

Spatial and temporal dynamics of plants
colonizing species-poor hedgerows

by

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Abstract

Hedgerows are increasingly being recognised as important in terms of landscape biodiversity. In Britain, recent hedgerows are not valued as highly as ancient hedgerows due to distinct differences in species-richness and historical significance. However, other potential ecological functions of species-poor hedgerows may have been overlooked, especially their potential role as corridors and habitats that help overcome the effects of habitat fragmentation. This thesis examines the spatial and temporal distributions of plant species in recent hedgerows in close proximity to remnant ancient woodland seed sources, and evaluates immigration, colonization and establishment processes that occur at this interface.

Transects were used to sample plant species distributions across the transition between remnant ancient woodland communities and adjoining Enclosure Act hedgerows in Northamptonshire. An analysis of the distribution of herbaceous plant species within the seed bank across the woodland-hedgerow transition is also presented. A census of colonizing woody plant species within the Experimental Hawthorn Hedgerows at Monks Wood, in Cambridgeshire was used to investigate the: i) influence of seed source availability, ii) immigration potential, iii) colonization and iv) establishment success under three hedgerow management regimes.

Woodland herbaceous plant species were found to have limited spatial and temporal dispersal strategies and species successfully dispersing into adjoining species-poor recent hedgerows were those able to reproduce vegetatively. The seed bank analysis showed that species of disturbed landscapes were dispersing into the woodlands, but were not successfully colonizing. Woody plant species dispersal was found to be operating at a larger spatial scale than herbaceous plant species. The abundance of seed sources and the availability of potential bird dispersers were found to correlate with the colonization success of woody plants within the Experimental Hedgerows, but the survival and establishment was related to hedgerow structure. The implications of these findings in relation to seed source-sink dynamics, corridor theory, habitat function, conservation and landscape planning were considered.

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Preface

My interest in hedgerow ecology started subconsciously through experiences growing up in the countryside as a child and by walking and cycling in my adolescent and adult life. When viewed from afar, hedgerows are the unseen element of a landscape, inadvertently providing structure, and texture to the fabric of what we see.

The cultural and ecological values of hedgerows were brought into the scientific and political fore by the researchers, Ernie Pollard, Max Hooper and Norman Moore, in the 1970s. They researched hedgerow history and ecology at the Institute of Terrestrial Ecology (now known as Centre for Ecology and Hydrology), Monks Wood, Cambridgeshire and published the widely accessible book 'Hedges' (Pollard *et al.* 1974). Max Hooper's correlation of woody-plant species diversity with hedgerow age inspired many to go out into the countryside and evaluate the heritage of their local landscapes. Max played a significant role in raising awareness of the rate of hedgerow removal from the British countryside as agricultural intensification gained momentum through the 1970s, and fuelled a thirty-year long campaign to produce legislation for hedgerow protection.

Whilst examining hedgerows of antiquity for an undergraduate dissertation (1992/3), I began to wonder if species-poor hedgerows were to increase in plant diversity over time and contribute to landscape biodiversity within present and future landscapes. Max Hooper accompanied me on one of my field days, although inspirational, he taught me that not all the answers to my questions were known.

Since embarking on this thesis, the topic of hedgerows, in terms of cultural and ecological importance, has rapidly grown. Hedgerow conservation is on the agenda at local, regional and

national levels of conservation organisations and government and is being addressed by European conservation policy-makers. The Hedgerows Regulations 1997 formalised the importance of hedgerows, affording protection for the most diverse and historically significant features of the British agriculture landscape. However, younger, species-poor hedgerows are not offered such protection and are still susceptible to removal; leading to loss in habitat, landscape connectivity and change in landscape character. Currently these hedgerows are considered as expendable elements in contemporary land use, and their potential for ecological function and landscape conservation is often disregarded.

1.1 Introduction

There is limited understanding about how hedgerows contribute to the wider context of landscape conservation and function. Hedgerows are mostly of anthropogenic origin. Although they are a major feature of agricultural landscapes, they are essentially non-productive in an agricultural sense and representative of semi-natural vegetation in an otherwise hostile landscape.

Despite the varied history of land use and origin, hedgerow networks exhibit properties of shape, and degree of connectivity to semi-natural habitats (Burel 1996). Both indirect and direct evidence has led to a consensus that hedgerows can function as wildlife corridors in agricultural landscapes, as they are thought to facilitate the movement of many species across hostile environments (Forman and Baudry 1984). Wildlife corridors are currently promoted in international conservation strategies and land use planning. The Pan-European Ecological Network and British Biodiversity Action Plan include hedgerows as important networks in modern-day agricultural landscapes and are thought to promote biodiversity and act as indicators of sustainable land-use.

Questions are being raised by policy-makers wanting to incorporate conservation and biodiversity issues into decision-making processes. Planners and landscape architects are also increasing their demands for information on how plants and animals are affected by changes in landscape structure (Selman 1993). The question of whether hedgerows reduce isolation of organisms in fragmented habitats is still unresolved. Recent theories (metapopulation and source-sink models) are seeking to explore species mobility between semi-natural habitats, as well as the sustainability of immigrant populations and their establishment. Many empirical

studies have focused on birds, mammals and invertebrates living and moving within hedgerows. Although species-poor hedgerows represent a substantial component within some regions in the British landscape, relatively few researchers have examined in detail plant immigration, colonization and successional processes that may occur within them.

The Hedgerows Regulations (Anon 1997a) protect only the most diverse and historically important hedgerows. Little protection is offered to species-poor hedgerows and consequently it is often assumed that species-poor Enclosure hedgerows have made only a limited contribution to the sustainability and biodiversity of landscapes. In spite of the increased attention on hedgerows in recent years, it is still uncertain if species-poor hedgerows actually increase in plant species diversity over time. Although many refer to the above ecological processes within semi-natural habitats, they are also applicable when studying hedgerow ecology and the potential of hedgerows to increase in diversity and contribute to landscape biodiversity.

The aim of this thesis is to examine whether ecological processes such as plant immigration, colonization and establishment may influence plant diversity in species-poor hedgerows. This thesis also considers how conservation strategies might be developed to facilitate plant community development in species-poor hedgerows; in turn promoting landscape function and biodiversity in agricultural landscapes. Whilst examining the spatial distribution of plant species colonizing species-poor hedgerows, this thesis asks specifically the following questions:

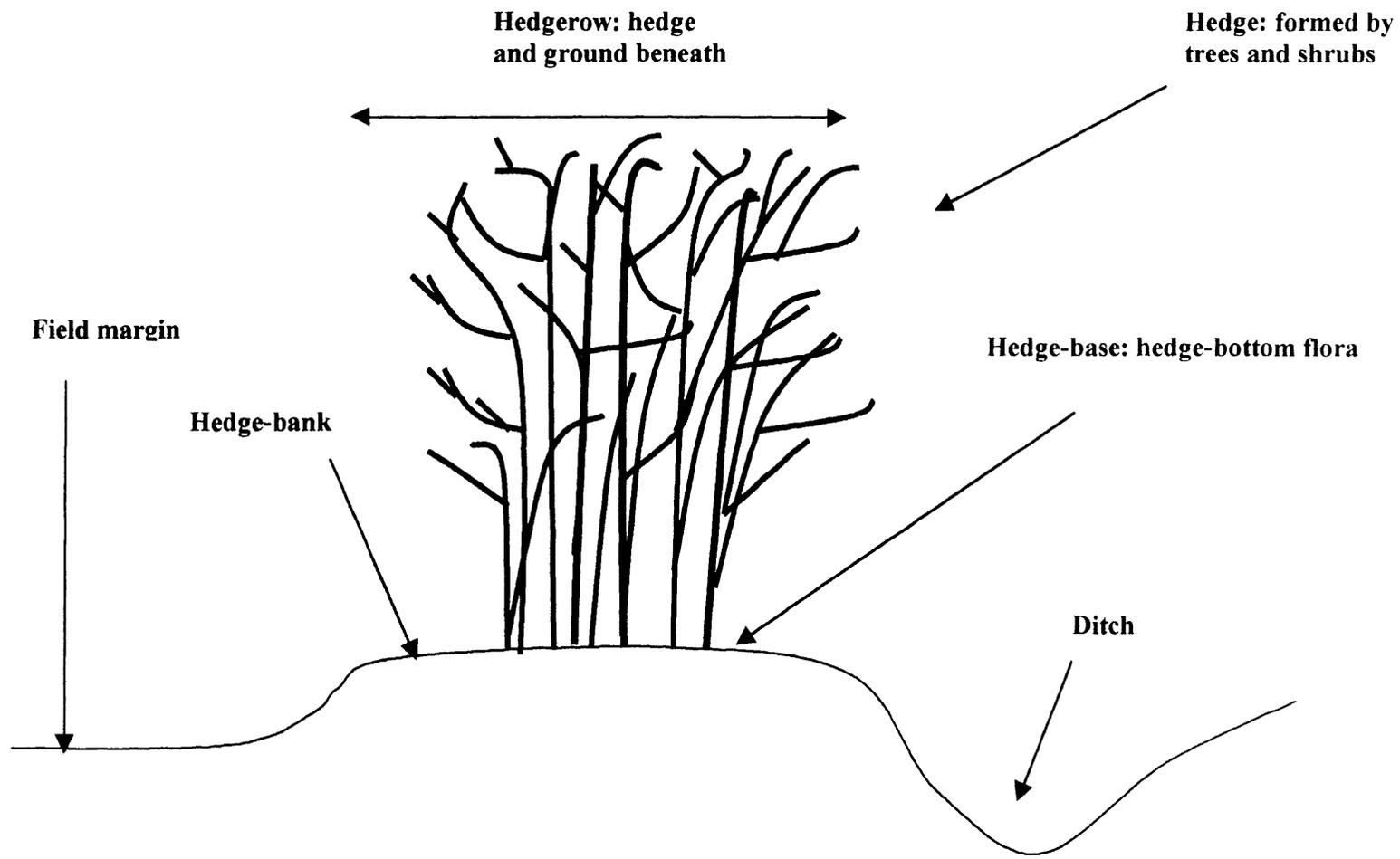
- do plant species from nearby woodland sources colonize species-poor hedgerows?
- at which spatial scales do plant immigration processes operate?
- which plant life history strategies contribute to the success of plants colonizing species-poor hedgerows?
- can the interpretation of spatial distributions of additional plant species increase the understanding of underlying ecological processes occurring in species-poor hedgerows?

1.2 Hedgerow definitions

Hedgerows are linear strips of woody trees and shrubs, which typically define land ownership, tenure, or a change in land use. The field and farm boundary hedge is a characteristic feature of the British countryside and, although their definitive role in boundary demarcation and livestock control has diminished in recent decades, their importance for wildlife conservation has increased (Cameron 1984, Blyth *et al.* 1991).

Shrub and tree species form the hedge proper (Bates 1937). The term hedgerow encompasses *the hedge and the immediate region on which it stands* (Bates 1937); the width of the hedge and the degree of overhang determine this. The ground under the hedgerow is commonly referred to as the *hedge-base*, and the vegetation found in this region is sometimes described as the *hedge-bottom flora* (Figure 1.1). At the edge of an arable field, there is often a strip of land between the ploughed soil and the hedgerow base: the *field margin*. The width of a field margin can vary according to farming practice. Local and regional variations in planting practice, management and origin can influence the overall structure of a hedgerow. Whether raised on a bank or on the level, the plant community of hedgerows can vary in composition according to the degree of shade, topography and hydrology (Bates 1937, Dowdeswell 1987).

Figure 1.1 A generalised cross section of a hedgerow and associated features



1.3 Background

1.3.1 Hedgerows as a habitat for wildlife

Few taxa are exclusively found in hedgerow habitats. Many species have an affinity with woodland habitats, while others, having accommodated the agrarian environment, utilise both hedge and the surrounding farmland (Pollard *et al.* 1974). Hooper (1976) estimated that 21 out of 28 species of mammals, 65 of 91 species of birds, and 25 of 56 species of butterflies can breed in lowland hedgerows in Britain. More recently, it has been estimated that 47 threatened species inhabit hedgerows in Britain, 13 of which are globally threatened species or rapidly declining ones (Anon. 1995, Wolton 1999).

Plant species within the hedgerow provide both habitat and food sources for many species which feed on leaves, nectar, lichens, fungi, dead wood and leaf litter, and fruits (Pollard *et al.* 1974). Standard trees within hedgerows also provide a valuable habitat to many groups of organisms. Older trees are especially important, providing nest-sites and song-posts for birds, roost-sites for bats, nest-holes for wasps and bees and a substratum for moss, lichens and fungi (Clements and Tofts 1992).

Until recently, few studies have examined how botanical composition and structure influence the habitat potential of hedgerows for animals. Tew (1994) found that for shrews (*Sorex* spp.), Bank and Field voles (*Clethrionomys glareolus* and *Microtus agrestis*), hedgerows can serve as a permanent habitat on arable farms. Wood Mice (*Apodemus sylvaticus*) exploit hedgerows as an alternative food source and habitat. Boone and Tinklin 1988 found that Harvest Mice (*Micromys minutus*) were dependent on hedgerows for refuge, particularly in winter, and the dense vegetation structure of a hedgerow was an important component of habitat requirements for Wood Mice and Bank Voles. They also proposed that although populations were retained within hedgerows, these mammals also move considerable distances into the surrounding landscape. Because of high concentrations of small mammals in hedgerows, specialist

predators such as Kestrels (*Falco tinnunculus*) concentrate their hunting efforts there (Tew 1994, Anon. 1999, Jackson pers. observ.)

Continuous hedgerows with emergent trees are known to provide valuable habitat for the Pipistrell bat (*Pipistrellus pipistrellus* 55kHz) (Oakeley and Jones 1998). In the Netherlands, *P. pipistrellus* was found to be almost entirely associated with linear landscape elements (hedgerow, tree lines and tree lanes), whereas the Serotine bat (*Eptesicus serotinus*) crossed into fields and meadows (Verboom and Huitema 1997).

Hedgerows provide cover, food, hibernation sites and migratory routes for amphibians in agricultural landscapes (Pollard *et al.* 1974, Boothby *et al.* 1996). Grass snakes (*Natrix natrix natrix*) are seen frequently in hedgerow bottoms, gaining protection when hibernating or basking in the sun, as well as finding food sources (small mammals) in an otherwise hostile agricultural environment (Pollard *et al.* 1974). Evidence of invertebrates utilising hedgerows is increasing (Dover 1994, Joyce *et al.* 1997, Petit and Usher 1998, Paoletti *et al.* 1999). Heteropteran species richness is strongly correlated with the floristic diversity of a hedgerow (Maudsley *et al.* 1997).

Lack (1992) considers hedgerows to be the single most important feature on farmland for breeding bird populations. Although the composition of bird communities in hedgerows varied on an Oxfordshire farm, there was a consistent presence of birds dependent on hedges throughout the year (Chapman 1939). A study within a parish in Huntingdon revealed that 70% of 48 bird territories were to some extent dependent on hedgerows and hedgerow trees (Wylie 1976).

Hedgerows that are allowed to develop good growth at the bottom, increasing in width, contained more bird species (Moore *et al.* 1967). Several bird species increase in incidence with hedgerow height (Green *et al.* 1994). Mason (1976) compared the breeding biology of the birds

within the Warbler family (Sylviidae). Whitethroats (*Sylvia communis*) were mainly found to be in hedgerows “with a greater vertical structure”. The Robin (*Erithacus rubecula*), Blackbird (*Turdus merula*) and Wren (*Troglodytes troglodytes*) were found to be more abundant in larger hedgerows (Parish *et al.* 1992). Sparks *et al.* (1996) found that many woodland bird species showed a preference for tall hedgerows, which were particularly favoured by the Wood Pigeon (*Columba palumbus*).

1.3.2 Hedgerow origin and plant species composition

Hedgerows exist to fulfil a practical function for land owners, providing barriers for livestock and partitions between land-use practices (Doubleday *et al.* 1994). Pollard *et al.* (1974) suggest that hedgerows originate from:

- planting from, or relict of, formerly extant woodland vegetation managed to form hedgerows around woodland assarts (farmland gained by small scale forest clearance);
- shrub development along previously non-hedged boundaries: for example natural colonization along water courses or fencerows;
- planting of trees and shrubs.

Plant species composition of hedgerows can vary geographically, depending on geology, history of land use, period of enclosure and local planting regimes (Moore *et al.* 1967, Cameron and Pannett 1980). ¹Several shrubs have limited distributions in the British Isles. For example *Viburnum lantana* and *Rhamnus cathartica* show preferences for dry calcareous soils and are more frequent in the south east of England, whereas, wet upland soils are favoured by *Alnus glutinosa*, *Betula* spp. and *Sorbus aucuparia* (Cameron 1984). *Corylus avellana* is a poor colonizer in the east (e.g. Huntingdon) (Pollard 1973) yet colonizes hedgerows more readily in wetter western regions (e.g. Shropshire and Wales) (Cameron and Pannett 1980).

The origin and floral composition of hedgerows is well understood (Bates 1937, Pollard 1973,

¹ For your reference, English and scientific plant names and their authorities are presented in Appendix 1.

Pollard *et al.* 1974, Boatman 1994, Cummins and French 1994). The floras of ancient land-boundaries share characteristic with the flora of ancient woodland (Pollard 1973). Hedgerows of ancient origin are often described as relict ancient woodland hedgerows and can be considered as ‘indicators’ of ancient woodland ‘ghost’ boundaries as they share a characteristic suite of plant species attributed to ancient woodlands (Pollard 1973). The presence of woody plant species, such as *Euonymus europaeus*, *Cornus sanguinea*, *Acer campestre*, *Ligustrum vulgare* and *Quercus* spp. along with the presence of *Mercurialis perennis*, *Hyacinthoides non-scripta*, *Primula vulgaris* and other woodland herbs, are indicative of relict ancient woodland communities (Pollard 1973, Helliwell 1975, Michelmore and Proctor 1994).

The term ‘ancient woodland indicator’ is applied to plants restricted to woodlands of ancient origin: those pre-dating 1600AD (*sensu* Rackham 1980). However, there can be no absolute certainty that a hedge was actually part of a wood without documentary evidence, although Pollard (1973) suggested that, given the poor dispersal powers of many characteristic shrub species and ground flora of woodland, a hedgerow containing these ‘indicator’ species must at least reflect the close proximity to an old wood, with the strong possibility that it was part of one.

Hooper (1965, 1966, 1970a, 1970b) observed variation in hedgerow tree and shrub diversity that could not be accounted for by variations in soil, climate or hedgerow management. A study of hedgerows in five counties found that 75% of the variation associated with tree and shrub species richness found in hedgerows could be explained by age. A further study generated the now widely known relationship between the age of a hedge and the number of species found in a thirty-yard length of a hedgerow (Hooper 1970b). Hooper stated that, in general terms, the rate of colonization of a hedgerow would equate to one new species each century. This assumption became known as Hooper’s Rule (Pollard *et al.* 1974) and was generally well accepted, particularly among historians (Anon. 1975, Cameron 1984, Hussey 1987), and educationalists (Jennings 1972) who used it as a tool for dating hedgerows and interpreting

historical landscapes. Ecologists and statisticians were more critical of this rule of thumb (Willmot 1980, Cameron and Pannett 1980, Johnson 1980). Hooper (1971) admitted that there was a margin of error within a range of a two hundred-year period. Regionally based correlations were recommended because of contrasting histories and periods of landscape development. Despite criticisms, Hooper (1976) still defended the basis for his general rule as a reasonable approximation of reality. Willmot (1980) revealed that dating hedgerows is an imprecise art; in one parish in Derbyshire, the age of hedgerows explained only 15% of the variation in woody plant species diversity. He proposed that other factors could contribute and the issue of tree and shrub variability within hedges was still unresolved. The use of Hooper's Rule can distinguish hedges of the Enclosure Act period from those of Stuart or Tudor times or the Middle Ages, but it cannot distinguish between hedgerows originating from Anglo-Saxon and Roman periods (Rackham 1986).

Up to the eighteenth century, field enclosure was localised and piecemeal (Rackham 1986). Much of England outside of the Midlands (for example, in Essex, Kent, Devon and Worcestershire) was enclosed before the fifteenth and sixteenth centuries (Darby 1976). After 1700 AD, agriculture in England came under a period of reform: vast areas (*ca*~2,000,000 acres (809,389ha)) of waste or common land was reclaimed, improved and enclosed with newly planted hedgerows (Hoskins 1955, Coppock 1976). The period of Parliamentary Enclosure affected large areas; involving the division and reallocation of land within nearly 3,000 parishes (Hoskins 1955). Some 618,000 acres (250,101ha) were enclosed between 1878-1914 under the General Enclosures Act, with small additions, totalling 30,751 acres (12,445ha), under the Commons Act 1876 (Coppock 1976).

Parliamentary Enclosure hedgerows were mainly planted with Hawthorn (*Crataegus monogyna*) (Darby 1976). Concentrations of Enclosure hedges varied on a national scale and planting of species other than *C. monogyna* occurred in some regions (Moore *et al.* 1967). Counties most affected by the transformation were Northamptonshire, Rutland, Huntingdonshire,

Bedfordshire, Oxfordshire, and the northern half of Buckinghamshire (Hoskins 1955). The rectilinear tidiness of field patterns produced by Parliamentary Enclosure Acts differed strongly from the small, slightly curved field patterns produced when furlongs or bundles of strips of land were common practice (Hussey 1987). These contrasting landscape features were indicative of epochal unplanned and planned periods of agricultural change that resulted from spatial and temporal alterations in agrarian practices (Darby 1976, Rackham 1986).

Most hedgerows include elements of grassland and arable weed plant communities, as field species set seed and establish at the base of a hedge (Michelmore and Proctor 1994). Adjacent land-use can substantially affect the composition of the herbaceous vegetation of hedgerows (Cummins and French 1994, Bunce *et al.* 1994, Hegarty *et al.* 1994). The hedge-bottom vegetation is commonly impoverished when fertiliser, herbicide drift, and where cultivation occurs too close to the hedgerow (Churchward 1995). In contrast, species-rich hedgerows are often associated with areas where less intensively managed farming occurs and where soils have a lower nutrient status (Hegarty *et al.* 1994). The impact of agricultural operations often led farmers and conservationists to view the hedgerow flora as consisting of agricultural weed species that are widespread and of little botanical importance (Boatman 1994).

Agricultural practice or disturbance by burrowing animals and domestic stock, provide opportunities for the establishment of annual and spreading perennial herbaceous species such as *Anthriscus sylvestris*, *Heracleum sphondylium*, *Cirsium arvense*, *Urtica dioica*, *Lamium album*, *Aegopodium podagraria* and *Galium aparine*. Conversely, less disturbed areas are often dominated by perennial grasses. Ploughing near the hedgerow base promotes *C. arvense*, which is thought to be tolerant of root fragmentation and is able to reproduce vegetatively. *Bryonia dioica*, *Galium aparine*, *Lamium alum*, *Papaver rhoeas*, *Ranunculus repens*, *Sonchus asper* and *Taraxacum* agg. significantly increased in abundance after conversion from pasture to arable farming (Mountford *et al.* 1994).

1.3.3 Hedgerow Management

The objective of hedgerow management, from a farmer's perspective, is to keep a hedgerow in shape and to promote new growth to ensure a stock proof barrier (Malden 1899). Hedgerows are managed by cutting and pruning trees and shrubs and clearing field margin vegetation. Hedge layering is a traditional method of hedgerow management (Lack 1992). Hedgerows that have been allowed to grow for five to ten years have the upright branches or pleachers partly cut through just above the ground, and bent over and woven around a series of stakes driven into the ground (Sturrock and Cathie 1980) (Plate 1). In many regions, farmers and land workers have developed local styles of hedge layering (Pollard *et al.* 1974), although in recent years many older practitioners have been unable to pass on their skills, as younger generations leave the farming community or else have adopted modern practices. Many traditional styles are now being reintroduced by conservation organisations, such as the British Trust for Conservation Volunteers.

Changes in farming practice have resulted in fewer staff employed to maintain hedgerows. Winter-sown crops can make seasonal access to hedgerows more difficult. Currently, the majority of hedgerows in the British Isles are maintained by a mechanical method - the flail cutter (Sturrock and Cathie 1980, Bunce *et al.* 1994, Helps 1994). Mechanical trimming may be done annually or at intervals of several years (Lack 1992). The mechanical flail cutter can cut a hedgerow with minimal passes up, down and along the top of the hedge.

Mechanical flail cutting can inflict damage to branches and stems of trees and shrubs. If trimming is not done with an upward stroke the cut surfaces will splinter, leading to dampness and considerable decay over time (Chapman and Sheail 1994) (Plate 2). *Crataegus monogyna* produces numerous shoots at the damaged tips, producing a bushy top with little new growth further down the shrub (Semple *et al.* 1994) (Plate 3). When trimming is too severe, all the young wood is removed, leaving behind only old wood; with limited regenerative ability. The old wood does not recover so well and the heart of the hedge becomes hollow (Chapman and

Plate 1 A traditionally laid hedgerow with stem weaving and positioning stakes



From www.hedgelayr.freemove.co.uk

Plate 2 Splintered stems and shoots along a hedgerow as a result of mechanical flail-trimming



With kind permission of Adam Kwolek

Plate 3 Altered hedgerow growth through mechanical hedge trimming: two trimming events are visible with numerous shoots at re-growth sites



By Janet Jackson

Sheail 1994). Flail cutting is thought to be one of the main causes of hedge deterioration, with hedge gappyness occurring after ten to twelve annual trims (Brooks 1975).

The composition of plant species in a hedgerow may be affected by regular mechanical trimming, as some shrub species may respond adversely to this treatment. *Crataegus monogyna* and *Fraxinus excelsior* are resistant to continued annual cutting, but other species like *Corylus avellana* and *Prunus spinosa* die quite quickly (Wolton 1994). Helps (1994) and Britt *et al.* (1996) regard over-grazing by farming livestock as another contributory factor leading to the deterioration of the hedgerow flora.

The value of a particular field boundary as a habitat depends largely upon its position relative to other habitats, management, and adjacent land use. Parish *et al.* (1992) proposed that short hedgerows, alongside arable land, would attract twice as many birds if they were allowed to grow. Additionally, strips of permanent pasture retained beside hedgerows and the planting of trees would be of further benefit. Arnold (1983) compared bird species in hedgerows of different structure and adjacent to varying land-use. He showed an increase in the number of bird species as the hedgerow structure increased in complexity and as arable land-use was replaced by grassland. Vegetated ditches along-side hedgerows were shown by Stoate and Szczur (1994) to increase the occurrence of nesting sites for Yellowhammer (*Emberiza citrinella*) and the Whitethroat (*Sylvia communis*).

Hedgerow management changes the structure of hedgerows. Coppicing and hedge layering have an initial impact on hedge structure but usually allow continued growth for a determined period (5-15 years). The modern practice of hedge flailing enforces a permanent change in the physical structure of hedgerows. With intensive regular trimming, growth is restricted reducing flower and fruit production of the woody plant species. It is recognized that, for wildlife conservation, the frequency and timing of trimming and other hedgerow management regimes is critical. To be of significant benefit, hedgerow management should not be prescribed *per se* but

designed to allow a mixture of structures within a farm landscape, with rotational management regimes (Sparks 1995); to provide food resources and nesting sites for a variety of species.

1.3.4 Hedgerow policy and legislation

Government and agricultural policy and market forces, particularly after World War Two, have emphasized productivity. Increased efficiency required a greater use of pesticides, herbicides and fertilizers, and promoted specialization, leading to land improvement, reduced diversity in cropping patterns, and the removal of hedgerows (Sturrock and Cathie 1980, Harvey and Bell 1990). Hedgerows have been removed because they were thought to harbour agricultural pests or have been accidentally damaged, for example by the once common practice of stubble burning (Moore *et al.* 1967). The Agricultural Acts 1957 and 1967 also made grants available for the removal of hedgerows for the expansion of arable fields within the 'Farm Improvement Scheme'.

Many internal farm hedgerows were 'grubbed up' to ease movement of larger machinery, whereas major land-boundaries and roadside hedgerows were more vulnerable from urban expansion and road development (Pollard *et al.* 1974, Peterken and Allison 1989). Modern-day demands and increased affluence have promoted land-use other than agriculture. Mineral and gravel extraction, landfill sites, airfields, leisure centres, sports fields, housing and shopping developments have all contributed to the overall decline of hedgerows to date, and have led to dramatic changes in local landscapes (Coppock 1968).

Hooper (1970a, 1974, 1978) estimated that an average annual rate of hedgerow loss of 5,000miles (8,046km) occurred between 1945-1970 (Table 1.1). Barr *et al* (1994) reported that the rate of hedgerow loss was declining. In the six-year period between 1984-1990, there was a total loss of 9,500km of hedgerows and between 1990-1993, 3,600km of hedgerows were removed.

Table 1.1 Estimated hedgerow removal rates (post-WWII) at selected intervals in England and Wales

Period	Extant hedges (km)	Time (yrs)	Total loss (km)	Annual rate (km yr ⁻¹)	reference (see below)
1945	804,635	-	-	-	*
1970	603,476	25	201,159	8,046	*
1984	563,100	14	40,376	2,884	+
1990	431,800	6	9,500	1,583	-
1993	377,500	3	3,600	1,200	-

*Hooper (1970a, 1974, 1978), + Assuming the estimates of Hooper are sound, then the calculations from his estimate and those of Barr *et al.* (1994) result in the estimate annual rate of loss between 1970-1984 as being approximately 2,884km yr⁻¹, - Barr *et al.* (1994).

Hedgerow loss has been recognised as a contributing factor to the decline of many species within agricultural landscapes. The declines of the Grey Partridge (*Perdix perdix*) and Red-legged Partridge (*Alectoris rufa*) have been attributed in part to hedgerow loss (Rands 1986, 1987, Dodds *et al.* 1995). Hedgerow removal may also have contributed to the decline of the Tree Sparrow (*Passer montanus*), Linnet (*Acanthus cannabina*), Reed Bunting (*Emberiza schoeniclus*), Song Thrush (*Turdus philomelos*), and Cirl Bunting (*Emberiza cirlus*) (Anon. 1996). However, Gillings and Fuller (1998) suggested that habitat degradation, on agricultural land, has had the greatest impact on bird populations.

Thirty years of lobbying by organisations concerned about hedgerow loss resulted in the introduction of legislation, in March 1997, to restrict the removal of hedgerows from the British countryside: The Hedgerows Regulations 1997. Landowners are now required to notify their local authority when they intend to remove a hedgerow (Anon. 1997a). If a hedge is deemed as 'historically and/or ecologically important,' then its removal without permission would result in charges of criminal damage (Wilson 1994). This Statutory Instrument was met with mixed responses from conservationists and regulatory bodies. Respondents to a consultation survey were concerned about the workability, enforcement, costs and the detailed criteria of the Regulations (Anon. 1997b). Some felt that the evaluation scheme provided in the Regulations, supported only the best and most historic hedgerows. Consequently, it is claimed that the Regulations have regional bias and protect only a small percentage (20%) of extant hedgerows in the British landscape (Anon. 1998b). Hedgerows unprotected from removal are mainly those

of the post-Parliamentary Enclosure Act period, considered as species-poor with little ecological and historical value.

On 29th May 1997 the Environment Minister Micheal Meacher announced that the The Hedgerows Regulations 1997 would be reviewed. A review group was set up, consisting of nominees from Government Departments, statutory agencies, and the main farming and conservation bodies. The group was charged with making new recommendations to strengthen hedgerow protection (Anon 1998b). To date, formal changes to the legislation have not yet been made. The review process may possibly propose a simplified evaluation system, and measures that may provide further protection for hedgerows along highways, complete examples of Enclosure landscapes, and the inclusion of UK Biodiversity Action Plan target species (Anon 1998b)

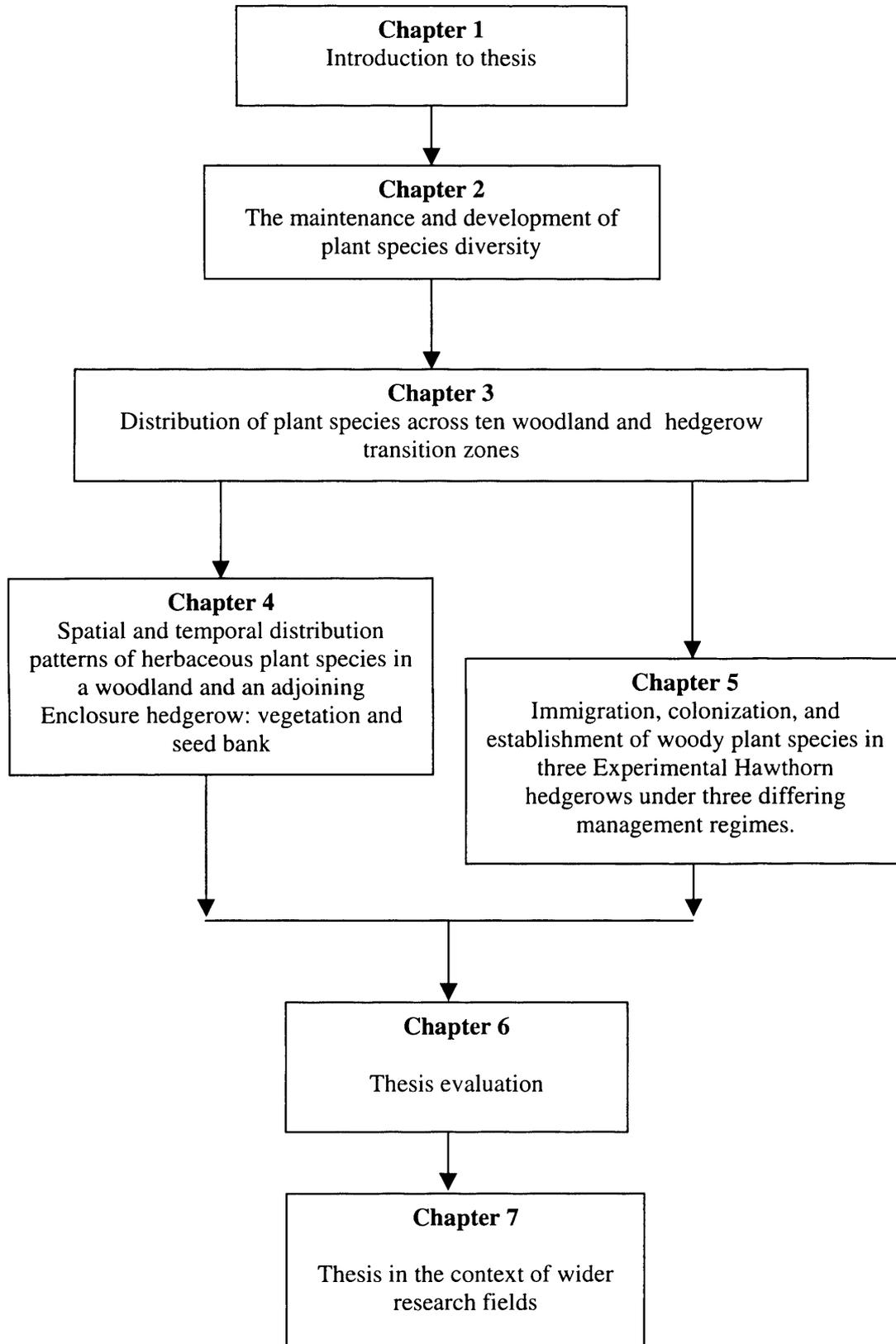
It is too early to assess the impact and success of The Hedgerows Regulations 1997. Various exemptions and legal loopholes are evident. During one Appeal Case, the definition of a hedgerow was found insufficient within the legislative framework which led to a wrongly placed retention notice (a refused application for hedgerow removal) (Jackson *et al.* 1999). A consultant ecologist revealed that in some instances hedgerow removal notices were being dealt with retrospectively, where the farmer had already removed the hedgerow in question (Anon pers. comm. 1999). There is a need to examine the effectiveness of the present evaluation system and the implementation of The Hedgerows Regulations 1997 within local authorities countrywide.

1.4 Thesis structure

Chapter 1 introduces the thesis, structure and composition of hedgerows, value to wildlife, methods of management, and recent developments in protective legislation. Chapter 2 reviews the diverse and rapidly expanding literature in landscape ecology and examines why hedgerows are valued as ecologically functioning components within agricultural landscapes. A concept map examines landscape and local scale influences that may affect the immigration, colonization and establishment of additional plant species in species-poor hedgerows. A conceptual model is presented which aims to clarify the role of these three ecological processes in plant community development within hedgerows.

The practical research of this thesis is presented as three separate but related studies (Figure 1.2). The first study, (Chapter 3) examines the spatial distribution and life history characteristics of both **herbaceous and woody plant species** in ten woodland-transects and adjoining Enclosure-Act-hedgerows in Northamptonshire. Chapter 4 focuses on the spatial distribution and temporal dynamics of **herbaceous plant species** in the vegetation and seed bank across a wood-hedgerow transition. The final study, Chapter 5, investigates the spatial and temporal dynamics of **woody plant species** immigrating, colonizing and establishing in three differently managed experimental hedgerows. These hedgerows are located at the Institute of Terrestrial Ecology Research Station (now known as the Center for Ecology and Hydrology (CEH)), Monks Wood, Cambridgeshire. Surrounding seed sources and immigration potential of woody plant species are evaluated and a spatial model is presented that analyses the distributions of additional woody plant species found in the Experimental Hawthorn Hedgerows. Chapter 6 brings together and evaluates the findings of these three studies and Chapter 7 discusses the relevance of this thesis in the research fields of landscape ecology and ecological conservation.

Figure 1.2 Structure of thesis



Chapter 2 The maintenance and development of plant species diversity in hedgerows

Can it be assumed that hedgerows are immune from ecological processes that occur in the surrounding landscape? This chapter introduces a literature review organised according to spatial scale: examining ecological process from the landscape and local perspective. Firstly, habitat fragmentation, species isolation, and the concept of wildlife corridors are introduced (Section 2.1). Section 2.2 reviews ecological research relating to plant community development, immigration processes, generative and regenerative strategies, and predation. Sections 2.3 and 2.4 introduce a concept map and model, which examines and aims to define the temporal, spatial and ecological processes that contribute towards plant species diversity within hedgerows.

2.1 Landscape scale factors

2.1.1 Habitat fragmentation

Fragmentation is defined by Opdam *et al.* (1993) as: ‘the destruction of habitat, leaving the remaining fragments scattered throughout the newly created landscape’. Fragmentation alters physical processes such as soil hydrology, nutrient cycles, wind profiles and radiation balance within a habitat patch (Saunders *et al.* 1991, Hobbs 1993). In the past, areas of natural habitat have probably always been fragmented into island-like enclaves (Wilson and Willis 1974); however past and current agricultural practice is accepted as the main cause of fragmentation of natural and semi-natural vegetation (Merriam 1988).

Fragmentation not only reduces the size of patches of semi-natural habitat but can reduce connectivity of linear landscape networks, such as hedgerows. This is achieved by the removal of hedgerows or whole patches of semi-natural habitat that they were once attached to, creating a landscape with few hedgerows, remote from other semi-natural landscape features.

Habitat boundaries created by the fragmentation of habitat patches are inherent components of heterogeneous landscapes where terrestrial ecosystems adjoin other habitats or varying types of land use (Wiens 1997) and can be considered as zones of floristic and ecological change (Wiens *et al.* 1985, Kent *et al.* 1997). Boundary types range from sharp, clearly defined changes in vegetation composition and structure (ecotones) to more gradual, diffuse transitional changes (ecoclines). Sharp boundary types tend to occur due to anthropogenic intervention (Kent *et al.* 1997).

Across habitat boundaries, abiotic and biotic vectors (wind, water and animals) may allow non-random directional fluxes, which reduce boundary resistance and increase interchange between the two landscape components. Wind is a complex vector subject to daily and seasonal change, but plays an important part in the movement of pollen, seeds and detritus material. Animal vectors are influenced by behavioural patterns and can be directed by complex responses to landscape patterns (Wiens *et al.* 1985).

In woodlands, for example, an edge may be regarded as a zone that experiences the external climate around the perimeter. The edge width can vary, and is measured by a marginal zone of altered microclimate and contrasting community structure from the forest interior (Matlack 1993). Woodlands have a low albedo and much radiative energy is converted into sensible and latent heat (Veen *et al.* 1996). Matlack (1993, 1994a) found that local radiation was a principle factor determining the forest microenvironment and that variation in radiation loading produced edge-orientated gradients at all sites open to direct sunlight. He suggests that localised aspects, temperature, gradients in vapour pressure deficit and litter moisture were all related to available light and were all simple functions of distance from the forest edge.

Other dynamic processes influence vegetation structure and composition. Woodlands provide 'roughness' to the landscape, causing turbulence to wind patterns particularly when woodlands are fragmented into several patches rather than large one. The combination of the low albedo

and roughness affects the atmospheric moisture content and the temperature of passing air currents (Veen *et al.* 1996). These abiotic variations will change seasonally, particularly in temperate woodlands regions.

The direct and indirect effects of altered microenvironments within forest edges manifest themselves in:

- modified plant species composition (Ranney *et al.* 1981, Fraver 1994);
- increased population densities of some species (Ranney *et al.* 1981, Williams-Linera 1990, Brothers 1993);
- altered physical structure (Ranney *et al.* 1981, Fraver 1994)
- increased species richness (Fox *et al.* 1997, Brunet and von Oheimb 1998).

The strength of the vegetation pattern at a woodland edge varies depending on the degree of canopy openness, edge aspect (Matlack 1994a) and strength and duration of disturbance (Laurance 1991, Matlack 1993, Fox *et al.* 1997). In recently formed woodland edges, the strength of the environmental gradient is high, and light-demanding competitive species are able to colonize the woodland edge. In older woodland edges, the vegetation develops, the canopy closes and the strength of the edge pattern diminishes over time (>55 years), as those species intolerant to shading are suppressed (Matlack 1994a).

Hedgerows, being linear and narrow, will be dominated by edge effects: potentially influencing plant species composition and vegetation structure. Hedgerow management may influence the degree to which edge effects influence microenvironments within the hedge-base. For example, tall-unmanaged hedgerows will cast a degree of shade, influencing light and temperature. However, if there is little undergrowth the unprotected base of the hedgerow will experience extremes in wind, and moisture loss. A hedgerow managed by layering will produce dense growth at the base of the hedgerow, reducing the effects of extreme variation in abiotic variables.

2.1.2 *Species isolation and dispersal*

The insularization of nature reserves and national parks by contrasting surrounding land-use has led to concerns for species survival (Noss and Harris 1986, Shafer 1990). The principles of island biogeographic theory (MacArthur and Wilson 1962; 1967) are often applied when considering habitat fragmentation, isolation, colonization and extinction in terrestrial ecosystems (Kent 1987, Dawson 1994). Unlike oceanic islands, patches of semi-natural habitats in agricultural landscapes are never totally isolated and even with varying degrees of isolation, immigration and colonization are always possible no matter how improbable (Harris 1984).

Survival of species found in fragmented semi-natural communities is governed not only by physical factors such as human activity and microclimate but is driven also by ecological processes such as reproduction, competition and predation (Forman and Godron 1986, Baudry 1989). Populations in fragmented semi-natural communities are dependent upon sustainable reproduction, population expansion and genetic exchange (to promote genetic flow and phenotypic plasticity) (Noss and Harris 1986, Fahrig and Greiz 1996). Interactions between any two spatially separated local populations may be dependent upon the degree of isolation. Isolation may lead to reduced immigration and increased extinction.

Survivorship in small isolated populations is affiliated with dispersability (den Boer 1981). At the landscape scale species with high dispersal powers will compensate the rate of local population extinction. Large patches could minimise local extinction rates and avoid isolation effects, whereas small patches could limit the extent of perturbations and catastrophic disturbance at the landscape scale and may act as 'stepping stones' for species colonization and migration (Forman *et al.* 1976, Spellerberg 1991).

Increased mobility of individuals seems to be the best strategy for survival in heterogeneous landscapes (Kozakiewicz 1993) and may depend on the size and quality of the habitat, the

distance between local populations, the dispersal attributes of the organism, and the degree to which the area separating the local populations is conducive to movement by the organism (Fahrig and Greiz 1996). Turner (1989) warned that conclusions or inferences regarding landscape pattern and process must be drawn with acute awareness of scale, as organisms of varying size and life histories will react to spatial scales differently. Some species are not affected by patchiness of habitat, since they disperse and utilise the landscape as a whole (Middleton and Merriam 1981). Other species, however, have limited dispersal ability and/or have specialised habitat and life history requirements and are less likely to survive in spatially isolated habitats unless the habitat area is sufficient to carry minimum viable populations (Shafer 1981, Jarvinen 1982)

Metapopulation dynamics focuses on the extinction risks of a global population by evaluating the local population dynamics: linked in space and time by inter-patch migration events (Hanski 1999). Smaller and spatially related habitat patches may be capable of sustaining viable populations through metapopulation dynamics. Many small and fragmented habitat patches that remain can contribute to the biodiversity of the landscape as a whole (Hanski 1987). However, some taxa with limited dispersal and migratory ability may react more slowly to changes in the global population and thus may be under greater risk of stochastic extinction processes. The immigration, colonization and establishment of spatially restricted individuals into neighbouring patches may be determined by population dynamics and processes occurring within inter-patch regions.

The metapopulation concept, although still developing, has been widely accepted in population biology and beyond. Although there are many advantages to the theory, there is a danger of blurring concepts and viewing any kind of patchiness at spatial or temporal scales as a metapopulation (Hanski and Simberloff 1997). In addition, habitat quality plays a significant role in the success of populations in fragmented habitats for example in the case of isolated

small mammal populations (van Apeldoorn *et al.* 1992). Local persistence of populations in habitat patches that are too small or poor in quality is questionable.

Pulliam (1988) proposed that individuals could regularly occur in 'sink' habitats, within which reproduction is insufficient to balance mortality. Nevertheless, populations may persist in such habitats if they are locally maintained by continuous immigration from more productive 'source' areas nearby and without such input, the 'sink' population would disappear. This concept calls for a greater understanding of the population dynamics, niche realisation, community structure and other controlling factors that limit reproduction within sink habitats (Pulliam 1988, Dawson 1994).

2.1.3 Hedgerow networks and corridor function

The corridor theory focuses on the plight of specialized species that have poor powers of dispersal. These species were once widespread but are now restricted to remnant habitats. Within modern agricultural landscapes, many taxa are dependent on small patches of remnant semi-natural habitat, or on neglected strips of land (Opdam 1991). Linear semi-natural habitats are found along highways, railroads, fence-lines, shelter-belts, power-lines, historic animal-trails, riparian strips and can either connect or sever the landscape (Noss and Harris 1986). Forman and Godron (1981) proposed that links of semi-natural vegetation form ecological networks. These networks provide migratory routes and alternative pathways: corridors that facilitate movement for wildlife in fragmented landscapes. The availability of these numerous optional routes allows the avoidance of localised disturbance and predators and increases opportunity for foraging (Forman 1995). Hedgerows within agricultural landscapes potentially provide one type of ecological network, providing corridors for species mobility in otherwise hostile environments.

During the 1980s, it became apparent that the protection offered to wildlife in isolated nature reserves and other protected areas would not conserve rare species and distinct ecological

communities in perpetuity (Kent 1987). This realisation gave greater importance to evaluating and researching functioning roles of landscapes elements in nature conservation. The proposed advantages of corridors in facilitating movement of organisms in fragmented landscapes became a popular concept among landscape planners and conservationists.

Due to the lack of direct empirical evidence to support the benefits of wildlife corridors, there was an uncertainty as to their ecological value and it was also necessary to point out the possible negative aspects of the corridor theory (Hobbs 1992, Simberloff *et al.* 1992, Dawson 1994). Corridors have inherent “edge” characteristics and could be hazardous for edge and predation sensitive species (Soulé and Gilpin 1991). However, for the most part, researchers and planners are willing to accept that corridors are beneficial to wildlife and should be maintained, acquired or created, rather than waiting for concrete evidence of corridor function (Hobbs 1992, Dawson 1994).

The importance of hedgerows to the corridor debate has received little attention (Dawson 1994). There is a consensus that the role of wooded linear elements of the landscape as functioning corridors is dependent upon their size and structure (Forman and Baudry 1984, Charrier *et al.* 1997). To date, much of the research in landscape context has focused on movements of invertebrates, mammals and birds but few studies have examined the role of hedgerows as habitats or corridors that enhance mobility of plant species.

2.2 Local scale factors

2.2.1 Plant community development

Traditionally, plant succession is considered to be directional or orderly, typically divided into two distinct phases of change in vegetation composition and structure: primary and secondary succession (Odum 1969). Primary succession relates to the colonization of skeletal habitats and the absence of existing vegetation. Pioneer species arrive, colonize bare ground, and create the conditions for later successional species to colonize and develop into a ‘climax’ community.

Secondary succession is associated with the disturbance of existing vegetation and the subsequent development of a plant community from extant seed banks and vegetation fragments in productive nutrient-rich soils. A major difference between primary and secondary succession is that many colonizers in secondary succession are dispersed in time rather than through space (Grubb 1987). However, Gleason (1917) suggested that communities are continuously changing in structure and composition through successional processes. In Gleason's view, the distribution of individual species is dependent upon the ability of plants to disperse and their environmental requirements. Because chance dispersal from seed sources varies in space and time, he proposed that two widely distant but essentially similar environments would develop different plant associations.

For plant species to coexist within stable but complex plant communities, plant species must have developed strategies to compete for resources, and to tolerate inter and intra-specific competition, external, biotic and abiotic pressures. The niche concept summarises the ecological attributes and abiotic tolerances of a species. Maximum relative-growth-rate, phenology, mortality and fecundity determine the ability of a species to compete or coexist with others (Grubb 1977, Crawley 1986). Selective pressure and evolutionary processes influence niche separation and/or alter the niche breadth (Crawley 1986). Niche separation allows individual species to coexist in a plant community by varying resource utilisation, whereas the expansion of niche breadth increases both tolerance and the competitive ability of an individual species. Adaptation may determine success or failure of individuals or populations within a given environment.

Of the many theoretical successional models, Connell and Slatyer (1977) proposed three which have been valuable to research in the field of community development:

- *The facilitation model*: places the emphasis on the influence of early colonists (pioneer species), which establish in unoccupied patches. Facilitation occurs when primary colonists act as nursery plants, improving opportunities for later successional species by offering shade

and reduced soil moisture loss (De Steven 1991, Callaway 1992, Callaway and Walker 1997). Pioneer species are often highly mobile and short-lived, but their presence changes the structure and nutrient properties of the soil and alters the immediate microclimate.

- *The tolerance model*: includes pioneer species that can appear dominant in a later phase of succession. They have been present from the beginning of the successional process, but have dispersed, colonised and established at a very slow rate. These species are tolerant to the highly competitive early stages of community development, shade and predation. These tolerances are dependent upon plant life history strategies.
- *The inhibition model*: includes the role of pioneer species that first arrive at the site. They prevent or suppress subsequent invasion by other species. Later successional species only succeed to colonise and become established when dominant species are damaged or die.

Each of these three models specifies a particular set of rules for community assembly during succession (Lawton 1987). Connell and Slatyer (1977) recognised that these proposed models may not necessarily be independent processes and may operate simultaneously. In the inhibition model, it was proposed that when an individual of a dominant species dies, the gap created may not necessarily be filled by a species of a later successional stage. The successor may be of a similar type or even the same species. If there was a lack of a seed source for the late successional species, continued community development would be arrested (McClanahan 1986). In isolated communities, continued community development would be dependent on either those species with long distance modes of dispersal, or in the case of secondary succession, those species that are able to regenerate from propagules of previous communities which lay dormant within the soil (Noble and Slatyer 1980). If seeds of later successional species were available, the transition in vegetation composition is then thought to be gradual (Connell and Slatyer 1977), as later successional species become established they will eventually shade the early colonists.

Pickett (1982) and Walker *et al.* (1986) observed plant succession in abandoned arable fields. All species identified at the end of the study were present at the onset. Instead of sudden shifts

in colonization, dominance, and extinction, each species changed in relative dominance gradually. Pickett (1982) proposed that differential tolerance, competition, replacement, and relationships with dispersers and predators were major influences in successional community development. In communities that included perennials, seeds and seedlings frequently encounter adult plants in their neighbourhoods and could be inhibited by them. Whether a population increases or decreases in abundance during succession depends, therefore, not only on the ability of its seedlings to grow in the presence of adult plants, but also on the ability to hold sites by suppressing establishment of seedlings under their own canopies (Peart 1989).

Tolerance and competitive ability of a species in plant communities may vary during different stages of development. Empirical field experiments have shown existing vegetation can facilitate germination of most tree species. This was thought to be the result of the combined effects of amelioration of moisture extremes, the provision of wetter micro-sites for germination, and a reduction in seed predation (De Steven 1991, Callaway 1992). However, the continued development of tree saplings into mature individuals can also be inhibited by herbaceous ground cover (Grime 1979).

2.2.2 Plant immigration processes

Evolutionary processes engender the development of particular seed size and morphology of plant species (Gadgil 1971, Salisbury 1975, Levin *et al.* 1984, Westoby *et al.* 1992, Venable and Brown 1993). Ridley (1930) revealed an exotic and diverse assortment of seed shape and size found in the Plant Kingdom around the world. He proposed that the appendages attached to many seeds were adaptations associated with methods or modes of dispersal. He formulated a basic classification of modes of seed dispersal based upon morphological characteristics of seeds; for example, winged appendages as an adaptation for wind dispersal, or hooks, hairs or burrs to attach or adhere to dispersal vectors. Dansereau and Lems (1957) developed and classified plant dispersal in terms of the mechanistic and functional properties of the seeds. These initial classifications of dispersal modes have been expanded to include contemporary

understanding of dispersal processes (van der Pijl 1982). Morphological, physiological and phenological traits of species, genera and/or family groups (phylogenetic traits) are reflected in modes of seed dispersal (Table 2.1).

Table 2.1 Further classification of dispersal strategies with explanatory processes (after: van der Pijl 1982, Howe and Smallwood 1982, Chambers and MacMahon 1994)

Term	Dispersal strategy and adaptation	Seed dispersal and adaptation
Ballists	release of tension in dead tissues	active: explosive capsules, creeping diaspores, passive: promoted by touch a seed falling or rolling
Barochory	seed size, weight	
Epizoochory	animal transport on external surfaces	attachment by hooks, hairs, burrs, adhesive coatings
Endozoochory	passive and active ingestion by animals	fleshy nutrients, chemical attractants
Dyszoochory	transported by animals and buried under soil surface	seed storage by rodents and birds,
Myrmecochory	transported by ants and buried under soil surface	ants attracted by elaiosomes (edible oil)
Anemochory	size reduction, high surface/volume ratio, propelled by air currents	dust size, plumes, wings, tumbleweeds, thrown by movement of parent plant (wind ballists)
Hydrochory	Resistance to sinking, surface tension, low specific gravity, water transport	Rain wash, rain ballists, submerged or floating

NB: Biotic and abiotic processes also act to either relocate or bury the seed (secondary dispersal) (Chambers and MacMahon 1994).

Pioneer plant species (early successional species) are commonly supposed to have exceptional powers of dispersal (Grubb 1987). One of the chief characteristics of a pioneer species, especially in disturbed-fertile sites, is their ability to arrive at the newly created sites rapidly (Walker *et al.* 1986, Wilson and Keddy 1986). It is axiomatic of classical successional theory, in that both the initial phases of primary and secondary succession, pioneer species tend to be small-seeded and wind dispersed (Fenner 1987). Salisbury (1975) regarded wind-dispersal as indiscriminate and wasteful, as propagules are widely distributed to every type of habitat, whether conditions are suitable for survival or not. Early successional tree species are characterised by numerous small wind-dispersed seeds or larger seeds with morphological adaptations to aid dispersal by wind.

Dispersal increases the evenness of spatial distribution of seeds within a landscape but selective evolutionary forces act against this process. Venable and Brown (1993) proposed four models

of dispersal strategies that link to particular ecological processes:

- **Risk reduction** (or bet-hedging): this strategy reduces global and temporal variation by widespread dispersal. Where efficient dispersal mechanism places less emphasis on fitness of individual seeds and more on multiplication ('r' selection) of small lightweight seeds.
- **Escaping negative consequences of crowding**: species in this category have a tendency to persist in seed-banks with an emphasis on local and temporal dispersal. This strategy waits for periodic disturbance or death of adult plant.
- **Escaping negative consequences of high concentrations of parents and siblings**: in shaded and competitive environments, the cost of seed production and dispersal are high. Emphasis is placed on the competition for space with a population and the varying concentration of parent plants. A greater proportion of offspring arising from vegetative reproduction.
- **Directed dispersal**: where seeds attract an appropriate vector or have the appropriate morphology to assist long distance dispersal away from highly competitive environments.

Plants that invest heavily on producing seeds that attract or use dispersal vectors rely upon the availability and behaviour of vectors. Many animals depend on fruits and seed in their diet, but relatively few depend mostly or entirely upon them for all dietary elements. Some plants have evolved to exploit a greater variety of dispersal agents, while others attract specialist groups (McKey 1980).²

Many woody plant species produce fruits and seeds that are attractive to birds (Sørensen 1981) and the ability of bird species to disseminate seeds of woody shrub species has been explored by direct field observation (Ridley 1930, Snow and Snow 1988). Early classifications of bird dispersal recognised three main groups (Ridley 1930, McAtee 1947):

- *adhesion*: when seeds attach to feathers or feet of birds;
- *alimentionation*: when birds eat seeds or fruits for nourishment. If seeds are large or numerous they are sometimes regurgitated; otherwise they pass through the alimentary

² From this point this review focuses primarily on the dispersal of seed by birds, because of the importance of this interactive process for woody plant species diversity in hedgerows.

canal and are deposited within the faeces in an unchanged or improved state for germination (Ridley 1930);

- *transportation*: when seeds or nuts are transported to a hiding place, cached, and stored for winter-feeding.

van der Pijl (1982) developed this classification further by sub-dividing the seed dispersal mode known as Ornithochory (dispersed by birds), into functional groups:

- *Epizoochores*: seeds that are accidentally carried. These include seeds with burrs, which are less frequently dispersed by birds and more commonly not specifically adapted for seed<>bird mutualism. However, mucilaginous-coated seeds are transported either by waterfowl when seeds attach to feathers in the water, or in the mud attached to feet.
- *Synzoochores*: seeds deliberately carried by birds because they offer a nutritious reward and remain edible after storage. This group is composed of a) *Stomatochores*: seeds that are immediately redeposited (e.g. dropped when perched on a branch or in flight); and b) *Dysozoochores*: seeds which are buried and stored in caches.
- *Endozoochores*: ingested seeds and fruit flesh. This group comprises of a) *Non-adapted diaspores*: seeds fed on indiscriminately (mostly by granivorous birds); and b) *Adapted diaspores*: which include the majority of ornithochorous seeds that are adapted to attract fruit-eating birds. Many woody plant species have seeds that are either coloured or are enclosed in ripening edible flesh and can withstand digestion and are excreted in a germinal state.

The 'adapted diaspores' of woody plant species are an important nutritional dietary component for birds. Palatability or other nutritional components influence bird preferences (Sørensen 1981). For example, the highly nutritious sloe berry (*Prunus spinosa*) can be ignored until all the available berries of *Crataegus monogyna* have been consumed (Sørensen 1981). Piper (1986) observed that frugivore choice correlated with the amount of pulp the fruit contained: larger fruits were selected preferentially.

The seasonal availability of fruits additionally influences feeding behaviour and preferences of

birds. Various fruits are produced throughout the year, depending on the phenology of plant species (Sørensen 1981, Snow and Snow 1988). In temperate climates however, the availability of fruits is greatest in the autumn. The phenology of fruiting patterns of woody plant species may be determined by disperser availability, indicating joint selective processes (coevolution). Stiles (1980) classified fruiting patterns into four groups:

- *summer small-seeded fruits*: the plant species that fruit early in the summer are available for fledglings (these plant species produce small seeds with tough outer coats, with a tendency to be sweet);
- *summer large-seeded fruits*: consist of larger seeds, all in the genus of *Prunus*;
- *autumnal high quality fruits*: are present during peak periods of bird migration (these are relatively large seeds with pericarps rich in lipids);
- *autumnal low quality fruits*: include the majority of bird-disseminated fruits (these fruits remain on the parent plant for longer and low rates of seed dispersal continue into the winter).

The efficiency of bird dispersers not only depends on their preferences for types of fruits and the time of year they feed on them, but also relates to the fruit handling ability of birds. Herrera (1995) describes legitimate avian dispersers as being small to medium-sized passerines. The body size of birds and the size and shape of bills are determinants of dispersal efficiency in frugivorous birds. Bird morphology determines the size of seed that birds are able to swallow completely or regurgitate. Fruit eaters often have very wide gapes, enabling them to swallow very large fruits whole (Herrera 1995).

Certain birds destroy the seeds they eat. Finches and buntings (*Fringillidae*) are for the most part dry-seed and grain eaters. They crush seeds with their strong bills and finally destroy them through digestive process (Ridley 1930). Seed predators often discard the pulp, whereas pulp predators will discard the seeds in favour of the fruit pulp (Snow and Snow 1988). The distinction between fruit predators and legitimate dispersers, however, is somewhat context-dependent. Fruit predators may sometimes act as dispersers when feeding on small-seeded

fruits, while dispersers may act as predators when feeding on large-seeded fruits (Herrera 1995).

2.2.3 *Generative and regenerative strategies*

The species composition of a seed bank reflects the differing temporal dispersal strategies of past and present components of the vegetation (Roberts 1981). Seed banks of arable fields and grassland have attracted a lot of research, largely because of their importance for agricultural practice (Cavers and Benoit 1989, Grime 1989). More recently, ecologists and conservationists have realised that seed bank studies can also offer an important insight into past, present and possible future changes in plant community composition (Grime 1989, Warr *et al.* 1993, Davies and Waite 1998).

Seed banks of arable soils are mainly composed of annuals, (with the majority being wind-dispersed) and can be dominated by one or two species with high densities (Kropac 1966, Roberts 1981). The frequency of cultivation and the use of modern selective herbicides influence the density and viability of arable seed banks (Roberts 1972). In regularly disturbed habitats, short-lived annuals and biennials tend to have persistent seed bank characteristics. Long-lived perennial species, associated with more stable environments such as woodlands, are less likely to remain persistently dormant within the soil (Hodgson and Grime 1990, Thompson *et al.* 1998).

Seeds enter the seed bank via immigration processes or by deposition from parent plants in the immediate vicinity. Seed banks are dynamic: seeds enter and leave, and, whilst in the seed bank, undergo physiological change which can affect their response to present and future environments (Roberts 1981). The number of seeds in the soil is determined by the rate of input in the seed rain, the rates of loss due to fungal disease and predation and losses to germination (Silvertown and Lovett Doust 1993). In semi-arid conditions, seed germination can be stimulated by a periodic interruption of drought by a rain season. In temperate climates, germination can be triggered by a period of chilling during the winter season; consequently,

seeds remain dormant for a comparatively brief period of time (Thompson and Grime 1979, Grubb 1988). Grubb (1988) emphasised the importance of disturbance signals as another major stimulant to seed bank activation and plant recruitment. Disturbance results in the alteration of abiotic conditions, such as soil temperature and light levels (Grubb 1977), combined with the physical movement of the soil that scours and brings buried seeds to the surface. These changes act as physiological triggers for seed germination (Grime *et al.* 1981). The seeds of some species are able to remain viable within the soil for long periods, whereas seeds of other species are able to germinate over wide ranges of abiotic conditions and appear to lack specific dormancy strategies (Thompson and Grime 1979).

Three seed bank strategies were initially identified by Thompson and Grime (1979). Transient seed banks are of plant species adapted to exploit spatial vacancies created by seasonally predictable damage or mortality within the vegetation. Species with persistent seed banks lasting more than one year are able to remain dormant within the soil until temporary or unpredictable disturbance events occur. This temporal strategy enables a plant species to remain in the locality when conditions are unsuitable for the maintenance of a population above ground. An intermediate group between these two seed bank types was also identified (Thompson and Grime 1979) but there were practical difficulties in obtaining data to differentiate it effectively. This initial classification lacked the capacity for comparative analysis of varying persistence of a species, with the consequence that a modified classification was later produced by Thompson *et al.* (1997) (Table 2.2).

Table 2.2 Thompson *et al.* (1997) classification of seed persistence strategies

Type	Strategy	Explanation
1	Transient	Species with seeds which persist in the soil for less than one year.
2	Short-term persistent	Species with seeds which persist for more than one year but less than five years
3	Long-term Persistent	Species with seeds that can persist in the seed-bank for at least five years.
4	Present	Species present but cannot be assigned to one of the three seed-bank types above

The successful colonization of a new habitat is dependent upon the availability of safe sites and opportunity for invasion. Harper (1977) proposed that a 'safe' germination site is not only determined by the necessary elements that it provides for seedling growth but also by the hazards it excludes. He defined a safe site as an area in which a seed may find itself which provides:

- the stimuli required for the breakage of seed dormancy;
- conditions required for germination;
- resources which are consumed during the germination process;
- absence of predators, competitors, toxic chemicals and pre-emergent pathogens.

Plant life history traits of seed size and germination phenology can also influence the apparent availability of sites for germination (De Steven 1991). Grime (1977) proposed that selective evolutionary processes have resulted in three distinct plant life history strategies. He proposed three permutations by which plant species respond to disturbance and physiological stress (Table 2.3).

Table 2.3 Basis of Grime's three primary life history strategies: adaptive response to levels of stress and disturbance (Grime 1977)

	Low stress	High stress
Low disturbance	Competitive species	Stress tolerant species
High disturbance	Ruderal species	-

Disturbance is a spatial and temporal influence on plant communities and can vary in extent, physical dimensions (area, volume), location and frequency (Glenn-Lewin and van der Maarel 1992). Stress is the influence of external constraints that limit the rate of dry matter production of all or part of the vegetation (Grime 1979). Stress can relate to both abiotic and biotic influences. Abiotic stress includes climatic and edaphic variation and biotic stress includes inter- and intra-specific competition and predation. Grime (1977) described plant species of each of the three primary life strategies (Table 2.4).

Table 2.4 Characteristics of plant species associated with the three primary life history strategies (Grime 1977)

Plant competitors	Stress tolerators	Ruderals
Rapid growth: shading of other plants	Slow growth	Short lived
Lateral spread: occupying space	Long lived	Rapid growth
Phenology: optimising conditions	Slow turnover of minerals	High production of dry matter
Rapid response to environmental variation	Infrequent flowering	Flowering at early stages of development
Response to physical damage	Vegetative reproduction	Rapid seed ripening
Phenotypic plasticity	Low morphological plasticity	Seed production followed by death of parent

Grime (1979) recommended further separation of these responses to disturbance and stress into two major stages of development: the regenerative phase and the establishment phase. The regenerative phase consists of a series of stages including seed release, seed dispersal, seed germination and seedling survival. The second, the establishment phase, is characterised by a variety of interrelating functions including: the capture of resources; the maintenance, replacement and enlargement of roots and shoots; survival of stress and physical damage; and the production of flowers and seeds. The success or failure of plant species, within these two phases, is determined by resistance to disturbance, competitive ability and/or tolerance to stress (Table 2.5).

Table 2.5 Regenerative strategies in terrestrial vegetation (after Grime 1989)

Strategy	Functional characteristics	Conditions where strategy is advantageous.
Vegetative expansion	New vegetative shoots that remain attached to parent plant until well established.	Productive or unproductive habitats subject to low intensities of disturbance.
Seasonal regeneration	Independent offspring produced by a single cohort	Habitats subjected to seasonally predictable disturbance by climatic or biotic factors.
Persistent seed or spore banks	Viable but dormant seeds or spores present throughout the year, some persisting more than 12 months.	Habitats subjected to temporally unpredictable disturbance.
Numerous widely dispersed seeds or spore	Offspring numerous, buoyant in the air, widely dispersed and often of limited persistence.	Habitats subjected to spatially unpredictable disturbance or inaccessible places.
Persistent juveniles	Offspring derived from an independent propagule, but seedling or sporeling capable of long term persistence in a juvenile state.	Unproductive habitats subjected to low intensities of disturbance.

2.2.4 Plant community development under predation pressure

It has been long recognised that the impact of plant predators, particularly grazers, can alter the progression of ecological succession. Where predation is intense, community development may be interrupted, creating a sub-climax community (Clements 1916, Tansley 1949). However, many researchers still fail to acknowledge the additional effect of plant predation, herbivory and parasitism on plant species composition and structure (Edwards and Gillman 1987, Connell 1990). Herbivory represents a selective process that acts on individual plants. This selection can be either:

- direct - where the preferences of a predator for seeds or a seedling of one species effectively eliminates it from the community before establishment; or
- indirect - where herbivory reduces the competitive ability of a plant (Edwards and Gillman 1987).

Predation can inhibit seedlings or vegetative shoots from developing and reaching establishment. Pre-dispersal predation occurs when large herbivores or insects remove substantial amounts of vegetative material of the parent plant, or destroy flowers and fruits. Birds, mammals and ants also remove seeds and fruits whilst they are still attached to the parent plants. Post-dispersal predation is the consumption of seeds, seedlings and vegetative shoots after dispersal.

Concentrations of seeds around a parent plant attract seed predators (Webb and Wilson 1985, Barik *et al.* 1996). Seed shadows of wind-dispersed tree species reach distances further away from the parent plants than those that are vertebrate-dispersed (Wilson 1993). Therefore, vertebrate-dispersed species could be regarded as being under a greater selective pressure to increase dispersal distances away from the parent plant to avoid predation. Janzen (1971) proposed that the attraction of seeds to predators could be an integral function of a dispersal mode. One strategy is to provide attractive edible fruits and seeds that attract potential predators. Some seeds will be sacrificed to predation, whilst others survive and are deposited or buried by the predators themselves (mammal and bird scatter-hoarding behaviour).

When predation equals seed or fruit production, the stability of the entire plant population is reduced. Harmer (1994) described the predicament of many foresters in attempting to manage natural regeneration in woodlands. He noted that seeds of *Quercus* spp. and *Fagus sylvatica*, in particular, suffer heavy predation from a variety of animals. He warned that natural woodland regeneration may be unsuccessful unless predators are adequately controlled. Observations in the New Forest demonstrated that tree regeneration was more successful when the intensity of grazing by large herbivores was reduced (Peterken and Tubbs 1965).

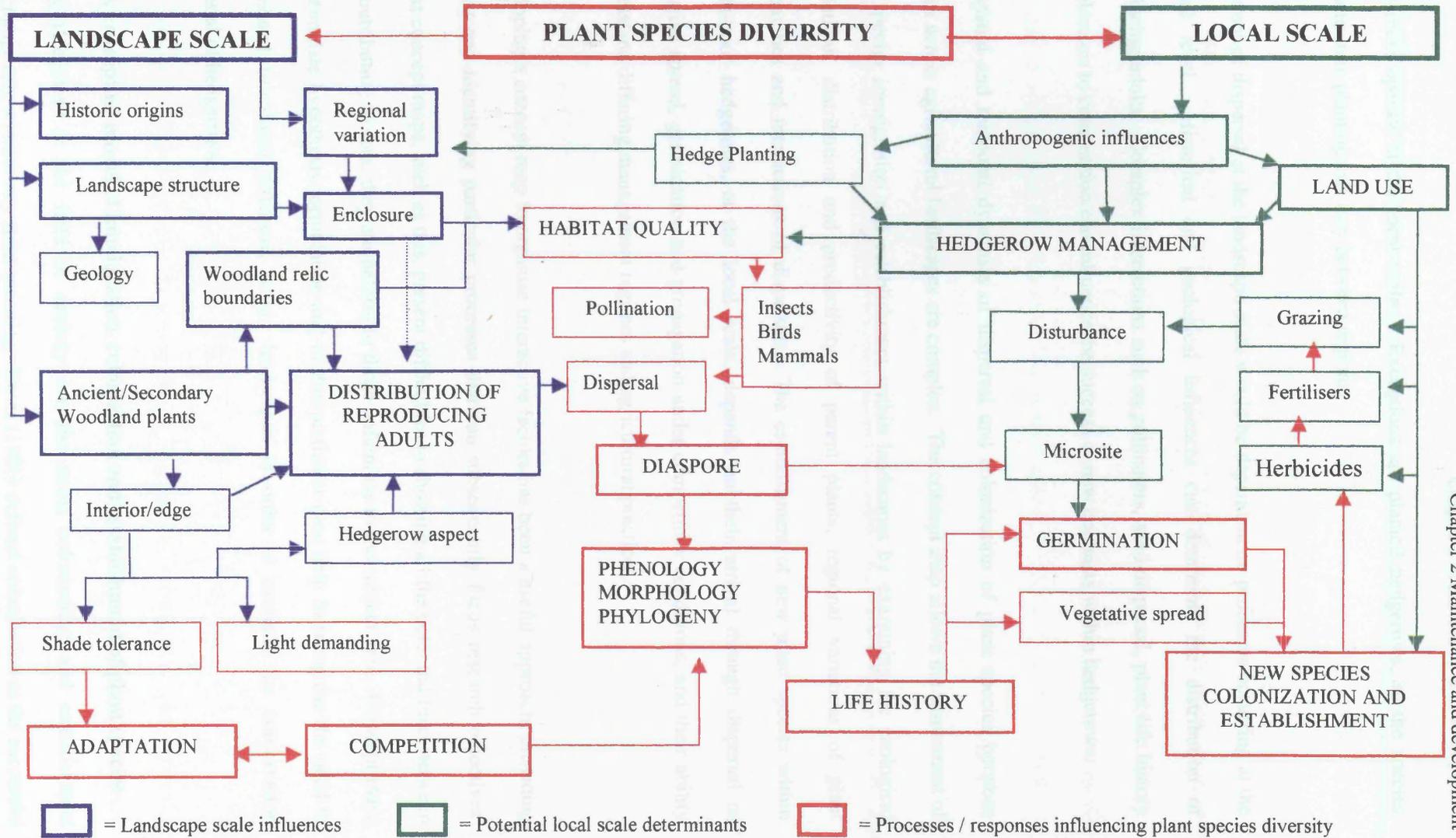
2.3 A concept map to focus research questions

Concept maps are a pictorial representation of ideas and concepts, which can be used to order complex arrays of information (Watson 1989). Concept mapping has proved a useful tool in a number of disciplines including chemistry (Pendley *et al.*, 1994; Bretz, 1996) and medicine (Holmes *et al.*, 1994), yet has only rarely been used in ecology (Cairns and Heckman, 1996). Given the complex nature of ecological studies, this is surprising, since concept mapping is a technique that can display the potential interactions between contributory factors and identify those areas that are of prime interest to the researcher.

A concept map is presented (Figure 2.1) (after Jackson and McCollin 1997) summarising interactions between ecological factors, emphasising the role of historical origins of hedgerows at a landscape scale and anthropogenic influences at the local scale. It illustrates possible determinants of plant species diversity of hedgerows. Landscape scale influences are depicted in blue boxes, potential local-scale determinants are green and processes or responses that may influence plant species diversity are coloured red. Ecological processes that are considered as major factors in each of these three categories are shown in upper case.

At the landscape scale, historical origins of hedgerows and geology influence the structure of the landscape at regional levels. Anthropogenic influences such as land use and hedgerow

Figure 2.1 A concept map that demonstrate the complexities when examining plant species diversity in hedgerows: indicating the importance of landscape and local factors.



management operate at the local scale. Exceptions are planted hedgerows, as the species composition in planting can vary between regions.

The extent of dispersal at the landscape scale would be dependent on processes occurring at the regional level. Historical and geological influences can determine the distribution of reproducing adults. Complex interactions such as pollinators, seed-dispersal, plant life history and tolerance to competition can influence the success of new colonists within hedgerows.

The spatial and temporal dynamics of dispersal and colonization of plant species between habitats across agricultural landscapes are complex. The concept map allows the assessment of plant species immigration and establishment within landscapes by examining the ecological associations, distribution and productivity of parent plants, regional variations of plant communities and interactions of dispersers. The establishment of new plant species within species-poor hedgerows, at the local scale, depends on their arrival through dispersal or vegetative spread, germination and propagation under competitive conditions, and their ability to withstand differing management regimes and agricultural practices.

Developing a concept map to organise interactive factors has been a useful approach, providing context and identifying particular processes that can subsequently focus research objectives. Whilst concept maps, such as this, present difficulties in showing all the potential links between the contributing factors, they are helpful to those unfamiliar to the subject area. Concept maps can stimulate hypothesis formulation and in this particular case help to recognise the need to understand functional processes within landscapes in order to evaluate the conservation potential of hedgerows.

2.4 A conceptual model of immigration, colonization and establishment of plant species

Many references in the field of ecology use the terms colonization and establishment interchangeably without any strict meaning. Davis (1986) defined colonization as the successful

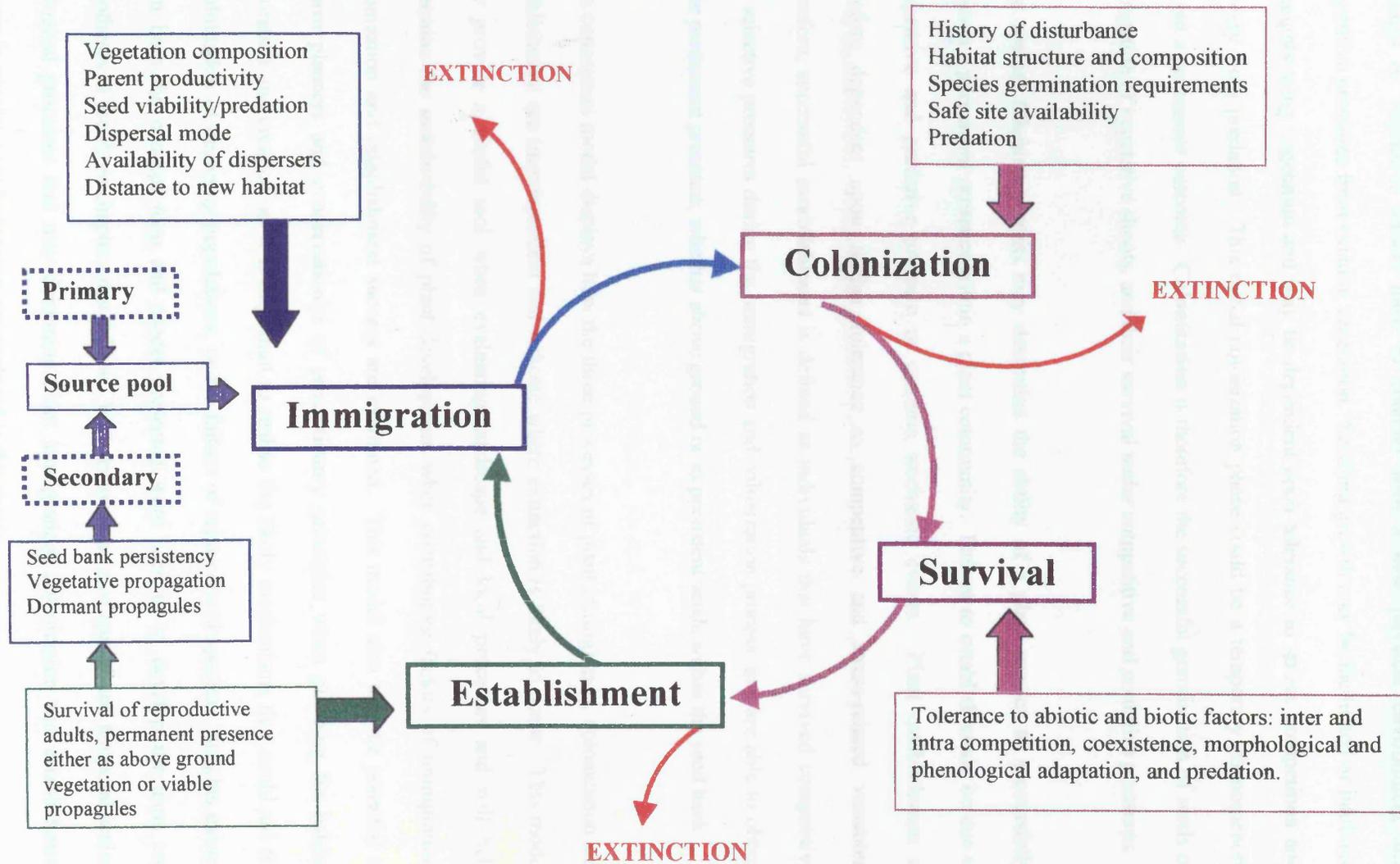
outcome of two independent processes: dispersal and establishment. van der Valk (1992) included seed dispersal, germination, vegetative propagation and colonization as integral components of the establishment process. Definitions of the terms' immigration, colonization, survival and establishment have been extracted from four dictionaries (Allaby 1992, 1994, Allen 1990, Meredith date unknown) (Appendix 2). Examining the terms above in more detail, the potential for confusion is evident. Within the ecological and botanical scientific dictionaries, immigration is defined in the context of gene flow, and survivorship is defined in terms of individuals of a population or in the context of natural selection. However, there is a lack of strict ecological use of the terms colonization and establishment. The non-scientific dictionaries tend to define colonization as an act – the process of establishing a new population- whereas establishment is taken to imply residence, or a sense of permanency.

In order to describe the relationships between the various processes that may influence immigration colonization and establishment of additional plant species in new habitats, a conceptual model was developed and is presented in this thesis (Figure 2.2).

Immigration processes are assumed to be dependent upon seed source composition, dispersal mode, availability of dispersal vectors, and distance to new habitat. A site may be colonized by a plant species through recruitment from seed or vegetative propagules (van der Valk 1992). *Primary immigration* is depicted as the dispersal of plant propagules not previously present in the new habitat. *Secondary immigration* is where species that were once established, are extinct in adult form. Propagules may be dormant within the seed bank or present as vegetative fragments.

For propagules of plant species dispersing into a new habitat, colonization and successful establishment is not guaranteed. Once a seed has arrived, several external conditions will determine successful colonization. Deposited seeds may be non-viable, attacked by fungal diseases, or preyed upon. Once germination or propagation requirements are met, growing

Figure 2.2 A conceptual model of plant species immigration, colonization, and establishment in hedgerows



seedlings or vegetative shoots have to contend with a new physical environment and competitive pressures from existing vegetation. Seedling growth may be facilitated or inhibited by neighbouring vegetation and may be dependent upon tolerance to stress, competition and recovery from predation. This initial colonization phase could be a temporary phenomenon, without a permanent outcome. **Colonization** is therefore the successful germination of seeds or propagation of vegetative shoots, and their survival under competitive and predatory pressures.

Plant species life-history traits may determine the ability of a plant species to successfully maintain a permanent presence within a plant community. Failure to establish could be due to competitive and predatory pressure or extreme stochastic events. Plant establishment is therefore dependent upon further tolerance to competitive and stress-related variables. Therefore, successful **establishment** is defined as individuals that have survived competitive and selective pressures during the immigration and colonization process, and are able to obtain some permanent presence, whether above ground or as persistent seeds within the seed bank.

This conceptual model displays how the three processes of plant immigration, colonization and establishment are interdependent and indicate where extinction is likely to occur. This model may provide a useful tool when evaluating landscape and local processes and will help determine the sustainability of plant development when contributing factors of immigration, colonization and establishment success are examined. This model also has the potential to inform planners and conservationists of precautionary principles when planning for habitat restoration and creation, as it is important to realise the likely mechanisms that could aid the rehabilitation of declining populations, or the failure of reintroduced species. Insights gained from both the concept map and model presented were used to develop the aims and hypotheses in the three chapters that follow. With an awareness of spatial and temporal scales, ecological processes that may determine plant immigration, colonization and establishment success in species-poor hedgerows are explored in this thesis.

Chapter 3 Distribution of plant species across ten woodland-hedgerow transition zones

3.1 Introduction

This chapter examines the distribution of plant species across the transition zone from two remnant ancient woodlands into adjoining species-poor Enclosure Act hedgerows; to ascertain if plant species found in nearby woodland sources were colonizing adjoining species-poor hedgerow (see Chapter 1). An investigation examined whether differing spatial patterns could be detected for groups of plants associated with particular community types and for individual plant species. This chapter also considered whether such variation was accounted for by differing life history strategies of individual plant species (see Chapter 2) found in woodland and hedgerow quadrats and species located in both habitat types (*Transition species*)

3.2 Study sites

Northamptonshire has around 1700 woodlands, covering around five percent of the county (Colston *et al.* 1996). Extant ancient woodlands located in the north-east region of Northamptonshire were collectively part of a former Royal Forest, known as Rockingham Forest (Anon. 1988) (Figure 3.1). The Forest region lies on Jurassic strata with mostly clay and outcrops of limestone. Large tracts of plateau land in the Rockingham Forest are capped with boulder clay, resulting in uniformly heavy soils (Peterken and Harding 1974).

Two large woodlands, within the Rockingham Forest Region, were chosen for study: Geddington Chase and Fineshade Wood. (Figure 3.2). Although commercially managed, both woodlands contain species-rich, relict ancient woodland communities. Geddington Chase (O.S. SP 88/98 910845) is an area of approximately 2.5 km², situated north-east of Kettering in Northamptonshire. In 1904, high forest management was introduced to Geddington Chase, replacing the long-established traditional woodland management of coppicing. Clear felling and the planting of *Quercus robur*, *Fraxinus excelsior*, *Larix decidua*, *Fagus sylvatica* and

Figure 3.1 Inset map position of Northamptonshire in the east of England. Main diagram: the position of Rockingham Forest circa 1286 in relation to present-day Northamptonshire and surrounding counties.

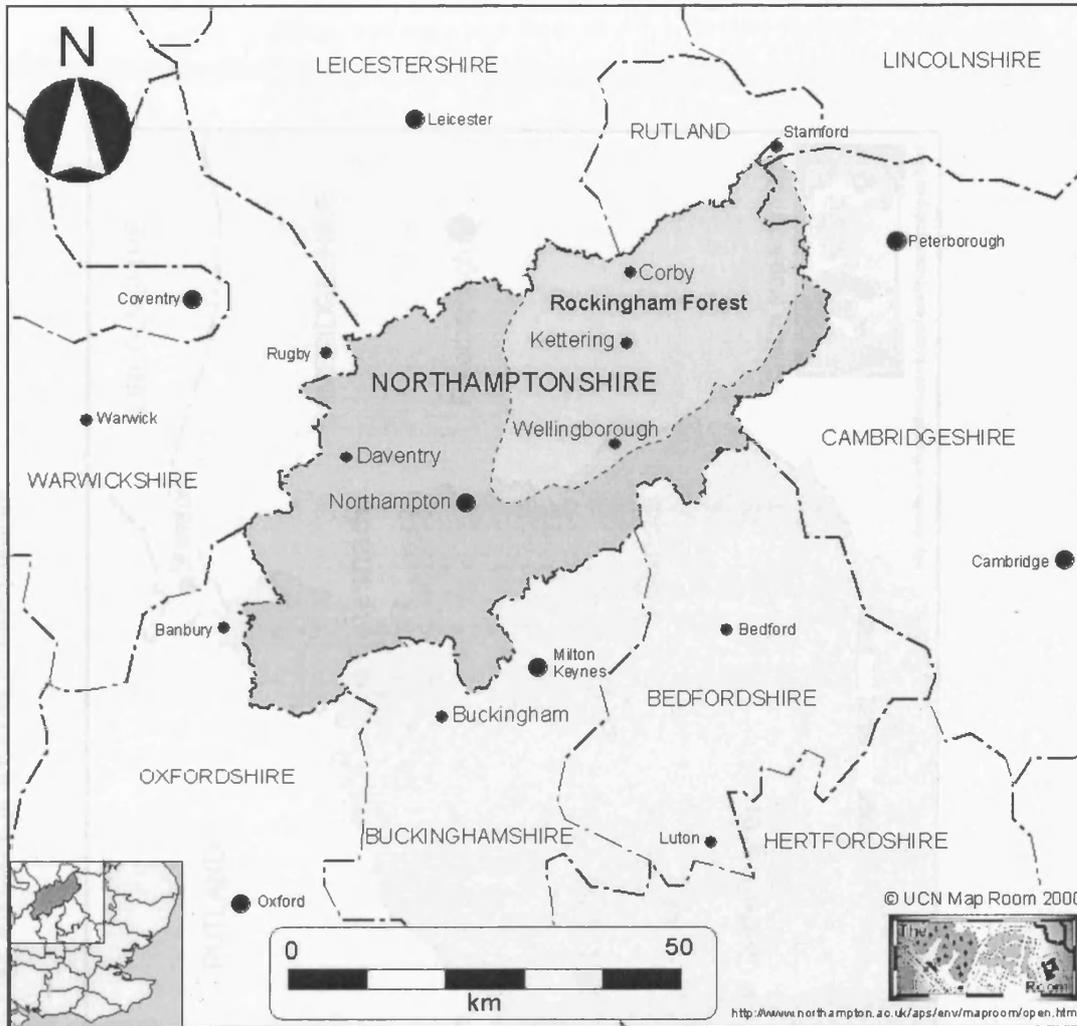
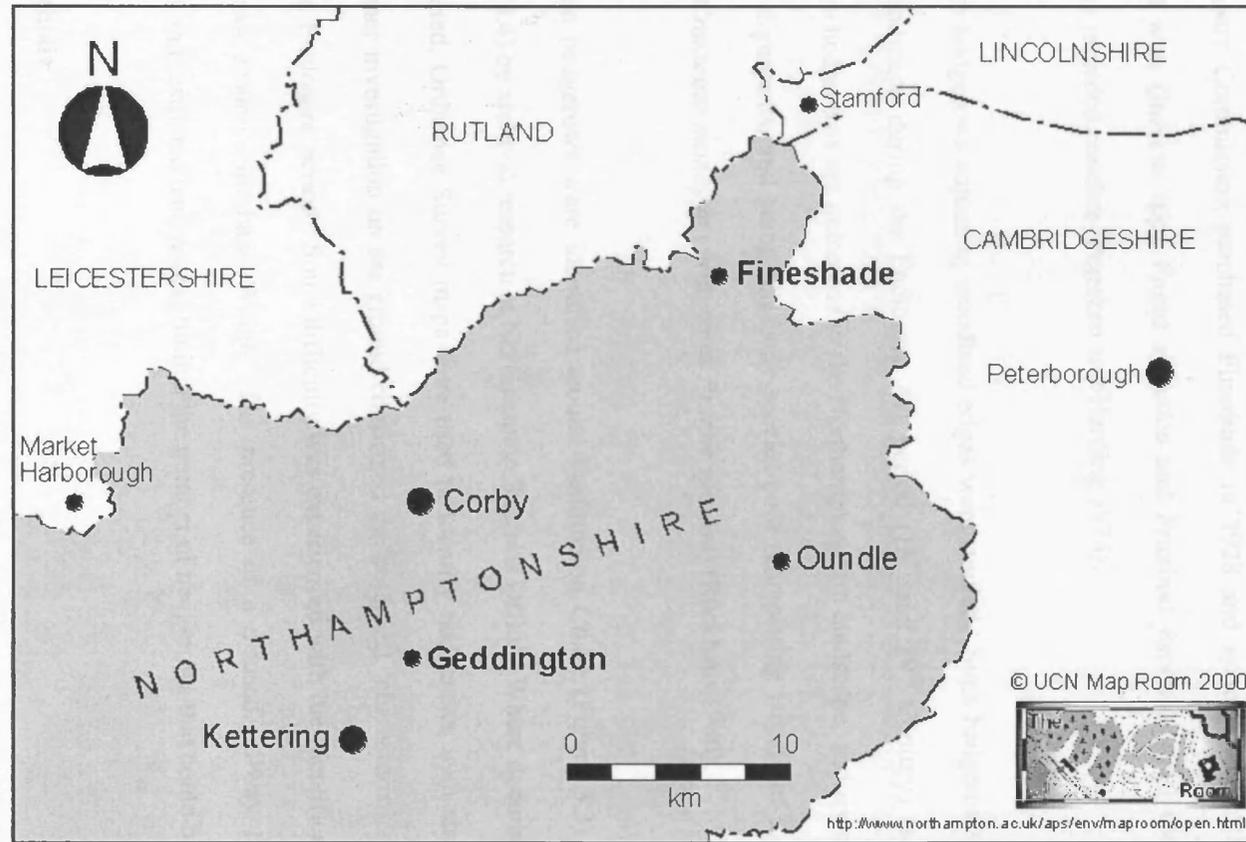


Figure 3.2 Location of Geddington Chase and Fineshade woodlands in north-east Northamptonshire



Populus serotina occurred throughout the site. After World War Two, additional non-native species were planted: *Larix decidua*, *L. kaempferi*, *Picea abies*, *P. sitchensis*, *Pseudotsuga menziesii* (Bellamy 1986). Fineshade (or Westhay) Wood is sited further north, near Stamford (O.S. SP 89/99 990981) and is approximately 5km² in size (Forestry Enterprise pers. com.).

The Forestry Commission purchased Fineshade in 1928 and systematically clear-felled and replanted with *Quercus* spp., *Fagus sylvatica* and *Fraxinus excelsior* until the 1960s, when replanting included conifers (Peterken and Harding 1974).

Enclosure hedgerows adjoining woodland edges were studied. Such hedgerows were installed in the landscape during the Enclosure Act period (18th and 19th Century) (see Chapter 2). Enclosure hedgerows are numerous in the Northamptonshire landscape, and are noted as having straight alignments, and being relatively species-poor (comprising largely of the woody shrub species *Crataegus monogyna* with some *Prunus spinosa*) (Rackham 1986).

Enclosure hedgerows were identified around Geddington Chase (Figure 3.3) and Fineshade (Figure 3.4) by archival research at Northampton Records Office. Where documentary evidence was limited, Ordnance Survey maps were used to identify hedgerows with straight alignment and further investigation on the ground confirmed the botanical 'characteristics' of hedgerows from the Enclosure period. Some difficulty was experienced with the identification of suitable hedgerows around Fineshade Wood. The presence of a disused railway track, hedgerow removal and restricted land access limited the number of hedgerows that could be surveyed.

3.3 Methods

A belt transect is a recognised method for systematic sampling across environmental gradients (Greig-Smith 1983, Shimwell 1971). The spatial scale over which plant species were distributed across woodland and hedgerow transition zones was uncertain, therefore a

Figure 3.3 Woodland-hedgerow transects sampled at Geddington Chase

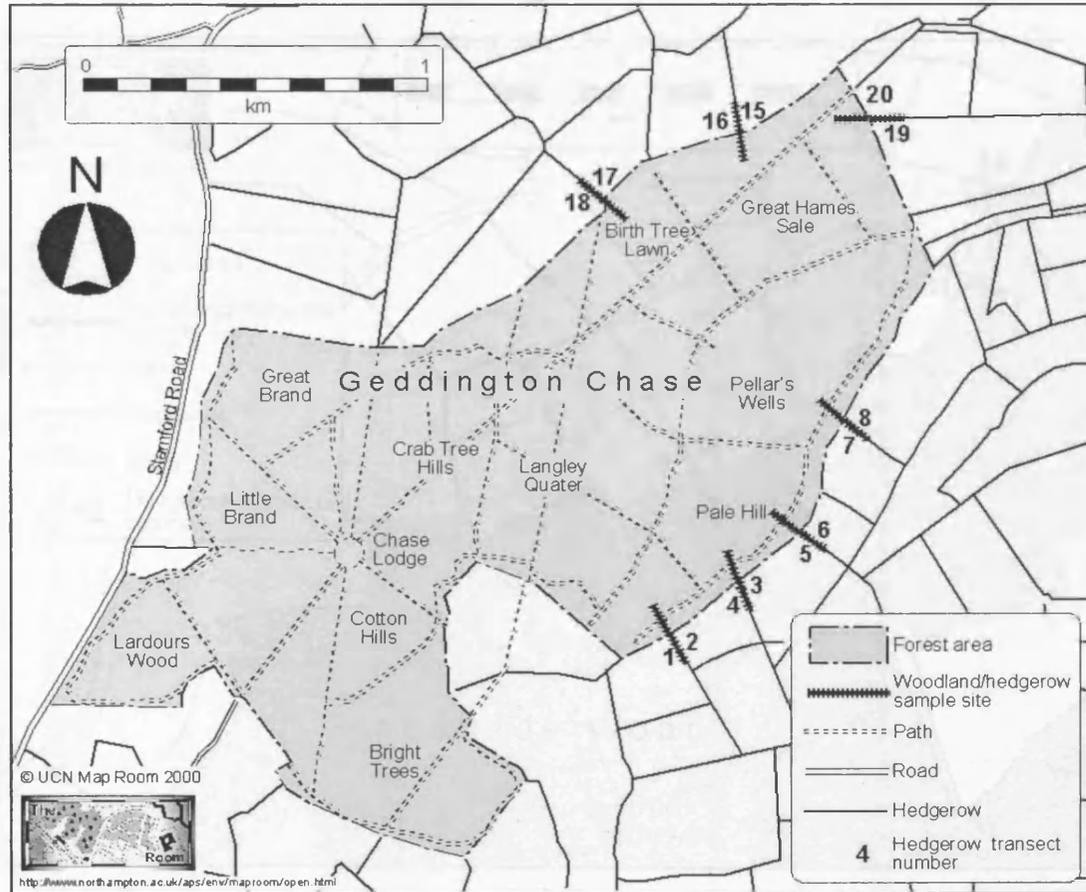
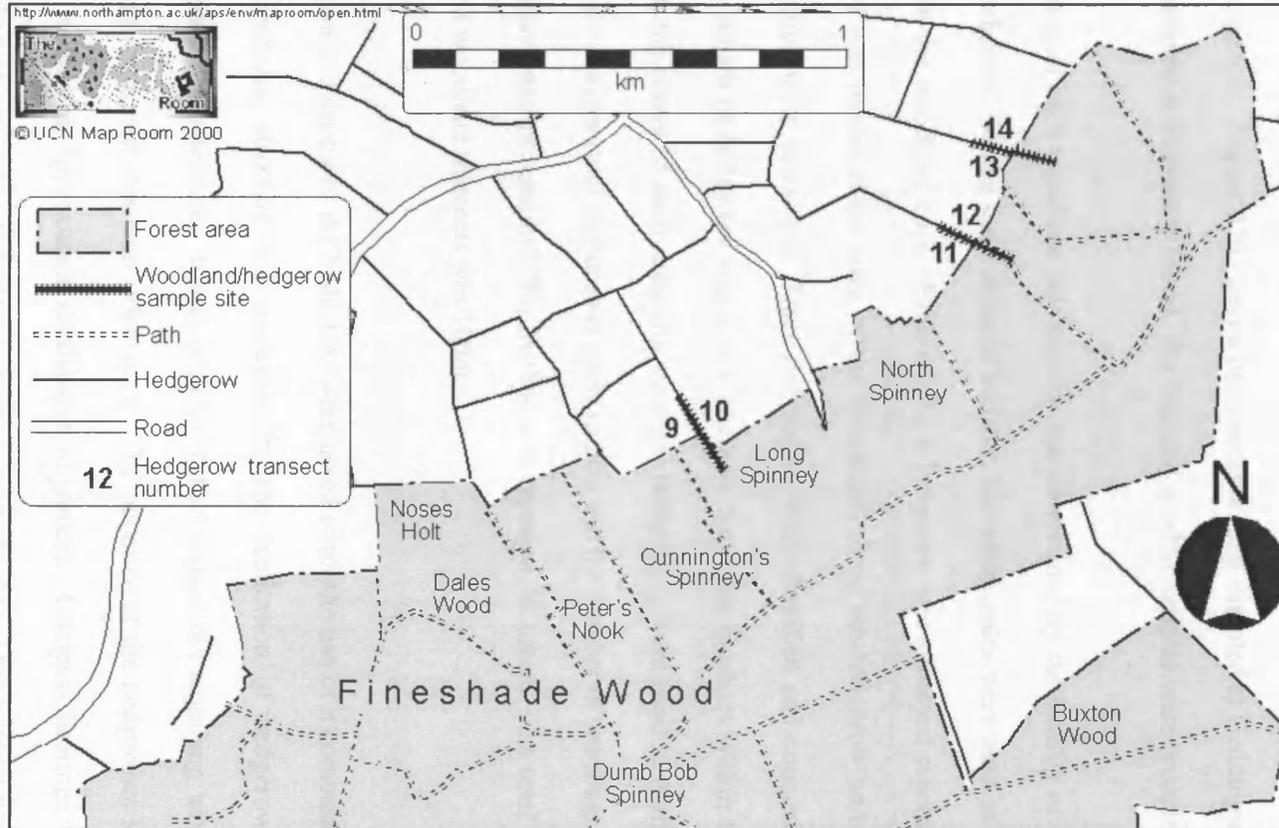


Figure 3.4 Woodland-hedgerow transects sampled at Fineshade



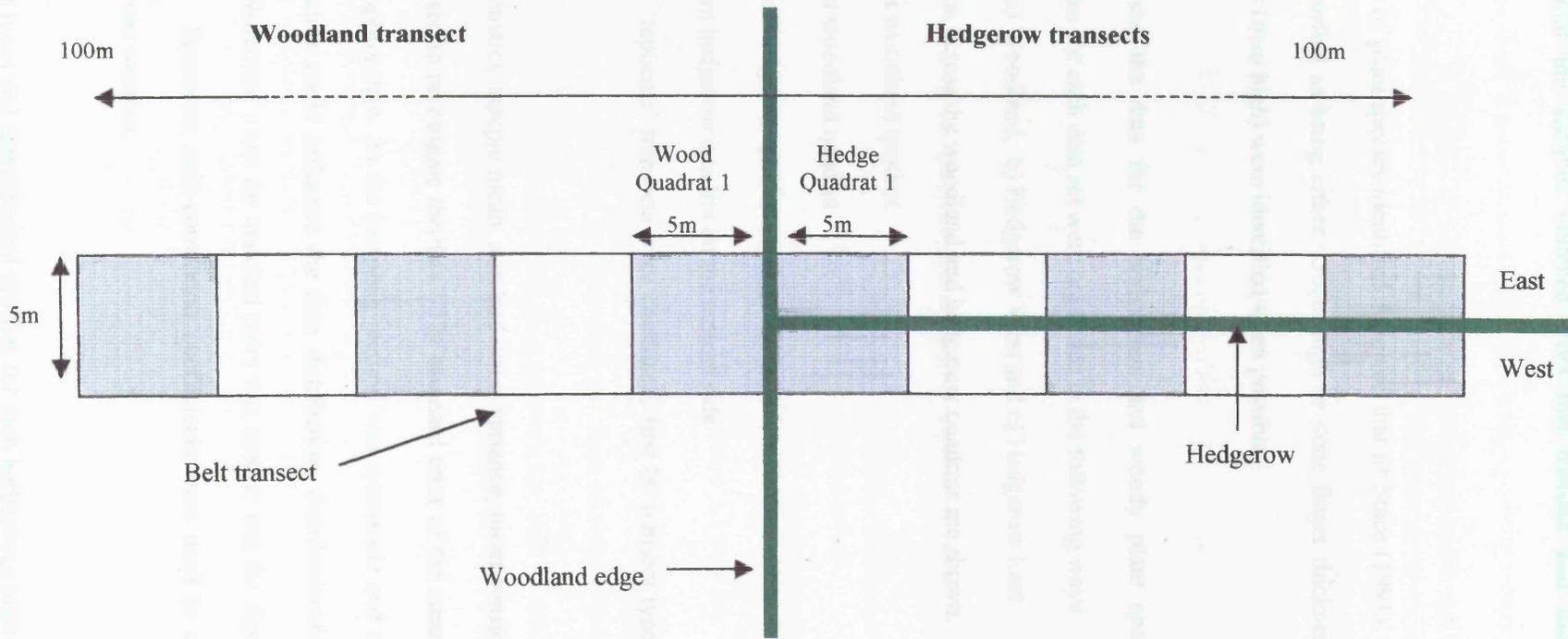
discontinuous belt-transect method was chosen for this survey to extend the sample area, as the spatial scales of the plant distributions unknown. The field work for this study occurred between May and June 1995.

Ten discontinuous belt-transects were sampled across woodland boundaries into adjoining Enclosure hedgerows (Figure 3.5). Seven belt transects were sampled at Geddington Chase and three were sampled at Fineshade Wood. Six hundred quadrat samples were recorded in total.

The positioning of each woodland belt transect was determined by the locality of the adjoining Enclosure hedgerow. Along the woodland transect, surveying poles were used to mark out the quadrats from the woodland edge. Each side of a hedgerow was surveyed separately. A 20m tape measure was placed at the edge of the woodland; along the hedgerow and alternate 5m lengths of hedge were measured. Trees and shrubs were identified and counted within each alternate 5m length of hedgerow and within alternate 5m x 5m quadrats within the woodland transects. In the centre of each sampling location, metre rules were used to mark a 1m x 1m quadrat to record presence of herbaceous plant species and the number of seedlings or suckering stems of woody trees and shrubs. This method was repeated 10 times. The total length of the hedgerow and woodland transects was 100m.

The orientation and aspect of the hedgerow were noted (with the use of a compass), along with hedgerow condition, structure and management. The replication of hedgerow aspect and orientation proved problematic. It was difficult to find hedgerows adjoining woodlands with absolute north-south and east-west orientation. The majority of the hedgerows located at the two study sites had an approximate north-south alignment. Compass bearings were used to categorise into east-west hedgerow aspect groups (Appendix 3.1). One transect was anomalous, (hedge transect 19/20 Transect 10) lying on an east-west orientation. Data within this sample were divided into aspect east-west groupings when compass readings were examined. Further

Figure 3.5 Strategy for alternate sampling in belt transects in woodland and adjoining hedgerow: shading = sample locations.



analysis proved that the samples obtained from this transect had minimal impact on amalgamated data.

The nomenclature of plant species identified followed that of Stace (1991). Young shrub/tree saplings were identified as being either <50cm high or <one finger thickness. Seedlings and suckering stems (<10cm high) were identified when possible.

During the analysis, the data for the herbaceous and woody plant species were treated separately. Samples for each data set were organised in the following ways:

- transect type: a) Woodland, b) Hedgerow West and c) Hedgerow East
- quadrat location across the woodland and hedgerow quadrats are shown:

e.g W1 = first woodland quadrat

W10 = last woodland quadrat

H1W = first hedgerow quadrat on the western side

H10E = last hedgerow quadrat on the eastern side

Data from the ten 'replicate' transects were combined, first by transect type, and secondly by quadrat location.

The descriptive statistics: sample mean, standard error, variance, mean confidence intervals and data range were used to investigate the data. The standard error of the mean (SE) is shown as error bars where appropriate. As the sampling method was systematic and unavoidable spatial autocorrelative factors could influence the data distribution, distribution-free-non parametric tests were used. Wilcoxon's test for matched pairs was used to test for significant differences between samples. Spearman rank-correlation coefficients were used to analyse the spatial relationships between samples.

Associated habitat types and autecological profiles for each herbaceous plant species identified, were obtained from the electronic database by Hodgson *et al.* (1995). Ten life history

characteristics were extracted from the data base (soil pH, life history, establishment strategy, leaf phenology, life form, regeneration strategy, seed bank, dispersal strategy, dispersule form and dispersule weight). A glossary of autecological terms is presented in Appendix 3.2.

Herbaceous plant species were divided into three community groups:

- 1) those located in the woodland quadrats only = Woodland group,
- 2) species located in the hedgerow quadrats only = Hedgerow group,
- 3) species located in both woodland and hedgerow quadrats = Transition group.

Autecological profiles of each community group were compared and tested using the Kruskal-Wallis test.

3.4 Herbaceous plant species results

3.4.1 Spatial distributions across woodland/hedgerow transition zones

A total of 70 herbaceous plant species were identified during this study. Distributions within each woodland and hedgerow transect are shown in Appendix 3.3 and 3.4. A summary of the number of herbaceous plant species in each transition transect are shown in Table 3.1. The standard error values indicate that the variation from the mean total number of plant species was largest between the woodland transects and least between the eastern sides of the adjoining hedgerows.

No significant differences were found between the total number of species in each transect in the woodland and hedgerow transects, or between each hedgerow aspect (using Wilcoxon test for matched pairs (Fowler and Cohen 1992)) (Table 3.2).

Table 3.1 Comparison of the total species number in each transect type (with mean and median number of species per transect, SE = standard error, and range)

Transect	Wood	Hedge	
		West	East
1	14	15	10
2	17	10	16
3	10	16	15
4	11	16	15
5	11	16	17
6	12	17	13
7	22	11	15
8	14	9	14
9	7	14	15
10	7	11	13
Mean	12.5	13.5	14.3
Median	11.5	14.5	15
SE	1.44	0.93	0.62
Range	7-22	9-17	10-17

Table 3.2 Results of Wilcoxon test for matched pairs: number of herbaceous plant species

	Hedge West			Hedge East		
	n	T	p	n	T	p
Woodland	9	6	non sig.	9	6	non sig.
Hedge East	9	10	non sig.			

The spatial distribution of the mean number of herbaceous plant species along the woodland-hedgerow transition showed a complex pattern. Species richness was higher in the hedgerows and into the woodland edge (Figure 3.6).

Herbaceous plant species per quadrat were organised into categories of most commonly associated habitat types used by Hodgson *et al.* (1995). Species richness of plant species most commonly associated with woodland and scrub communities were found to be higher at the woodland edge and further into the woodland (Figure 3.7a). The mean number of species were located within the adjoining hedgerow, but were found to decline in number with distance from the woodland edge. Hedgerow and road verge species were mostly located in the hedgerow transects (Figure 3.7b). Species associated with pasture and meadow habitats (Figure 3.7c) were most frequently located in the hedgerow transects, whilst those associated with river and mire habitats (Figure 3.7d) were more frequent along the woodland transects.

Figure 3.6 Spatial variation in the mean number of herbaceous plant species per m² across the sampling sites (Error bar = SE)

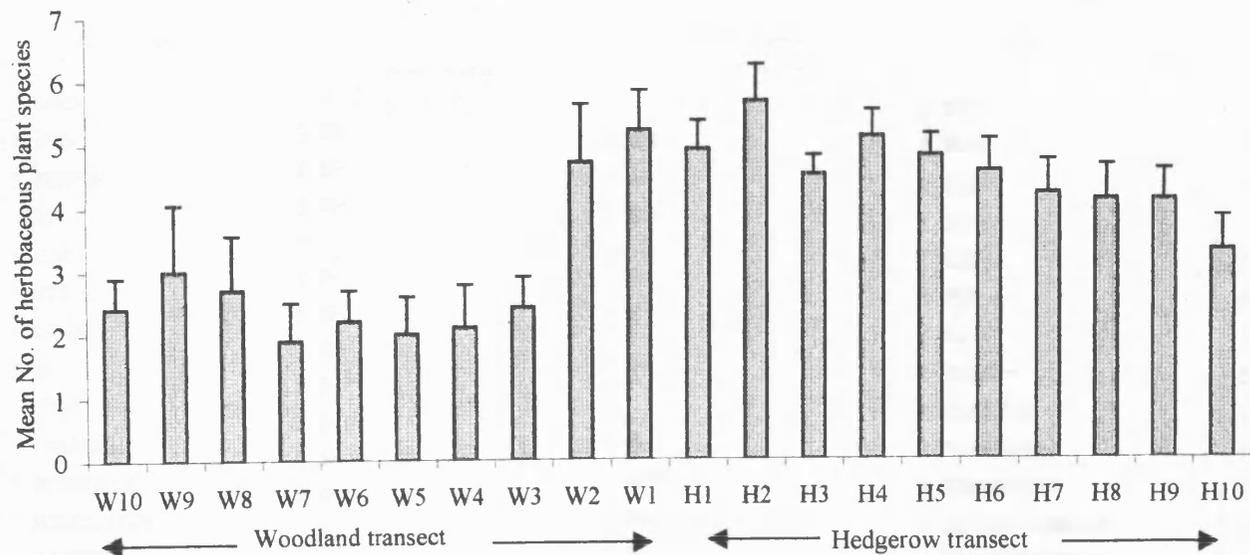
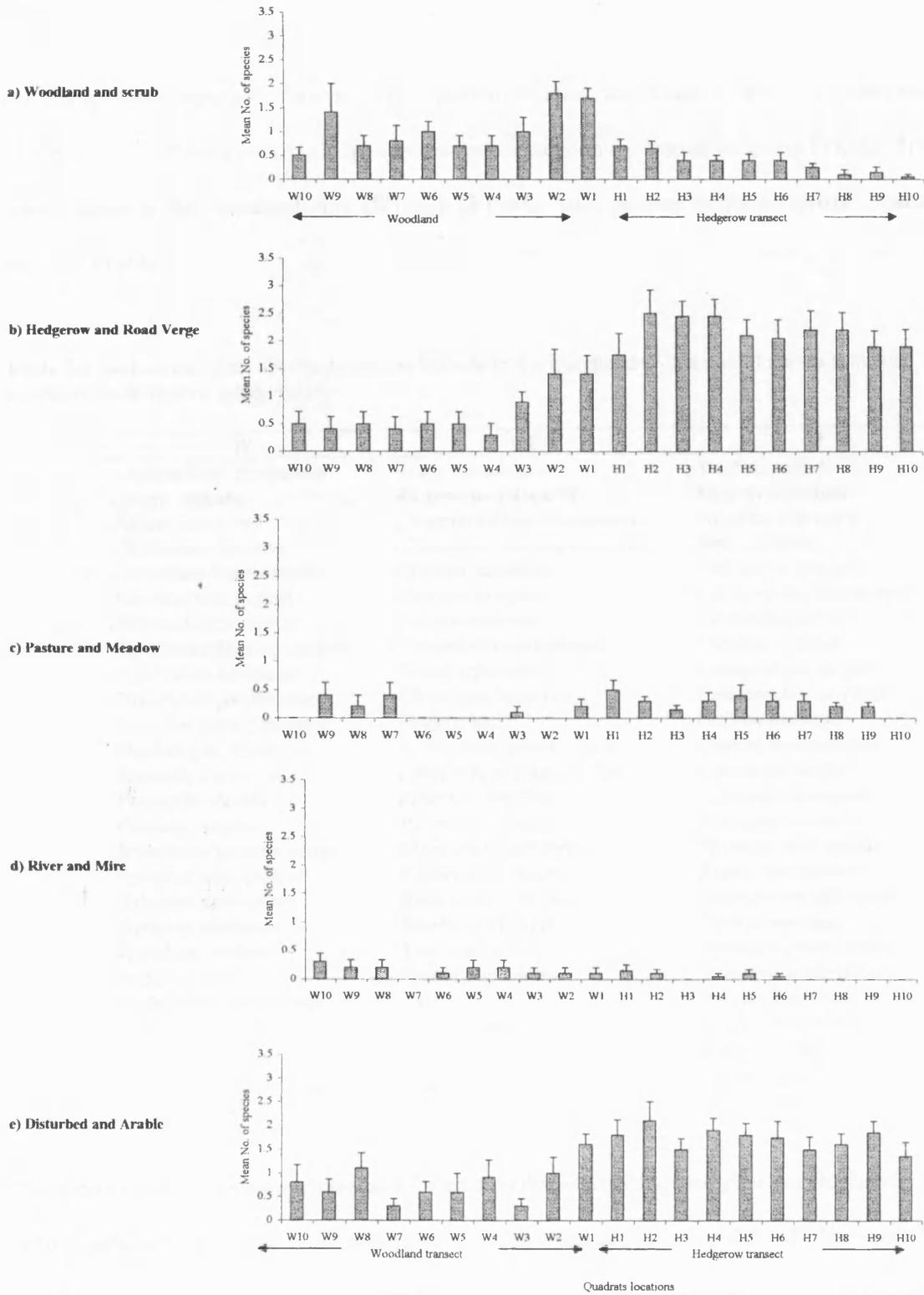


Figure 3.7 Mean Number of species in each habitat group across the sampling sites



Herbaceous plant species associated with disturbed habitats declined in number along the woodland transects (Figure 3.7e).

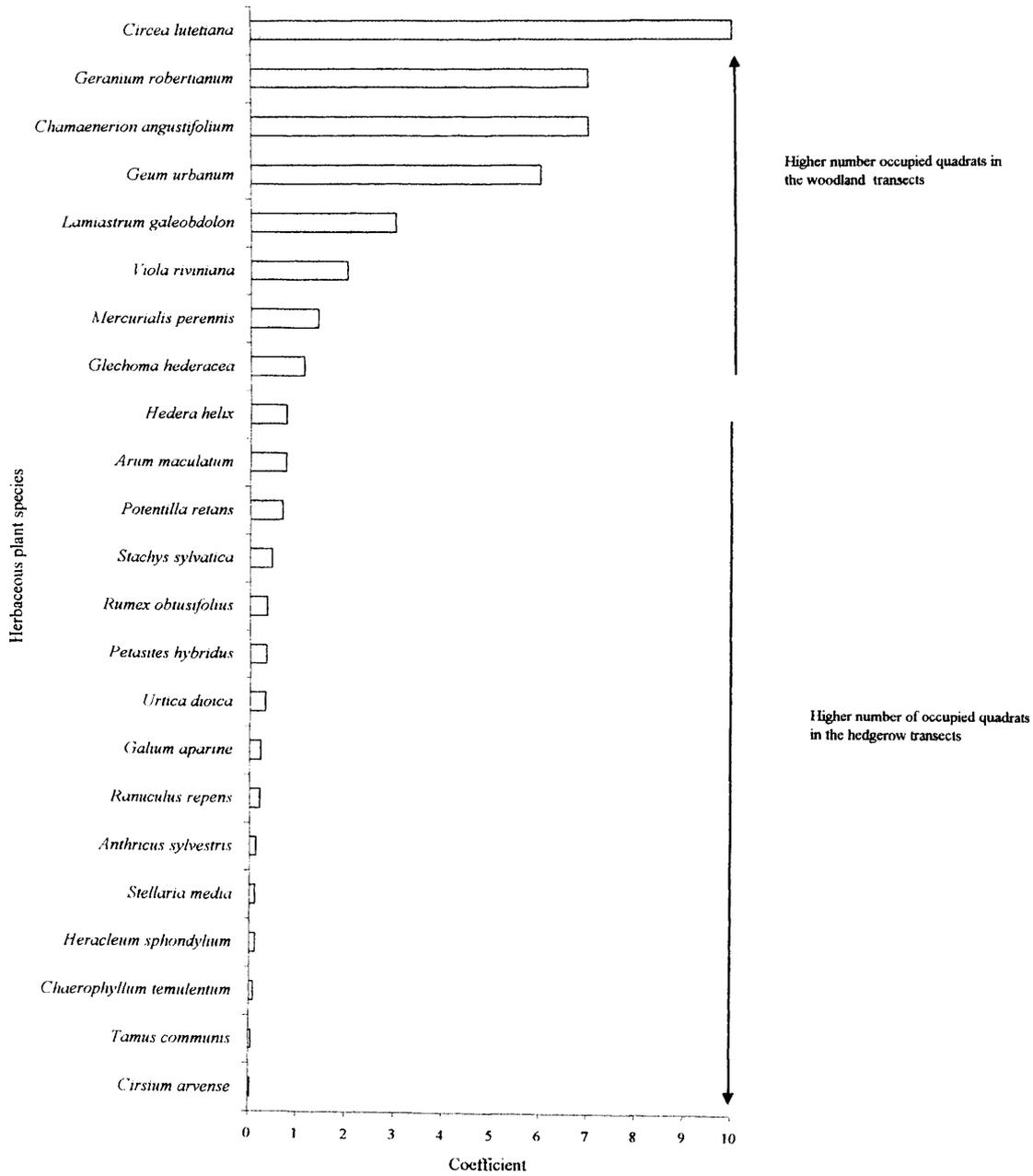
For comparative purposes, data for each quadrat location and transect type were combined (Appendix 3.5). Twenty-three (33%) species were located in the transition group (T), 22 (31%) were located in the woodland only (W) and 25 (36%) were present in the hedgerow quadrats only (H) (Table 3.3).

Table 3.3 Herbaceous plant species found exclusively in the woodland (W), across the transition zone (T) or within the hedgerow quadrats (H)

W	T	H
<i>Aegopodium podagaria</i>	<i>Arum maculatum</i>	<i>Achillea millefolium</i>
<i>Ajuga reptans</i>	<i>Anthriscus sylvestris</i>	<i>Alliaria petiolata</i>
<i>Allium ursinum</i>	<i>Chaerophyllum temulentum</i>	<i>Angelica sylvestris</i>
<i>Cardamine flexuosa</i>	<i>Chamaenerion angustifolium</i>	<i>Bryonia dioica</i>
<i>Cerastium holosteoides</i>	<i>Circaea lutetiana</i>	<i>Calystegia sepium</i>
<i>Dactylorhiza fuchsii</i>	<i>Cirsium arvense</i>	<i>Capsella bursa-pastoris</i>
<i>Filipendula ulmaria</i>	<i>Galium aparine</i>	<i>Centaurea nigra</i>
<i>Hyacinthoides non-scripta</i>	<i>Geranium robertianum</i>	<i>Cirsium arvense</i>
<i>Hypericum hirsutum</i>	<i>Geum urbanum</i>	<i>Conopodium majus</i>
<i>Hypericum perforatum</i>	<i>Glechoma hederacea</i>	<i>Convolvulus arvensis</i>
<i>Lonicera periclymenum</i>	<i>Hedera helix</i>	<i>Galium mollugo</i>
<i>Moehringia trinervia</i>	<i>Heracleum sphondylium</i>	<i>Geranium dissectum</i>
<i>Myosotis sylvatica</i>	<i>Lamiastrum galeobdolon</i>	<i>Geranium molle</i>
<i>Potentilla sterilis</i>	<i>Petasites hybridus</i>	<i>Lapsana communis</i>
<i>Primula vulgaris</i>	<i>Potentilla reptans</i>	<i>Myosotis arvensis</i>
<i>Scrophularia auriculata</i>	<i>Mercurialis perennis</i>	<i>Plantago lanceolata</i>
<i>Scrophularia nodosa</i>	<i>Ranunculus repens</i>	<i>Rumex sanguineus</i>
<i>Solanum dulcamara</i>	<i>Rumex obtusifolius</i>	<i>Sisymbrium officinale</i>
<i>Stellaria nemorum</i>	<i>Stachys sylvatica</i>	<i>Taraxacum agg.</i>
<i>Tussilago farfara</i>	<i>Stellaria media</i>	<i>Veronica chamaedrys</i>
<i>Vicia sepium</i>	<i>Tamus communis</i>	<i>Veronica hederifolia</i>
<i>Viola reichenbachiana</i>	<i>Urtica dioica</i>	<i>Veronica persica</i>
	<i>Viola riviniana</i>	<i>Vicia tetrasperma</i>
		<i>Viola arvensis</i>
		<i>Viola hirta</i>

The total number of occupied quadrats for each herbaceous plant species was calculated. The ratio coefficients for woodland-hedgerow quadrat occupation are graphically presented in Figure 3.8. Highest coefficient values indicate higher quadrat occupancy in the woodland quadrats. In particular, eight species (*Glechoma hederacea*, *Mercurialis perennis*, *Viola*

Figure 3.8 Ratio coefficient values for each herbaceous species between woodland and hedgerow quadrats



riviniana, *Lamiaeum galeobdolon*, *Geum urbanum*, *Chamaenerion angustifolium*, *Geranium robertianum* and *Circea luteiana*) were increasingly more frequent in the woodland quadrats.

The spatial distribution of percentage site occupancy in the combined data across the woodland and hedgerow transition zone are displayed in Figure 3.9. *Circea lutetiana*, *Geranium robertianum*, *Chamaenerion angustifolium*, *Geum urbanum*, *Lamiaeum galeobdolon*, and *Viola riviniana* were found more frequently in woodland transects (Figure 3.9a). *Mercurialis perennis* and *Glechoma hederacea* occupied a higher number of quadrats in the woodland transects and occurred in fewer quadrats along the hedgerow transects with distance away from the woodland edge. *Mercurialis perennis* was found to have the highest percentage site occupancy in the woodland edge region of the woodland and hedgerow transition (W1 = 0-5m and W2 = 10-15m).

Potentilla reptans, *Stachys sylvatica* and *Hedera helix* were found more widely spread across the woodland/hedgerow transects (Figure 3.9b). *Heracleum sphondylium*, *Rumex obtusifolius* and *Urtica dioica* were also found to be widely distributed but were more frequently found within the hedgerow quadrat samples. The percentage site occupancy of *Rumex obtusifolius* declined along the hedgerow transect with distance away from the woodland edge, whereas percentage site occupancy of *Urtica dioica* declined into the woodland edge and along the woodland transect.

Seven herbaceous plant species (*Arum maculatum*, *Stellaria media*, *Anthriscus sylvestris*, *Chaerophyllum temulentum*, *Tamus communis*, *Cirsium arvense*, and *Petasites hybridus*) had a higher percentage site occupancy within the hedgerow transects (Figure 3.9c). The spatial distribution of site occupancy also shows that these species were found in the woodland edge.

Figure 3.9 Spatial distribution of percentage site occupancy along the woodland/hedgerow transition zone

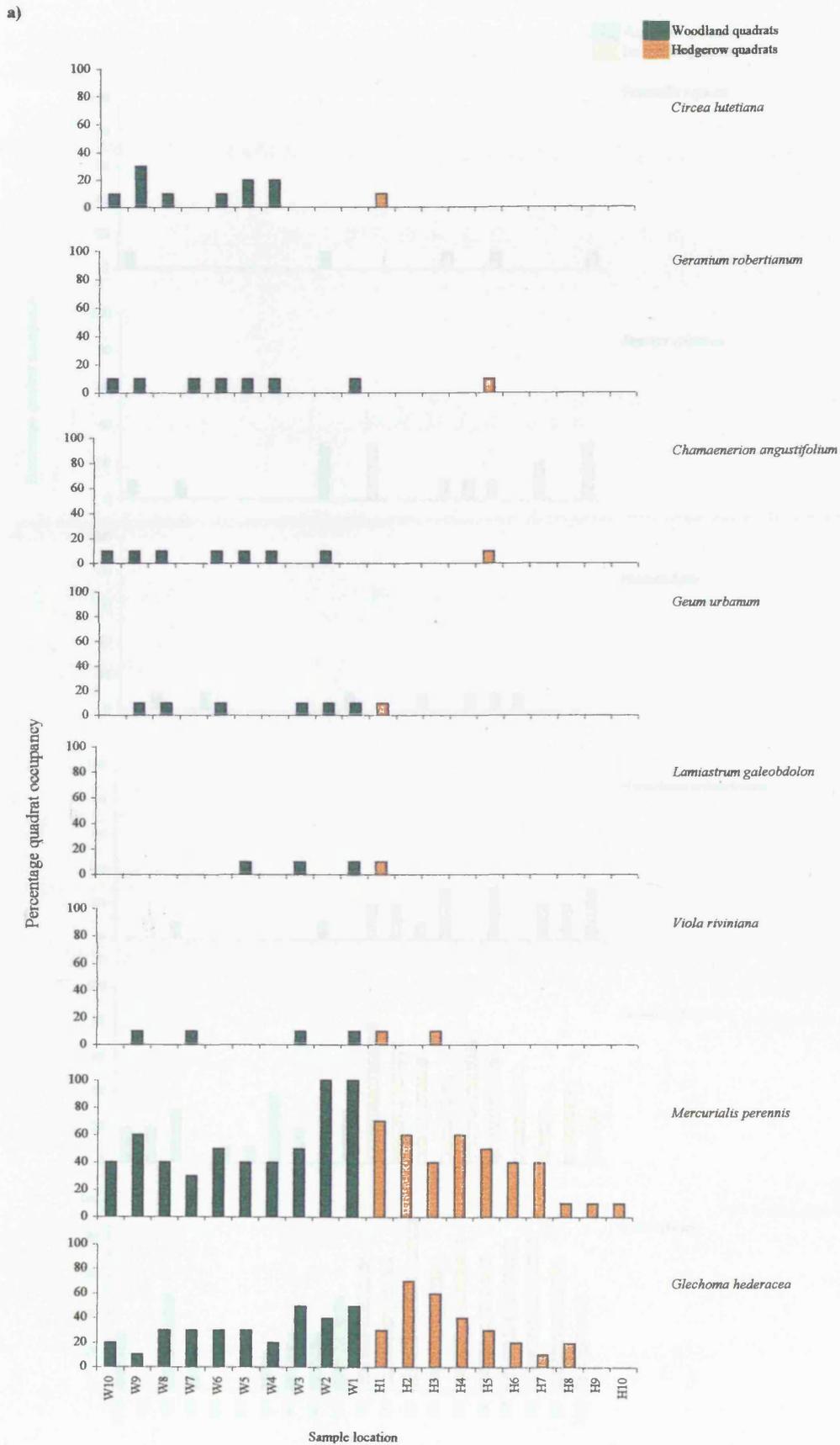


Figure 3.9 Spatial distribution of percentage site occupancy along the woodland/hedgerow transition zone

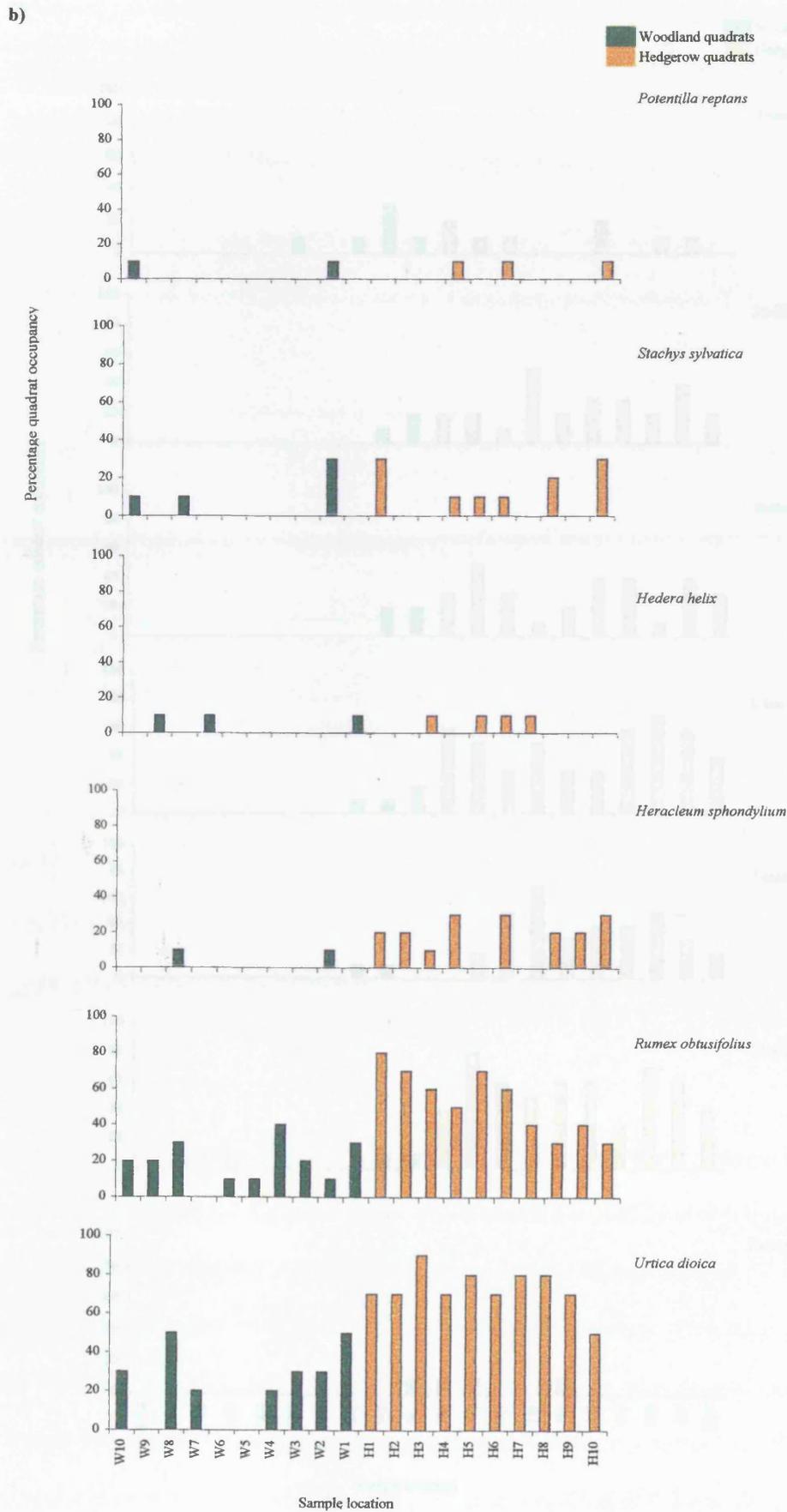
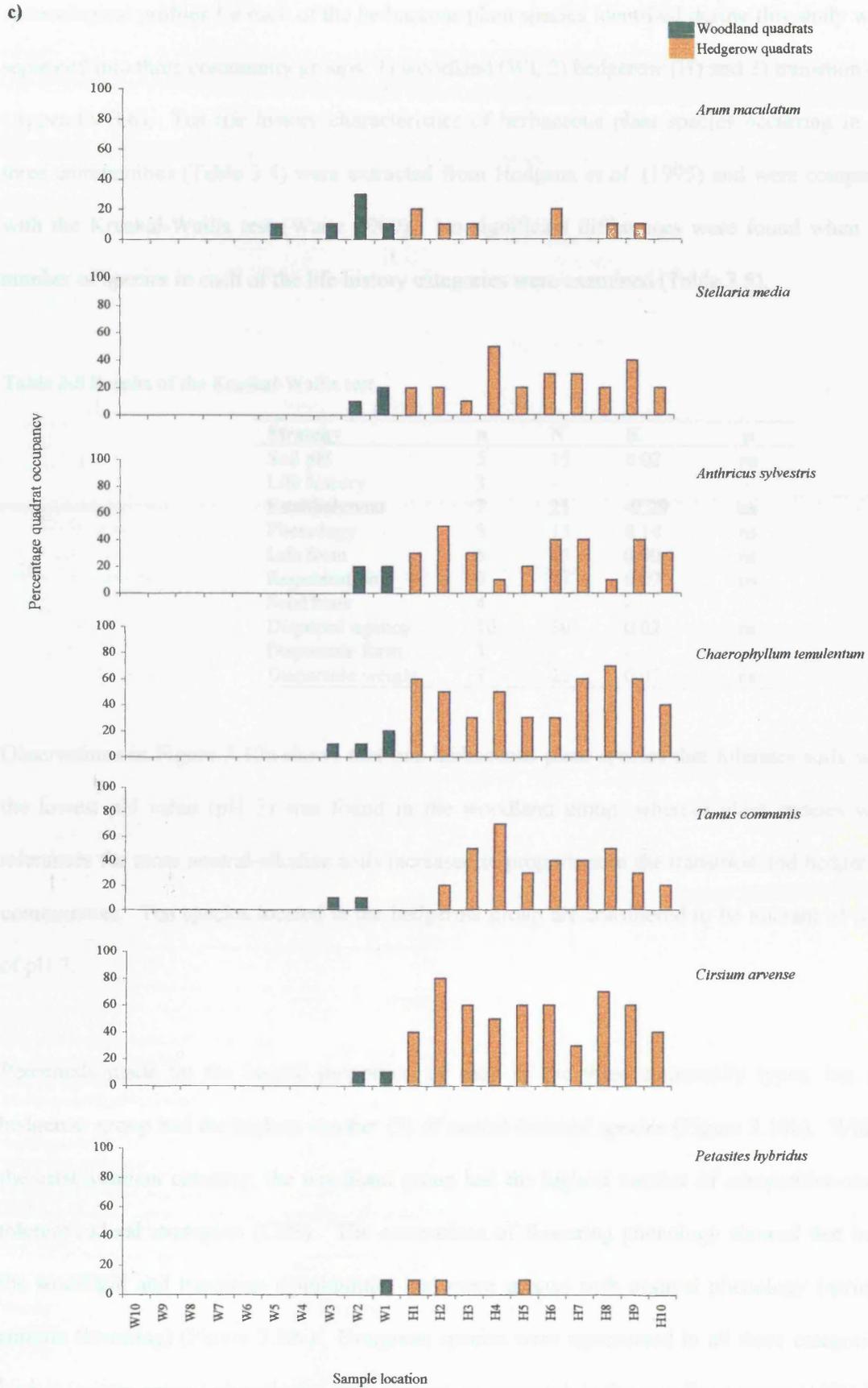


Figure 3.9 Spatial distribution of percentage site occupancy along the woodland/hedgerow transition zone



3.4.2 Autecological profiles of three community groups

Autecological profiles for each of the herbaceous plant species identified during this study were separated into three community groups: 1) woodland (W), 2) hedgerow (H) and 3) transition (T) (Appendix 3.6). Ten life history characteristics of herbaceous plant species occurring in the three communities (Table 3.4) were extracted from Hodgson *et al.* (1995) and were compared with the Kruskal-Wallis test (Waite 2000). No significant differences were found when the number of species in each of the life history categories were examined (Table 3.5).

Table 3.5 Results of the Kruskal-Wallis test

Strategy	n	N	K	p
Soil pH	5	15	0.02	ns
Life history	3	-	-	-
Establishment	7	21	-0.29	ns
Phenology	5	15	0.14	ns
Life form	5	15	0.00	ns
Regeneration	9	27	0.07	ns
Seed bank	4	-	-	-
Dispersal agency	10	30	0.02	ns
Dispersule form	3	-	-	-
Dispersule weight	7	21	0.07	ns

Observations in Figure 3.10a shows that one herbaceous plant species that tolerates soils with the lowest pH value (pH 3) was found in the woodland group, whereas plant species with tolerances for more neutral-alkaline soils increased in proportion in the transition and hedgerow communities. Ten species located in the hedgerow group are considered to be tolerant of soils of pH 7.

Perennials made up the largest proportion of each of the three community types, but the hedgerow group had the highest number (9) of annual-biennial species (Figure 3.10b). Within the establishment category, the woodland group had the highest number of competitive-stress tolerant-ruderal strategists (CSR). The comparison of flowering phenology showed that both the woodland and transition communities had more species with aestival phenology (spring–autumn flowering) (Figure 3.10c). Evergreen species were represented in all three categories. Vernal (winter-spring) phenologies were present, as expected, in the woodland group (10%) but

Table 3.3 Autoecological profiles: number of herbaceous plant species in each community group

Soil pH			
	Wood	T	Hedge
pH3	1	0	0
pH4	3	2	0
pH5	5	4	4
pH6	7	10	8
pH7	5	7	10
Total	21	23	22

Life History			
	Wood	T	Hedge
Perennial	18	20	12
Annual-biennial-perennial	3	1	1
Annual-biennial	0	2	9
Total	21	23	22

Establishment strategy			
	Wood	T	Hedge
Competitor	0	4	0
Stress tolerant/competitor	2	3	0
Stress tolerant	2	1	1
CSR	11	6	6
Competitive Ruderal	3	8	7
Stress tolerant/Ruderal	3	0	5
Ruderal	0	1	3
Total	21	23	22

Leaf phenology			
	Wood	T	Hedge
Spring-autumn	9	7	4
Always evergreen	7	8	7
Partially evergreen	3	4	5
Winter-spring	2	1	2
Autumn-early summer	0	3	4
Total	21	23	22

Life Form			
	Wood	T	Hedge
Woody: buds < 250mm	2	1	0
Buds below ground	4	6	3
Buds soil level & buds < 250mm	12	12	8
Bud < 250mm	1	1	2
Therophytes	2	3	9
Total	21	23	22

Regeneration strategy			
	Wood	T	Hedge
Unknown	1	1	0
Vegetative propagation and widely disp. seeds	1	2	0
Vegetative propagation only	4	2	0
Seed and vegetative propagation	6	5	3
Seed bank and vegetative propagation	4	4	4
Seed only	0	6	5
Seed bank only	2	2	6
Widely dispersed seeds	1	1	2
Seed and seed bank	2	0	2
Total	21	23	22

Seed bank			
	Wood	T	Hedge
?	1	0	0
Transient	9	13	2
Persistent	8	7	12
Intermediate	3	3	8
Total	21	23	22

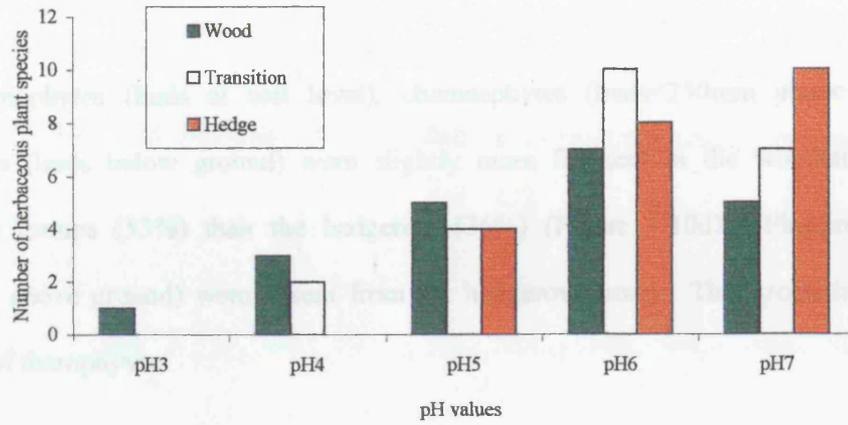
Dispersal agency			
	Wood	T	Hedge
Wind capsule & mucilaginous	1	0	0
Wind: capsule	6	0	1
Anim: ingested	2	3	0
Aquatic	2	1	1
Anim: ant dispersed	3	3	2
Wind: plumed	1	3	2
Wind: winged	1	1	3
Anim: adhesive	0	7	3
Anim: mucilaginous	0	0	1
UNSP	5	5	9
Total	21	23	22

Dispersule form			
	Wood	T	Hedge
Seed	2	5	2
Fruit	5	14	9
Fruit and seed	14	4	11
Total	21	23	22

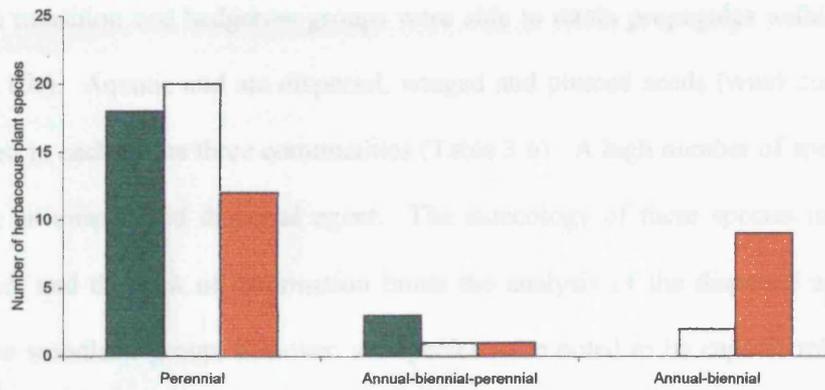
Dispersule Weight			
	Wood	T	Hedge
Spore	1	0	0
< 0.2mg	6	2	3
0.21-0.50mg	3	3	3
0.51-1mg	2	3	2
1.01-2mg	4	6	5
2.01-10mg	4	6	7
> 10mg	1	3	2
Total	21	23	22

Figure 3.10 Number of herbaceous plant species with different life history strategies in three plant community groups across a woodland-hedgerow transition zone

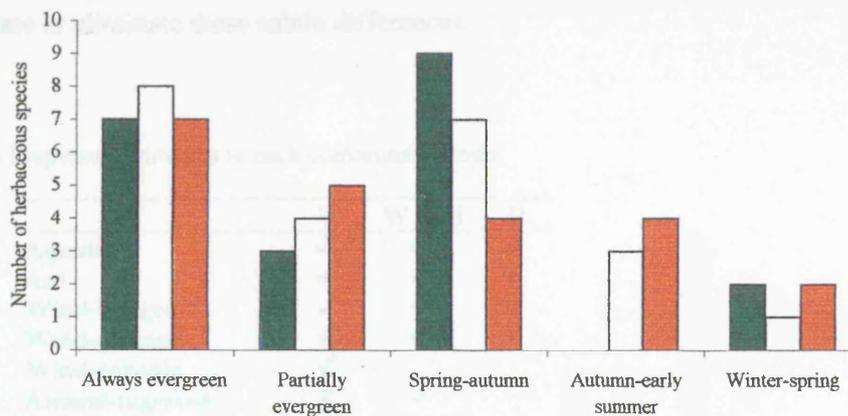
a) Soil pH



b) Life history



c) Phenology



were also present in the hedgerow (9%) and transition (4%) community groups. Hibernial (autumn-early summer) phenological strategies were not located within the woodland samples.

Hemicryptophytes (buds at soil level), chamaephytes (buds < 250mm above ground) and geophytes (buds below ground) were slightly more frequent in the woodland (56%) and transition groups (53%) than the hedgerow (36%) (Figure 3.10d). Phanerophytes (buds > 250mm above ground) were absent from the hedgerow group. This group had the highest number of therophytes.

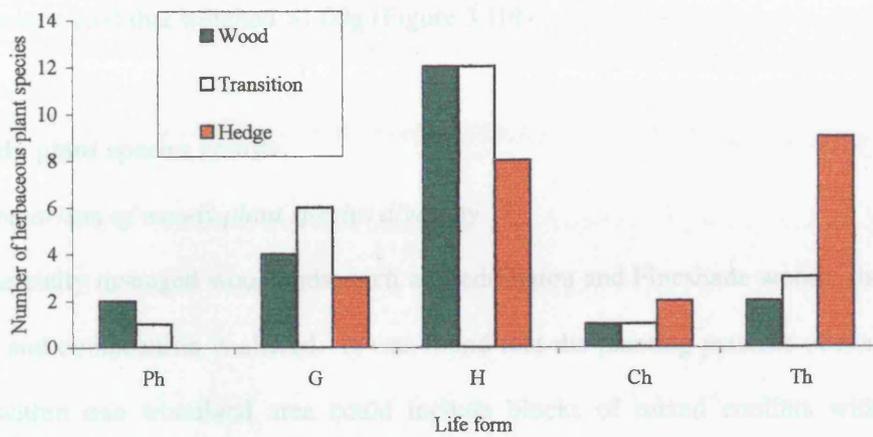
Non significant trends in the data for the regeneration strategies indicated that more species within the transition and hedgerow groups were able to retain propagules within the seed bank (Figure 3.10e). Aquatic and ant dispersal, winged and plumed seeds (wind-dispersal) were all represented in each of the three communities (Table 3.6). A high number of species were listed as having an unspecified dispersal agent. The autecology of these species may not be fully understood, and the lack of information limits the analysis of the dispersal agency category. Within the woodland group, however, six species were noted to be capsule released and wind dispersed. The highest value in the transition group (7) was for the adhesive seed and animal dispersed category. These results may highlight the need for further investigation to substantiate or eliminate these subtle differences.

Table 3.6 Dispersal Strategies in each community group.

	W	W & H	H
Aquatic	✓	✓	✓
Ant	✓	✓	✓
Wind-winged	✓	✓	✓
Wind-plumed	✓	✓	✓
Wind-capsule	✓		
Animal-ingested	✓	✓	
Animal-adhesive		✓	✓
Animal-mucilaginous			✓

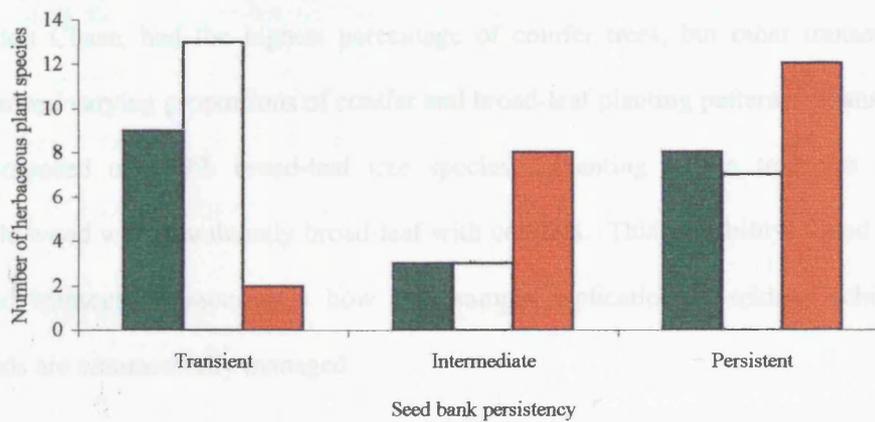
Figure 3.10 Number of herbaceous plant species with different life history strategies in three plant community groups across a woodland-hedgerow transition zone (cont.)

d) Life form

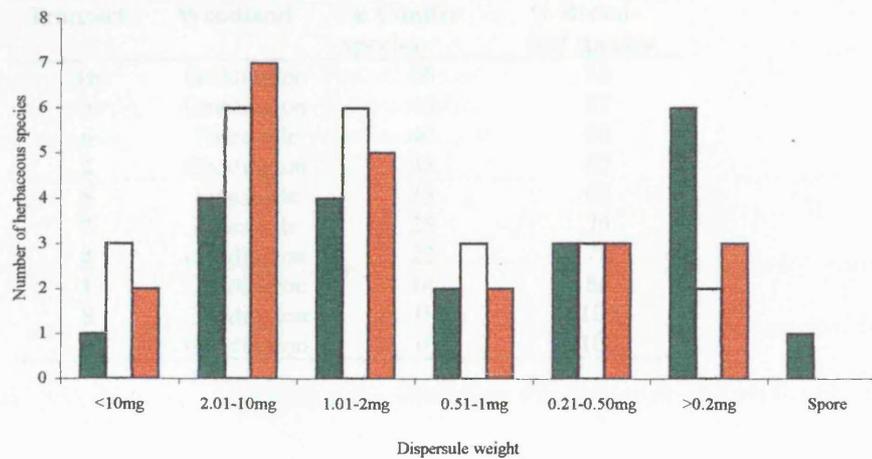


Ph = Phanerophytes G = Geophytes H = Hemicryptophytes Ch = Chamaephytes Th = Therophytes

e) Seed bank strategy



f) Dispersule weight



Twelve herbaceous plant species (57%) produced seeds that weighed <1.00g in the woodland group. Fifteen species (65%) in the transition group and 14 (63%) species in the hedgerow group produce seed that weighed >1.00g (Figure 3.10f).

3.5 Woody plant species results

3.5.1 Comparison of woody plant species diversity

In commercially managed woodlands, such as Geddington and Fineshade woods, the vegetation structure and composition is altered. It was found that the planting patterns of non-native tree species within one woodland area could include blocks of mixed conifers with broad-leaf species, or broad-leaf species only. Some variability in tree species composition was expected between the woodland transects. The proportion of conifer and broad-leaf tree species was calculated as a percentage of the total number of species (Table 3.7). Transect 10, sited in Geddington Chase, had the highest percentage of conifer trees, but other transects into this wood showed varying proportions of conifer and broad-leaf planting patterns. Transects 8 and 9 were composed of 100% broad-leaf tree species. Planting within transects surveyed in Fineshade wood were dominantly broad-leaf with conifers. This variability, found between the woodland transects, demonstrates how true sample replication is seldom achieved where woodlands are commercially managed.

Table 3.7 Proportions of conifer and broadleaf trees species in the woodland transects

Transect	Woodland	% Conifer species	% Broad-leaf species
10	Geddington	66	33
3	Geddington	43	57
6	Fineshade	40	60
2	Geddington	33	67
5	Fineshade	33	67
7	Fineshade	25	75
4	Geddington	22	78
1	Geddington	14	86
8	Geddington	0	100
9	Geddington	0	100

During this study, 23 species of *established* trees and shrubs, 12 species of *saplings*, and 11 tree and shrub species of *seedlings* were identified. The mean number of species per woodland and hedgerow transect are displayed in Figure 3.11. Analyses using Wilcoxon's test for matched pairs between the number of established woody plant species in the woodland transects and hedgerow transects showed that significantly more species were located in the woodland transects (Table 3.8). A significant difference was also found between the number of species on each side of the hedgerow transects.

Table 3.8 Results of Wilcoxon test for matched pairs: number of established woody plant species

	Hedge West			Hedge East		
	n	T	P	n	T	P
Woodland	9	3	<0.02	9	0	<0.02
Hedge East	9	3.5	<0.05			

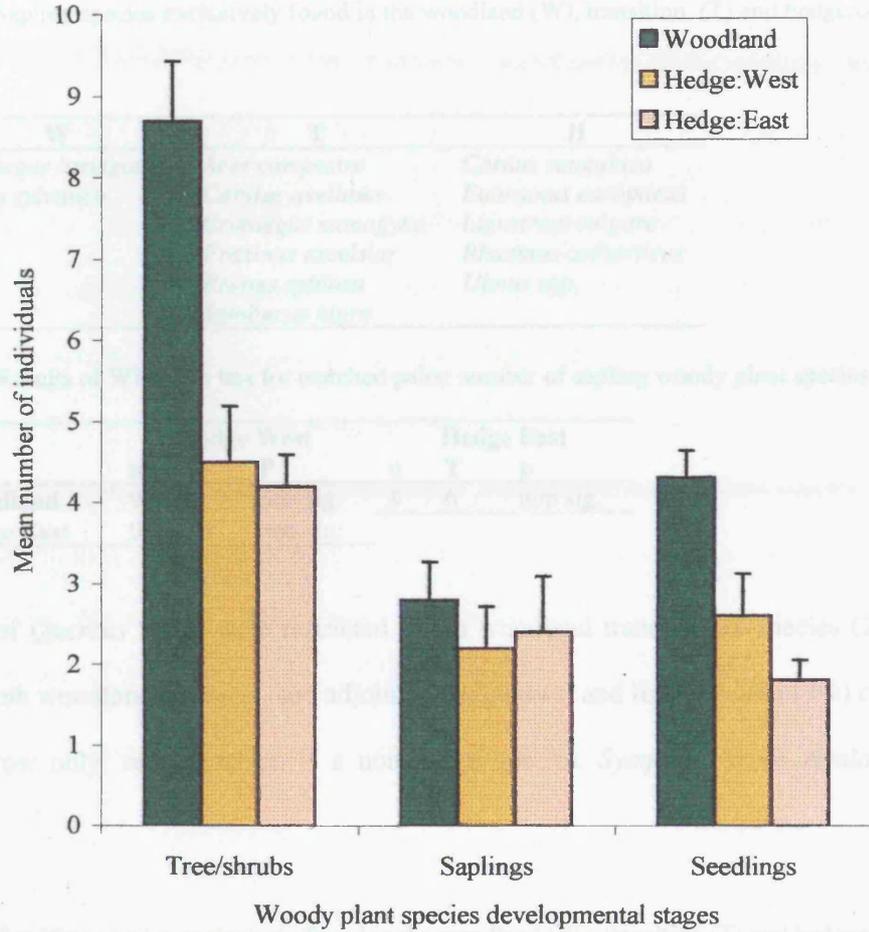
Nine (39%) of the total number of established woodland plant species were restricted to the woodland transects, five of which are regarded as non-native species. Ten species (44%) were found in both woodland and hedgerow transects and four species (17%) were located in the hedgerow transects, but not within the woodland (Table 3.9).

Table 3.9 Established woody plant species exclusively found in the woodland (W), transition (T) and hedgerow quadrats (* = non-native species)

W	T	H
<i>Betula pendula</i>	<i>Acer campestre</i>	<i>Cornus sanguinea</i>
<i>Chamaecyparis lawsoniana</i> *	<i>Acer pseudoplatanus</i> *	<i>Euonymus europaeus</i>
<i>Crataegus laevigata</i>	<i>Corylus avellana</i>	<i>Ligustrum vulgare</i>
<i>Fagus sylvatica</i>	<i>Crataegus monogyna</i>	<i>Rhamnus catharticus</i>
<i>Larix decidua</i> *	<i>Fraxinus excelsior</i>	
<i>Picea abies</i> *	<i>Malus sylvestris</i>	
<i>Pinus nigra</i> *	<i>Prunus spinosa</i>	
<i>Pinus sylvestris</i> *	<i>Quercus robur</i>	
<i>Salix caprea</i>	<i>Sambucus nigra</i>	
	<i>Ulmus</i> spp.	

Two species of *saplings* (9% of total number of established species) were restricted to the woodland transects. Six species (26%) were found in both woodland transects and adjoining hedgerows, and five (22%) species were located in the hedgerow transects only (Table 3.10).

Figure 3.11 Mean number of woody plant species in three developmental stages, in the woodland and each side of adjoining hedgerow transects



No significant difference was found between number of species of saplings in the woodland and hedgerow transects nor was any variation found between the hedgerow aspects (Table 3.11).

Table 3.10 Sapling species exclusively found in the woodland (W), transition (T) and hedgerow (H) groupings

W	T	H
<i>Crataegus laevigata</i>	<i>Acer campestre</i>	<i>Cornus sanguinea</i>
<i>Fagus sylvatica</i>	<i>Corylus avellana</i>	<i>Euonymus europaeus</i>
	<i>Crataegus monogyna</i>	<i>Ligustrum vulgare</i>
	<i>Fraxinus excelsior</i>	<i>Rhamnus catharticus</i>
	<i>Prunus spinosa</i>	<i>Ulmus</i> spp.
	<i>Sambucus nigra</i>	

Table 3.11 Results of Wilcoxon test for matched pairs: number of sapling woody plant species

	Hedge West			Hedge East		
	n	T	P	n	T	p
Woodland	9	7	non sig.	9	6	non sig.
Hedge East	9	10	non sig.			

Seedlings of *Quercus robur* were restricted to the woodland transect, six species (26%) were found in both woodland transects, and adjoining hedgerows; and four species (17%) occurred in the hedgerow only: one of which is a non-native species, *Symphoricarpos rivularis* (Table 3.12).

Table 3.12 Seedling species exclusively found in the woodland (W), transition (T) and hedgerow (H) quadrats (*= non-native species)

W	T	H
<i>Quercus robur</i>	<i>Acer campestre</i>	<i>Euonymus europaeus</i>
	<i>Acer pseudoplatanus</i>	<i>Ligustrum vulgare</i>
	<i>Crataegus monogyna</i>	<i>Rhamnus catharticus</i>
	<i>Fraxinus excelsior</i>	<i>Symphoricarpos rivularis</i> *
	<i>Prunus spinosa</i>	
	<i>Sambucus nigra</i>	
	<i>Ulmus</i> spp.	

The number of seedling species was significantly higher in the woodland transects, compare with the hedgerow transects (Table 3.13).

Table 3.13 Results of Wilcoxon test for matched pairs: number of seedling woody plant species

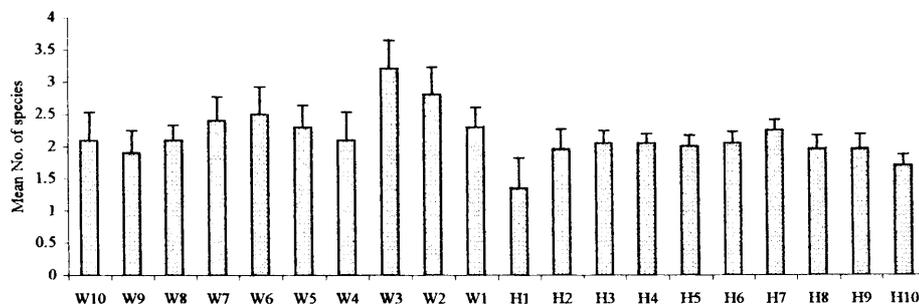
	Hedge West			Hedge East		
	n	T	P	n	T	p
Woodland	9	1	<0.02	9	0	<0.02
Hedge East	9	1	<0.02			

When the two hedgerow aspects were compared, significantly fewer seedling species were located on the eastern side of the hedgerows.

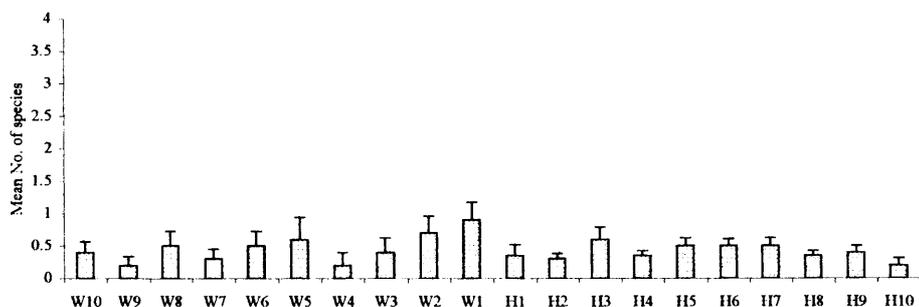
The data for the woodland and combined hedgerow transects were amalgamated to provide a measure of the mean number of woody plant species per quadrat. The spatial distribution of the mean woody species diversity, across the woodland-hedgerow transitions, for established individuals, saplings and seedlings, are displayed in Figure 3.12. In each case, the woodland edge region contains the highest species richness. Established woody plant species increase in species richness into the woodland edge. Greater variability was found in the distribution of the sapling species, the mean number of species were found to decrease into the woodland edge region. A higher number of seedling species was found in the woodland transects; compared to the hedgerows transects, and there was less spatial variation in species diversity across the woodland edge.

Figure 3.12 Spatial distribution of the mean number of woody plant species per quadrat
(Error bar = SE)

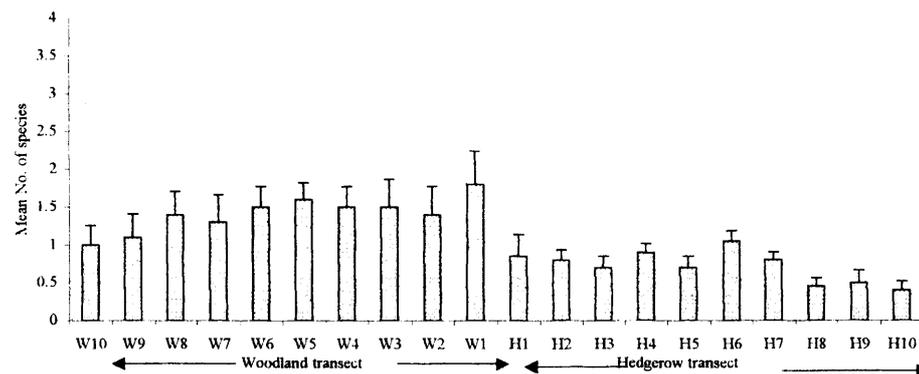
Tree and shrub: established



Saplings



Seedlings



Quadrat location

3.5.2 Woody plant species composition of hedgerow transects: Hooper's Rule

The number of woody plant species found in the hedgerow transects was converted to species per 30m length (Table 3.14), a comparable length to fit Hooper's Rule (see Chapter 2). The mean number of 1.7 shrub species suggests that the hedgerows are around 150-200 years old, concordant with the periods of Enclosure.

Table 3.14 Number of woody plant species in hedgerow transects, conversion to the number of woody species number per 30m length of hedge, and management types.

Transect	Total No.	per 10m	per 30m	Hedge management
1	4	0.4	1.2	Box
2	9	0.9	2.7	Old lay / box + gaps
3	4	0.4	1.2	Old coppice / tall
4	7	0.7	2.1	Tall / unmanaged
5	6	0.6	1.8	Box / fence
6	5	0.5	1.5	Box
7	8	0.8	2.4	Tall + gaps
8	5	0.5	1.5	Tall
9	5	0.5	1.5	Oldlay / box
10	3	0.3	0.9	Box

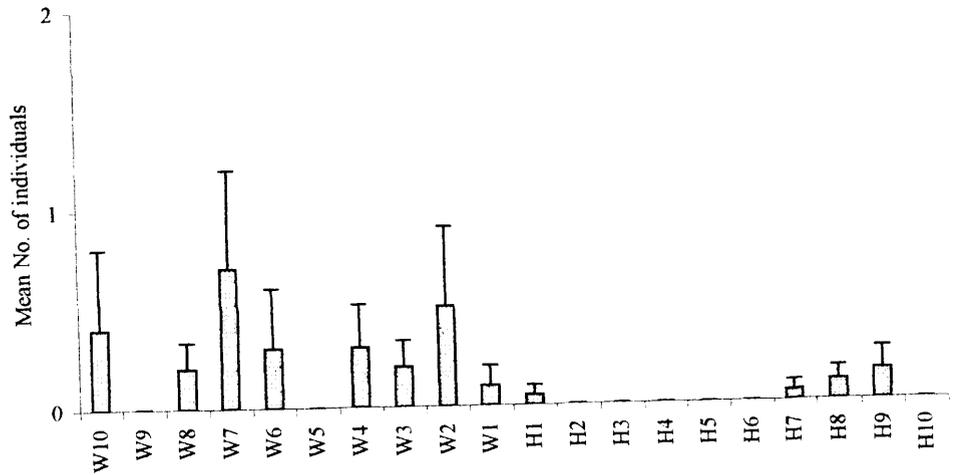
3.5.3 Spatial distribution and abundance of individual woody plant species along the woodland-hedgerow transects

The following results represent the combined data for all ten woodland and twenty hedgerow transects. Three wind-dispersed tree species (*Acer campestre*, *Acer pseudoplatanus* and *Fraxinus excelsior*) (Ridley 1930), were found in both the woodland and hedgerow transects. The majority of established individuals of *Acer campestre* were located in the woodland transects, but some occurred in the hedgerow transects (up to 70-90m away from the woodland edge) (Figure 3.13). Saplings were intermittently found in the woodland transects, and in one hedgerow location, close to the woodland edge. The seedlings of *Acer campestre* were concentrated around the woodland edge and hedgerow quadrats nearest the woodland, reaching a peak at around 10-40m into the woodland.

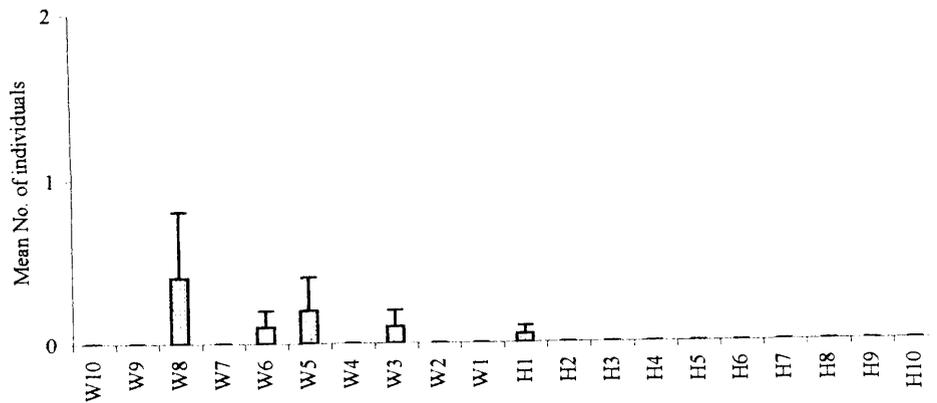
Established individuals of *Acer pseudoplatanus* were confined to the woodland transect (Figure 3.14). No individuals were found in the first two woodland samples at the woodland edge.

Figure 3.13 Spatial distribution of *Acer campestre* (bar = SE)

Established individuals



Saplings



Seedlings

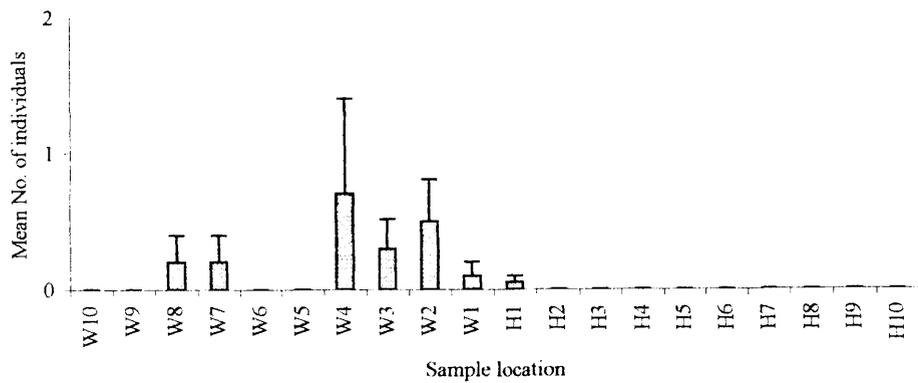
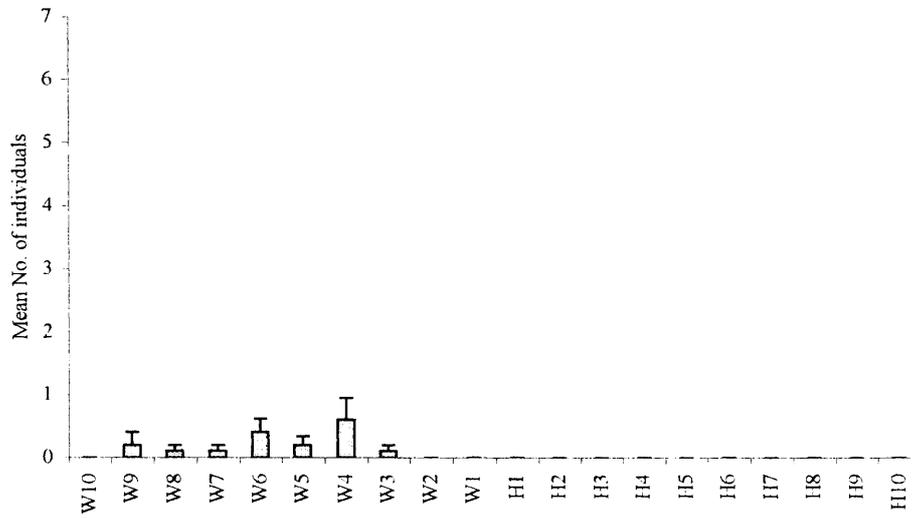


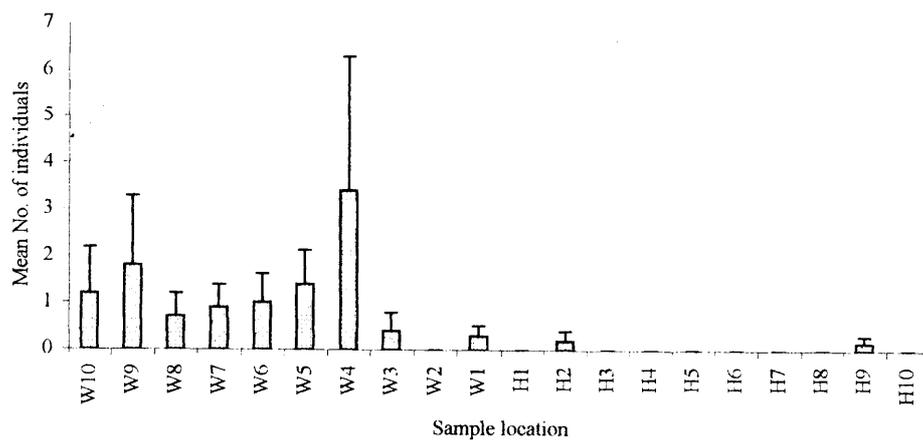
Figure 3.14 Spatial distribution of *Acer pseudoplatanus* (bar = SE)

Established individuals



Saplings: none found

Seedlings



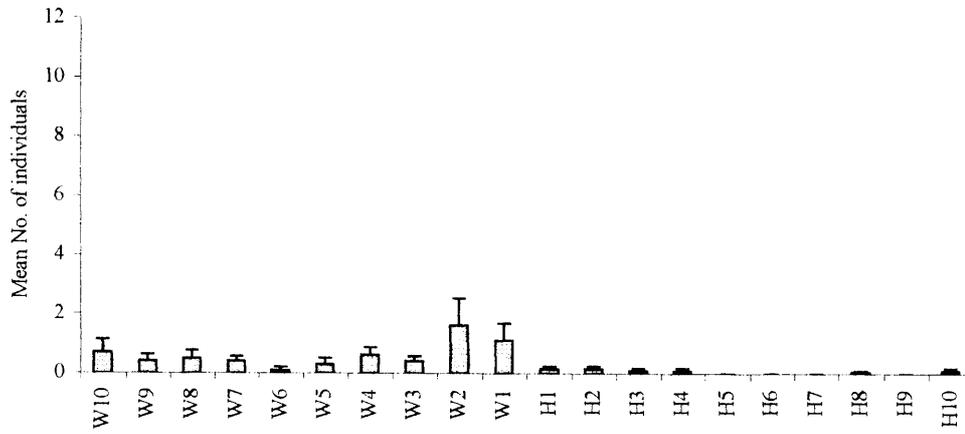
Saplings of this species were absent. Seedlings seem to be most abundant around 40m into the woodland. Some seedlings were located in the first woodland sample, and in two locations along the hedgerow transects (10m and 90m).

Established individuals of *Fraxinus excelsior* were discovered in both the woodland and hedgerow transects (Figure 3.15) (there is a possibility that individuals in the hedgerows were planted during the Enclosure period). Established individuals were most abundant in the two woodland samples nearest the woodland edge). Saplings were found less frequently, but were most common in the second woodland sample (10-20m). Saplings of *Fraxinus excelsior* were located at the ninth quadrat location (90m along the hedgerow transects), which match the location of established individuals. The distribution of the seedlings of this species declined in abundance in the adjoining hedgerows toward the woodland edge and peaked in abundance 30m into the woodland. This species is wind-dispersed and these results indicate that seeds can disperse up to 50m away from the woodland edge. Established individuals of *Corylus avellana*, described by Hodgson *et al.* (1995) as being dispersed by animal vectors, were variable but common within the woodland transects. Only one individual was found in twenty hedgerow transects, 50m away from the woodland edge (Figure 3.16). Few saplings were found. Those located occurred at the woodland edge, and 40-50m into the woodland. Seedlings of this species were not recorded.

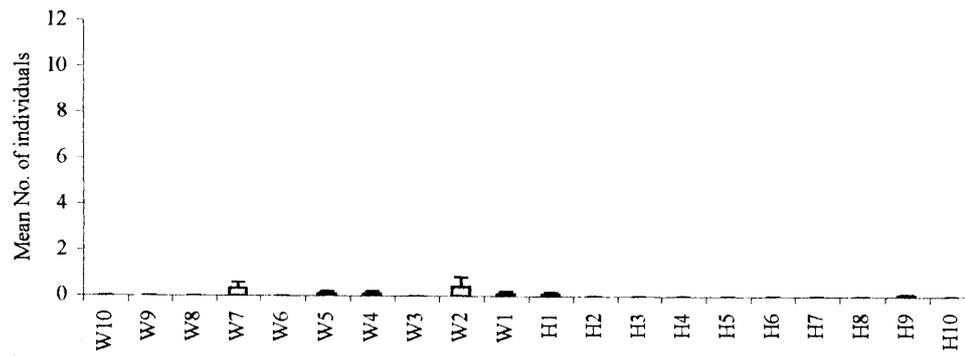
The spatial distribution of *Quercus robur*, within both the woodland and hedgerow transects, may be a result of varying planted regimes or a complex edge effect (Figure 3.17). *Quercus robur* is dispersed by both mammal and bird vectors (Ridley 1930). This species was most abundant 50-60m into the woodland. Saplings were not located. The abundance and distributions of seedlings did not correspond with the abundance and frequency of established individuals. Seedlings were located at the first two woodland samples and 40-50m into the woodland. Seedlings were not located in the hedgerow samples.

Figure 3.15 Spatial distribution of *Fraxinus excelsior* (bar = SE)

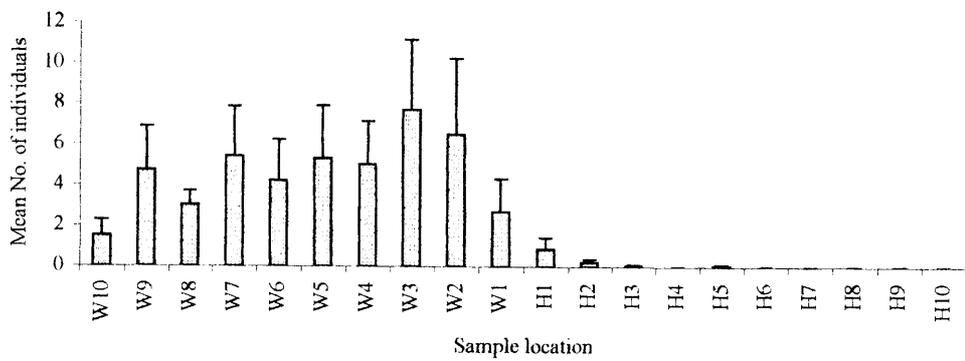
Established individuals



Saplings



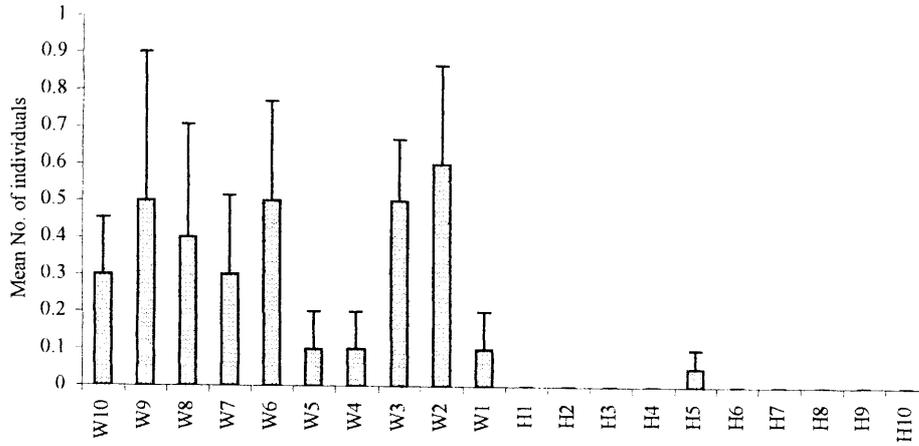
Seedlings



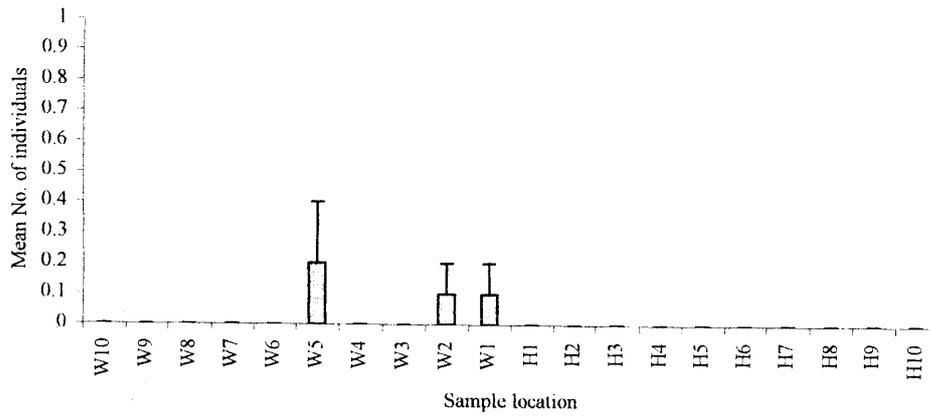
Sample location

Figure 3.16 Spatial distribution of *Corylus avellana* (bar = SE)

Established individuals



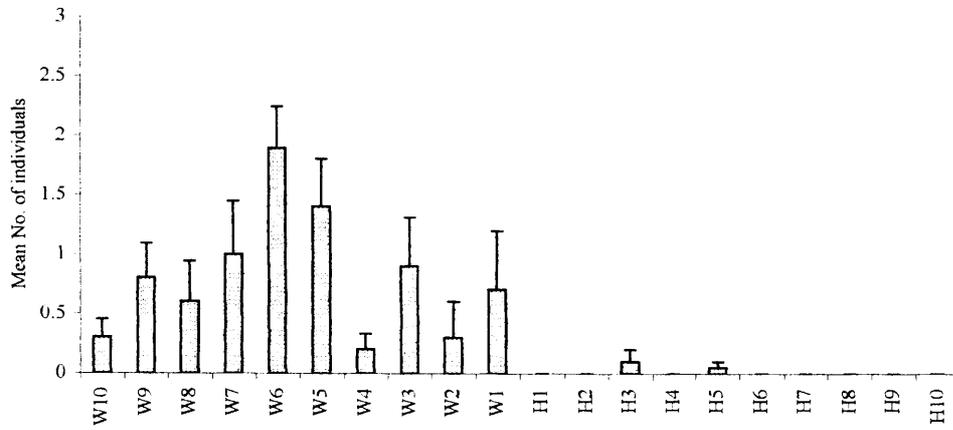
Saplings



Seedlings: none found

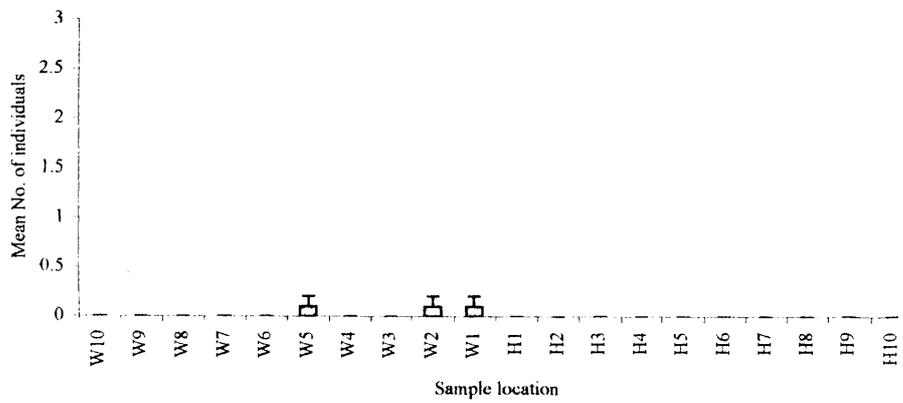
Figure 3.17 Spatial distribution of *Quercus robur* (bar = SE)

Established individuals



Saplings: none found

Seedlings



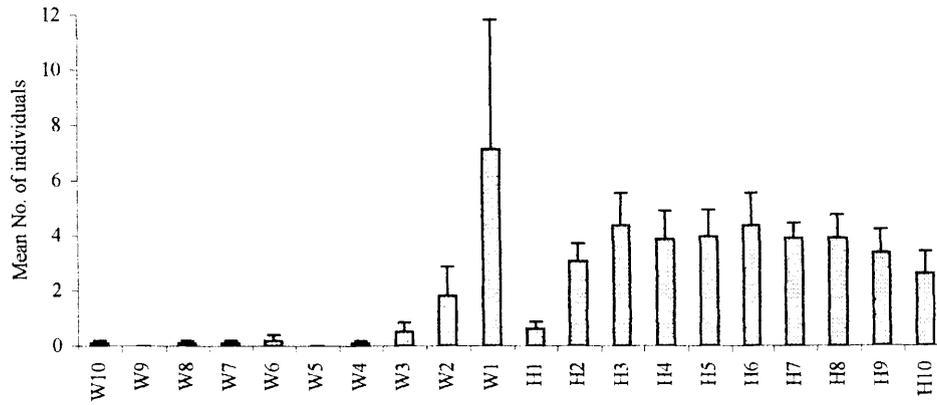
According to Grime *et al.* (1988), birds disperse seven of the woody shrub species recorded in this study. Three species (*Prunus spinosa*, *Sambucus nigra* and *Ulmus* spp.) were more frequent and abundant along the hedgerow transects. *Prunus spinosa* was found to be consistently abundant within the hedgerow samples further away from the woodland but decreased in abundance nearer the woodland edge (Figure 3.18). The abundance of established individuals rises at the woodland edge and decreases rapidly along the woodland transect. The spatial distribution of the saplings was similar, but with a less pronounced abundance at the woodland edge. The seedlings (or suckering stems) also displayed similar spatial distributions to the established plants. Fewer individuals were found further along the woodland transects.

The spatial distributions of established individuals of *Sambucus nigra* (Figure 3.19) have some similarity with those of *Prunus spinosa*. However, saplings were absent within the woodland edge and less frequent along the adjoining hedgerow. The seedlings of *Sambucus nigra* were distributed along the hedgerow transects and into the woodland edge. From the inspection of Figure 3.20, established individuals of *Ulmus* spp. were found more frequently along the hedgerow transects, rising in abundance towards and into the woodland. The distribution of the saplings was restricted to the hedgerow transects (60-100m away from the woodland edge). Seedlings (or suckering stems) were found 40-100m away from the woodland edge, and in two woodland locations in the woodland transition zone.

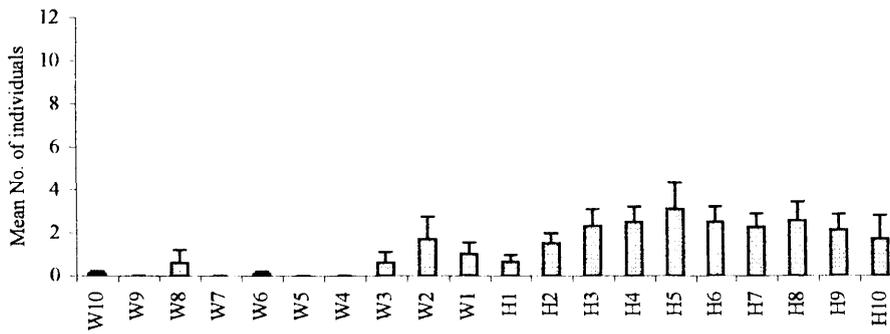
Three species of shrub (*Cornus sanguinea*, *Euonymus europaeus*, *Ligustrum vulgare*) were occasionally found within the twenty hedgerow transects (Appendix 3.7). Established individuals of *Cornus sanguinea* were located in the hedgerow transects, near to the woodland edge (0-20m along the hedgerow transects). Established individuals, sapling and seedlings (or suckering stems) of *Euonymus europaeus* and *Ligustrum vulgare* were all found in close proximity to each other, (*Euonymus europaeus*: 10-50m away from the woodland edge, *Ligustrum vulgare*: 30-90m away from the woodland edge).

Figure 3.18 Spatial distribution of *Prunus spinosa* (bar =SE)

Established individuals



Saplings



Seedlings / suckering stems

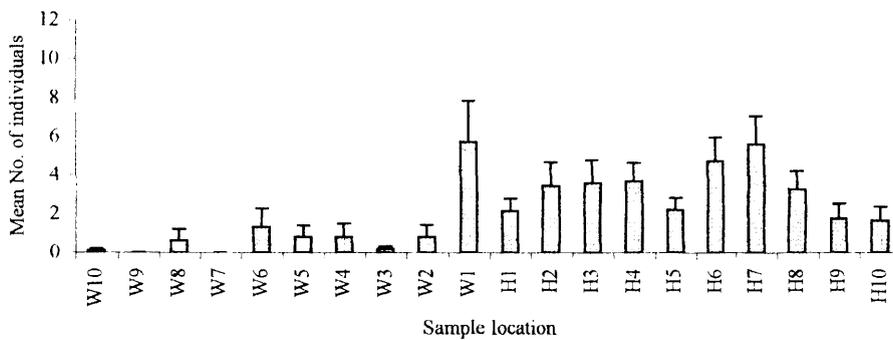
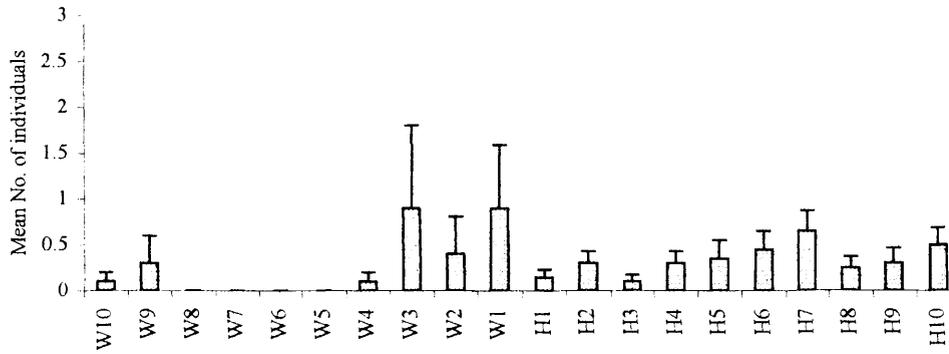
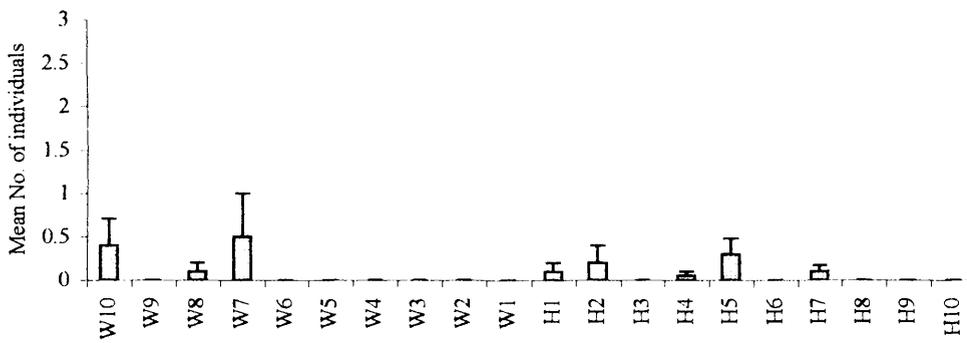


Figure 3.19 Spatial distribution of *Sambucus nigra* (bar = SE)

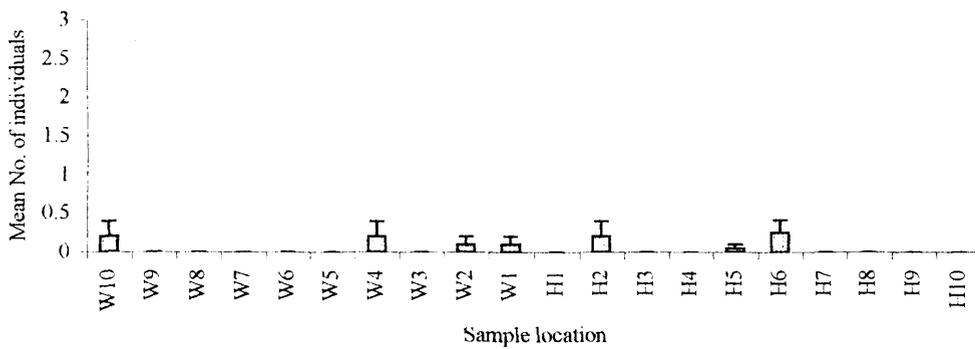
Established individuals



Saplings



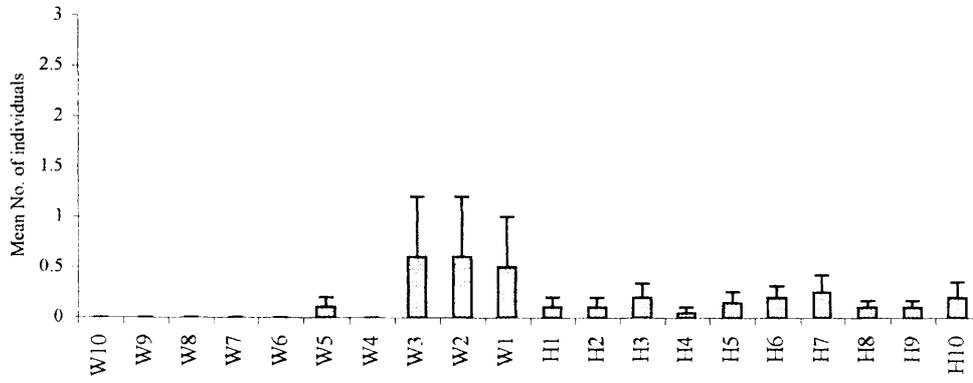
Seedlings



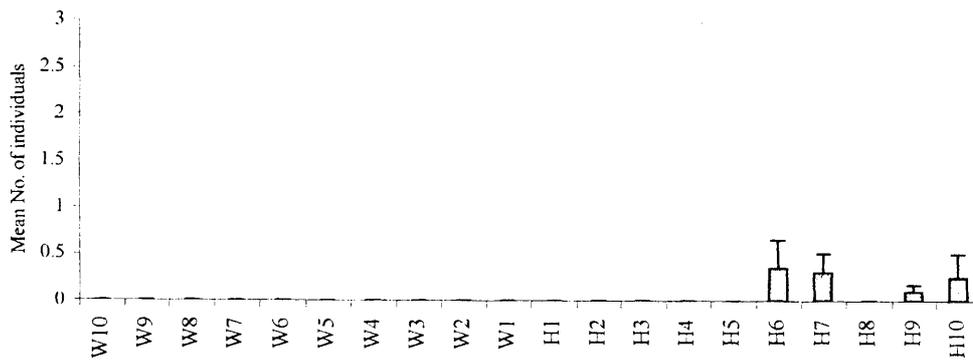
Sample location

Figure 3.20 Spatial distribution of *Ulmus* spp. (bar = SE)

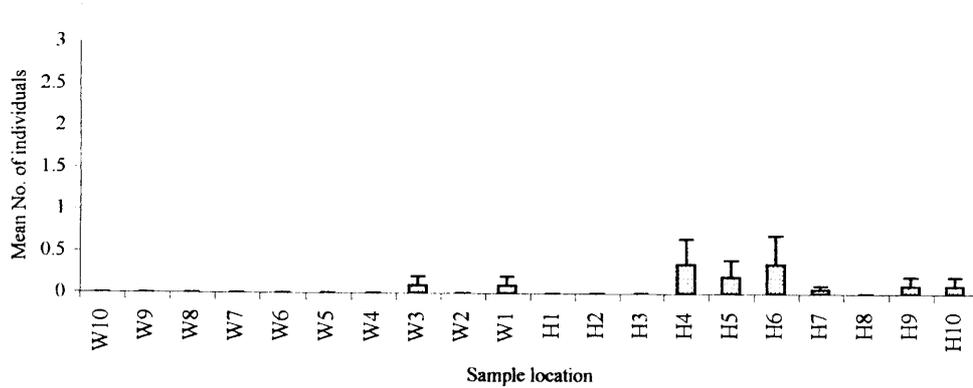
Established individuals



Saplings



Seedlings / suckering stems



Established, saplings and seedlings of *Rhamnus catharticus* showed little association with the proximity and composition of the woodland transects.

3.6 Summary of results

The spatial distribution of herbaceous plant species across the woodland-hedgerow transitions displayed declining species richness from the woodland edge into the woodland. Patterns of distribution were also found to fall into three distinct groups across woodland and hedgerow transitions: 1) herbaceous plant species restricted to the woodland transects, 2) species located in both the woodland edge and the adjoining Enclosure hedgerows (transition group) and 3) those species found in the hedgerow transects only (Table 3.2). These differing distributions reflected the autecologies and strategies for survival of individual species under varying degrees of disturbance and stress across an environmental gradient.

The results suggested that various life history strategies could contribute to the differences in herbaceous vegetation of the woodland, woodland/hedgerow and hedgerow community groups. Other studies of woodland vegetation across woodland edges (Ranney *et al.* 1981, Matlack 1994b, Fox *et al.* 1997), found that the vegetation across woodland transition zones to comprise of both shade-tolerant woodland plant species and light-demanding plant species from the external landscape. Results from comparing phenological characteristics confirmed this. In addition, it is proposed that in external landscape habitats such as hedgerows may be less hospitable to woodland species if a higher soil pH is experienced.

The herbaceous plant species with the phanerophyte life form were located in the woodland and transition community groups, and absent in the hedgerow community. Phanerophytes have perennating buds or shoot apices borne on aerial shoots and are less tolerant to drought, cold and exposure to strong winds (Allaby 1992). Results suggest that these species inhabit hedgerows next to woodlands, possibly because of the physical protection from extreme microclimates within the hedge base.

Larger seeded herbaceous plant species were more widely distributed across the woodland-hedgerow transition. Seed dispersal is considered to decrease in distance with increased seed weight; the distance of seed-fall decreases as the weight of a seed increases. However, this does not take into account distance travelled via seed dispersal vectors. The analysis investigating the modes of seed dispersal was inconclusive. This was mainly due to the lack of autecological knowledge of many herbaceous plant species.

The distribution and occurrence of woody plant species was examined separately. The results suggest that the processes that determine the distribution of the herbaceous plant species and woody plant species operate at different spatial scales. This study revealed that all but one non-native tree species were confined to the woodland transects. The naturalised tree species *Acer pseudoplatanus* occurred as seedlings in both the woodlands and adjoining hedgerows: indicating successful wind dispersal out of the woodland edge. Two other wind-dispersed but native tree species (*Acer campestre* and *Fraxinus excelsior*) were found as adult, seedling and saplings in the woodland transects and adjoining Enclosure hedgerows.

The spatial distribution of two cache-hoarding-animal-dispersed woody plant species, *Corylus avellana* and *Quercus robur*, suggests that dispersal has occurred out from the woodland into the adjoining hedgerows. Bird-dispersed shrub species were found more frequently and abundantly in the hedgerow transects than in the woodland transects. Five shrub species were absent in the woodland transects but present in the hedgerows surveyed. It is very likely that individuals of these species have entered the hedgerows via bird dispersal. Seed sources of these five species were not detected in the woodland surveys. It is suggested that long distance dispersal strategies influence the scale at which shrub species colonize new hedgerow sites.

The absence of any plant species within the transects surveyed need not indicate failed immigration or colonization. The vast majority of dispersing individuals or propagules must fail to reach suitable sites for colonization and establishment (Harper 1977, Davis 1986, Scupp

and Fuentes 1995). The presence or immigration of individuals reflects the varying contribution of seed banks, the seedling bank and differential seed dispersal (Glenn-Lewin and van der Maarel 1992).

De Steven (1991) stated that seed germination and emergence represent a critical phase in establishment and may contribute a significant 'bottleneck' for the establishment for any species in succession. She found that vegetated cover facilitated germination of most of the tree species in her study of old field succession. Enhanced germination probably resulted from the combined effects of amelioration of moisture extremes, provision of wetter micro-sites and reduced susceptibility to seed predation. In communities that include perennials, seeds and seedlings are usually inhibited by adult plants (Peart 1989). Varied conditions across woodland/hedgerow transitions may contribute to the differing composition of plant communities found in this study, as life histories strategies may equip individual plant species to disperse and tolerate varying degrees of stress and competition.

It has been established that certain plants can either spread vegetatively or colonize from seed in secondary woodland adjacent to ancient woodland (Rackham 1975, Peterken and Game 1984, Hughes and Fahey 1988, Dzwonko 1993, Matlack 1994b, Brunet and von Oheimb 1998). In this study, 22 herbaceous plant species were found across the woodland/hedgerow transition. Eight species were assessed as dispersing from woodland into adjoining Enclosure hedgerows in varying degrees. Previous records of a woodland herbaceous plant species, Dog's Mercury (*Mercurialis perennis*) spreading into hedgerows from adjoining woodland (Pollard *et al.* 1974, Rackham 1975, Peterken and Game 1981) are supported in this study and evidence suggests that *Glechoma hederacea* may also be capable of spreading out from the woodland edge and along the adjoining hedgerows.

The study in the next chapter focuses upon the spatial distribution of herbaceous plant species in the vegetation and seed bank along a single woodland transect and adjoining hedgerow. The

scale of this study was reduced in order to improve the possibility of detecting subtle change in spatial distribution.

Chapter 4 Spatial and temporal distribution patterns of herbaceous plant species in a woodland and adjoining Enclosure hedgerow vegetation and seed bank.

4.1 Introduction

The previous chapter showed that plant life history strategies may influence immigration, colonization and establishment of plant species into hedgerows that are in close proximity to woodland. Grime *et al.* (1988) stated that primary ecological strategies are recurrent types of specialisation associated with particular habitat conditions or niches. They maintain that the recognition of these strategies is the key to understanding the structure and dynamics of ecological communities. By exploring common attributes of successful dispersers and colonists in both the vegetation and seed bank across a woodland-hedgerow transition zone, an insight could be gained into the processes and the spatial dynamics that contribute towards composition and distribution of herbaceous plant species.

A seed bank study was designed to investigate spatial patterns of seed dispersal from the woodland into the hedgerow and vice versa. The presence of plant species in the woodland and/or hedgerow vegetation may reflect the net effect of dispersal, colonization and establishment success. The seed bank, on the other hand, may reflect dispersion patterns of potential colonists not detected in the vegetation.

4.2 Study site

The site for this study was located in Geddington Chase. Details of this woodland are described in Chapter 3. The location (Transect 9, Hedge transects 17/18: see Figure 3.3) was chosen for the following reasons:

- a) this area of Geddington Chase was not intensively planted with conifer trees;
- b) the adjoining hedgerow could be positively identified as a Parliamentary Enclosure Act boundary;

- c) there was good access for transporting soil samples.

4.3 Method

4.3.1 Field survey and sampling

Data were derived from three continuous belt transects, 50m in length from the woodland edge into the woodland and each side of the adjoining hedgerow. Each sample site was located at 5m intervals along the hedgerow (Figure 4.1). The hedgerow seed bank samples were taken at 1m intervals along each 5m section of the hedgerow (Figure 4.2). The woodland transect was set on the opposing trajectory of the adjoining hedgerow the using a compass. A 5m x 5m quadrat was used to demarcate the woodland sample sites. The woodland seed bank samples were taken from each of the corners of the 5m quadrat and one from the centre. Within each woodland and hedgerow sample location:

- a) the presence and absence of woody shrub and herbaceous plant species was recorded;
- b) soil samples were taken and combined and placed into a labelled, plastic bag and sealed;

Bulb planters are considered as appropriate tools for sampling soils in seed bank studies (Warr *et al.* 1993, 1994). A standard sized bulb planter (top circumference = 7cm, base circumference = 5cm, height = 10cm) and trowel were used to extract soil-sub-samples (once a sample was extracted the surrounding soil was then used to fill in the hole, so it would not act as a pitfall trap for invertebrates). Soil volume for each bulb planter core was 19.85cm^3 and the total volume of soil for each quadrat sample was 99.25 cm^3 . A total 150 soil samples were taken (or 30 combined samples).

Sampling for this study took place on April 7th 1997, during the optimum period for seed bank studies (March-April), recommended by Warr *et al.* (1993). At other times of the year, transient seeds are difficult to detect and quantify. Species with transient seed banks are in a continuous flux, as seed input and germination occur simultaneously. The transient seeds are at their lowest density during the early spring, before the new seasonal seed input. Sampling should take place

Figure 4.1 Belt transect sampling.

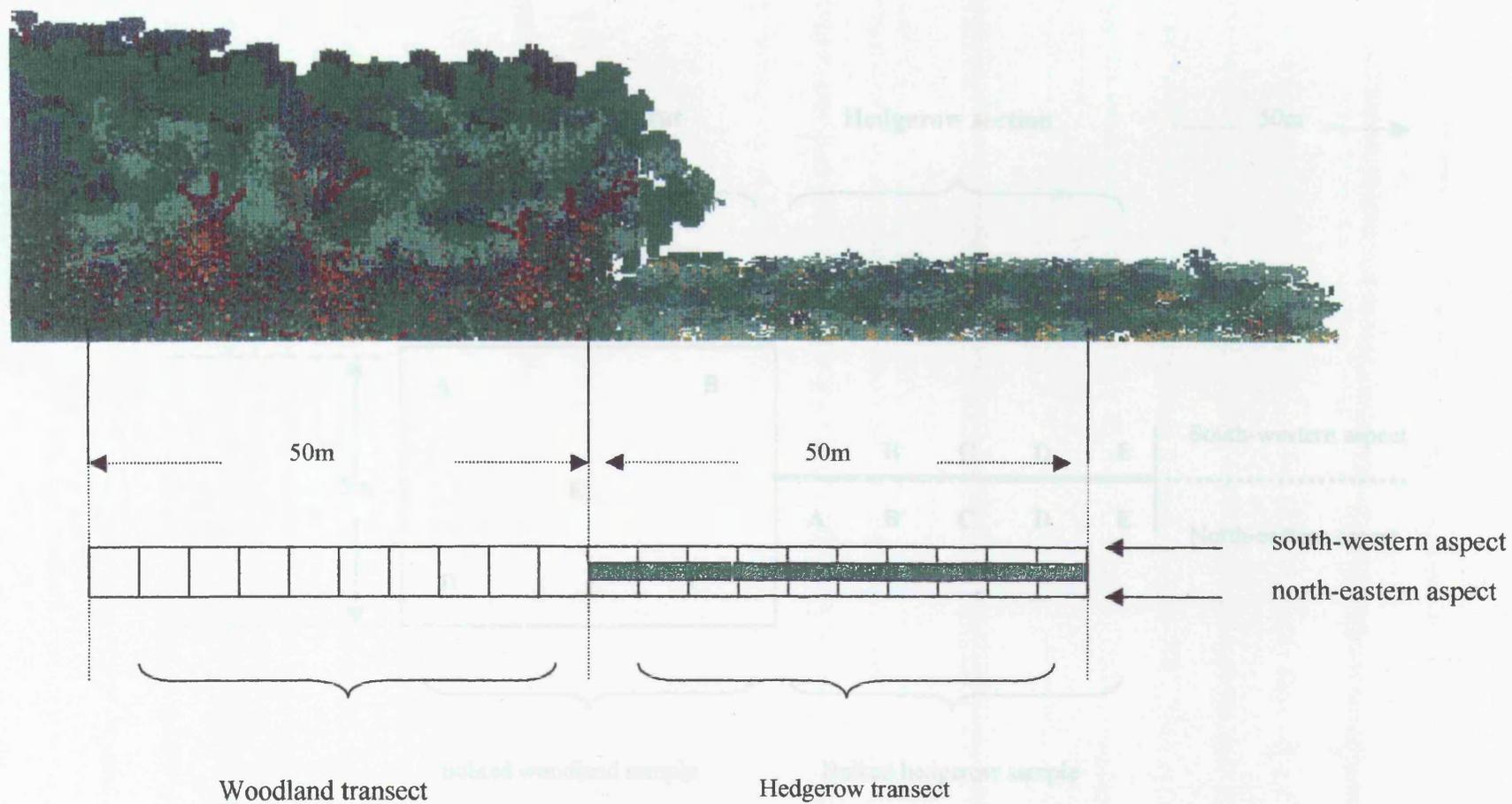
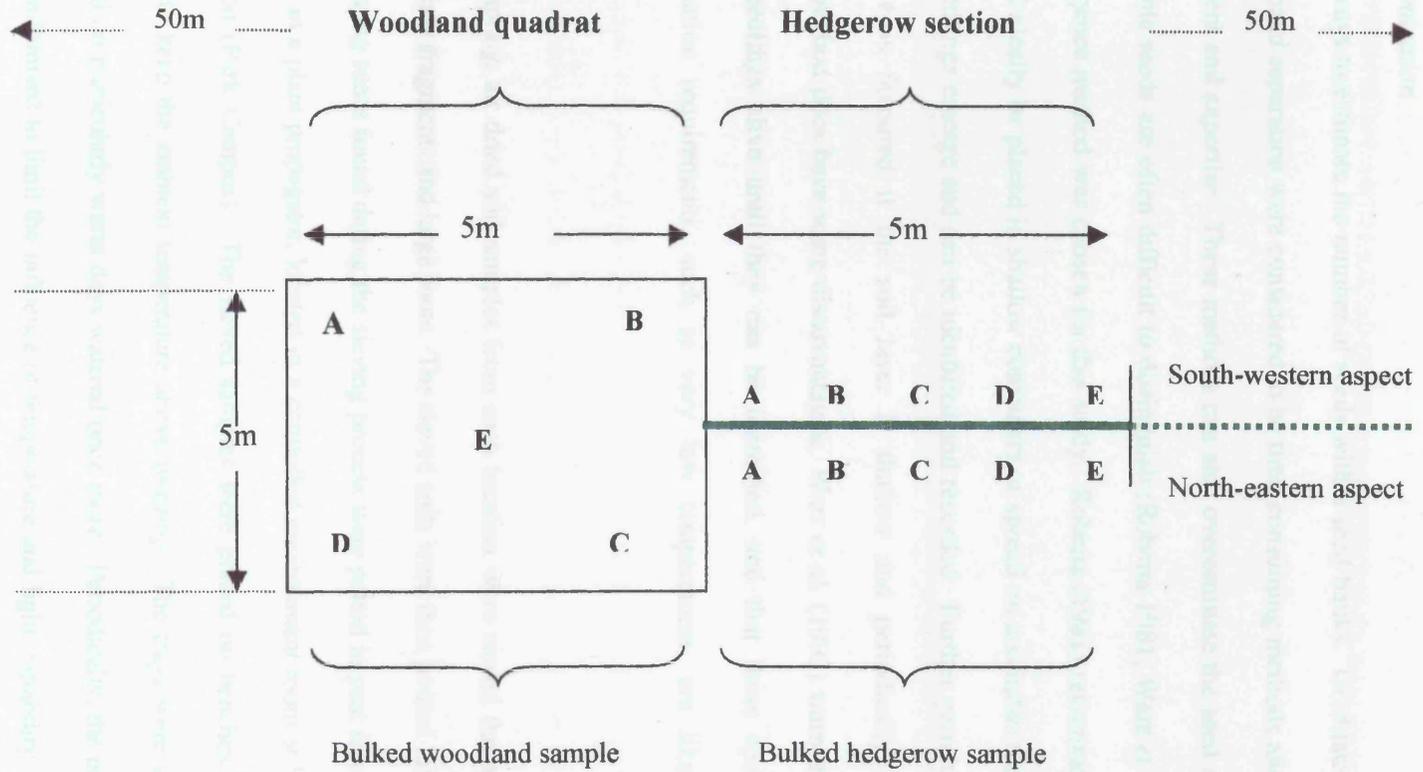


Figure 4.2 Seed bank sampling strategy.



before the remaining, more persistent, species in the seed bank germinate at the beginning of May (Warr *et al.* 1993).

4.3.2 Seed bank germination

There are several ways to estimate the number of seeds within seed-banks. Graduated sieving, seed flotation and hand separation were considered to be time-consuming methods and required specialised equipment and expertise. These methods can also overestimate the seed number as viable and non-viable seeds are often difficult to distinguish (Roberts 1981, Warr *et al.* 1993). The seedling emergence method was chosen for this study. Roberts (1981) recommended that soil samples should ideally be placed in shallow containers or spread on a suitable medium and kept moist until seedlings emerge and can be identified and recorded. Further germination and seedling emergence is favoured if the soil layer is shallow and periodically disturbed. Nevertheless, this method does have some disadvantages. Warr *et al.* (1993) warn that care is needed to keep seedlings alive until they can be identified, and that those species with specialised germination requirements, such as very low temperatures, are likely to be underestimated.

Two days after sampling, air dried soil samples from each location were sieved through a 1cm mesh to remove woody fragments and large roots. The sieved soils were then poured into labelled seed trays. Germinating seeds found during the sieving process were potted in peat free compost, labelled, and placed in a plant propagator, located in a controlled environment room at University College Northampton (Park Campus). The sieved samples were placed on benches in a cool greenhouse, heated to keep the ambient temperature above freezing. The trays were watered at least once a day, and on particularly warm days watered once more. Periodically, the placements of each tray were randomised to limit the influence of temperature and light variability within the greenhouse. Once emerging seedlings were identified, they were removed and recorded. Those seedlings that could not be identified were potted and kept until they had reached a stage of development that enabled identification.

Seedling emergence began 18th April 1997 and continued until March 1998. Periodically, when no seedlings had emerged, the soils were stirred to stimulate further germination of remaining seeds. Some invasion of a greenhouse weed (*Oxalis corniculata*) was noted in the collected soil samples and in a control seed-tray containing only peat-free compost. This did not present a problem, as this was a non-native invasive species and was readily identifiable.

4.4 Analysis

Data for each transect type were compared using the Wilcoxon's test for matched pairs. The spatial arrangements of species within the vegetation and seed bank were evaluated by direct and indirect gradient analysis (*sensu* Whittaker 1973). Species association with habitat types and autoecological characteristics of herbaceous plant species was derived from the Electronic Comparative Plant Ecology database (Hodgson *et al.* 1995). Further information regarding the herbaceous plant species identified during this study was derived from a variety of literature sources, including Stace (1991), Sutton (1995) and Thompson *et al.* (1997).

The analysis of the data was divided into three groups: 1) herbaceous plant species found only in the seed bank, 2) species found in both the vegetation and seed bank, 3) species found in the vegetation only. The aim of this division was to simplify the analysis and interpretation of the spatial distributions of the herbaceous plant species and to elucidate the processes that influence species composition and community structure across the woodland and hedgerow transition zone.

A non-parametric correlation technique, Spearman Rank Correlation, aims to assess the strength of association between two comparable sets of data, where data do not satisfy the assumptions of parametric statistical techniques. This non-parametric test of association was used to compare the spatial distribution of herbaceous plant species present in vegetation and seed bank with distance; correlation coefficients, in this case, were used to reflect a measure of spatial association.

Ordinations were produced with the use of a multivariate computer package (CANOCO - CANONical Community Ordination), a package developed in 1985 as an extension of the computer ordination program DECORANA (ter Braak and Smilauer 1998). Ter Braak (1995, 1996) describes ordination as the collective term for multivariate techniques that summarize large data sets into homogenous groups or scatter diagrams on a few ordination axes. Ordination is used to recover underlying or latent structures within the data set that influence species community composition. The inclusion of environmental parameters into ordination analyses allows explanatory variables to be identified.

Principal Component Analysis (PCA) can be considered to be an extension of fitting straight lines and planes by least squares regression (ter Braak 1995). In this investigation, it was hypothesised that the species composition of the vegetation and seed bank across a woodland and hedgerow transition would be influenced by a linear spatial gradient. Therefore, a linear multivariate analysis was seen as the most appropriate. With large data sets, without environmental variables, PCA can identify linear trends and reduce the variability within the composition of community data. Species abundance (response variable) may seem to change linearly through short sections of environmental gradients (explanatory variable), so a linear response model may be a reasonable basis for analysing quantitative abundance data spanning a narrow range of environmental variation (ter Braak and Prentice 1988).

Presence/absence data for the vegetation survey and abundance of species within the seed bank were analysed separately. Data were entered into a matrix on an EXCEL spreadsheet and the computer software WCANOIMP 1.0 converted the matrices into the data format for CANOCO software. Firstly, the 'only species available data' option was chosen. This option interprets extracted patterns from all the variation in the data (indirect gradient analysis). Secondly, linear gradient analysis (PCA) was chosen. Interspecies correlation and data centered by species options were taken. The data were not transformed during these analyses. The effect of

collinearity was tested, as recommended by Philippi (1993). The test is where the square root of the ratio of the largest eigenvalue of the correlation matrix and the lowest eigenvalue found is above 30. Collinearity was not found in any of the ordinations performed.

Detectable linear trends are response curves of species. In linear methods, the species score is defined by the linear regression coefficient of the data for the species k ; thus, resultant species scores are slope parameters (ter Braak and Smilauer 1998). Samples scores are the positions along ordination axes. Sites are arranged along axes on the basis of species composition. The result of ordination is a diagram in which sites are represented by points in two-dimensional space. Points positioned closely together represent sites that are similar in species composition; those found widely spaced are more dissimilar (ter Braak 1995). In PCA, ordination axes are unconstrained, reflecting theoretical gradients that best explain the species data. These theoretical latent variables minimise the total residual sum of squares after fitting straight lines to the species and sample data. The first PCA axis (or theoretical variable) is the variable that best explains the species data. The second and later axes also explain the species data subject to the constraint of being uncorrelated to the previous PCA axes. This indirect gradient method can also pick out general patterns of coincidence of several species. Clusters of species can represent sub-communities within larger community data sets (ter Braak 1995).

Biplots produced by PCA display species abundance in the space defined by the ordination axes. The software packages CANODRAW 3.1 and CANOPOST 1.0 were used to draw diagrams: sample sites are displayed as points and arrows represent species. These arrows point in the direction of maximum variation in the species abundance and their length is proportional to this maximum rate of change. Consequently, species on the edge of the diagram are the most important for indicating sites differences; species near the center are of minor importance (ter Braak and Prentice 1988).

Sørensen's similarity coefficient is a simple mathematical expression that describes similarities

or associations between plant communities (Waite 2000). In this chapter, this index of similarity was used to compare the distribution of presence/absence data of plant species within the vegetation and the seed bank and between woodland and hedgerow transects.

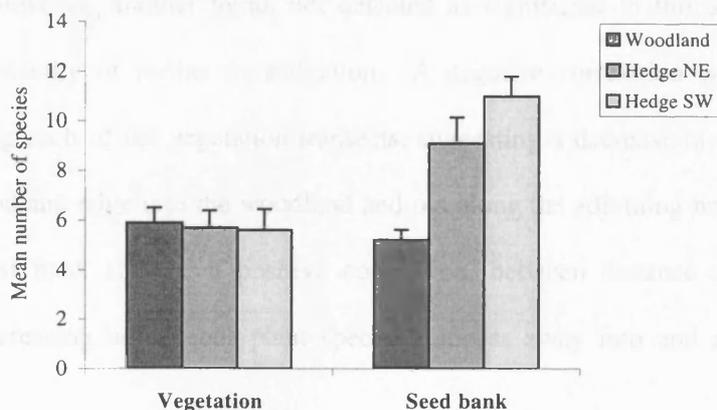
Sørensen's Index = $2a/(2a+b+c)$, where **a** is the number of quadrats where a species coincides in corresponding quadrats in each data set, **b** is the number of quadrats where a species is present in the first data set but absent in the corresponding quadrat of the second data set and **c** is the number of quadrats where a species is present in the second data set but absent in the first data set.

4.5 Herbaceous plant species vegetation and seed bank

4.5.1. Herbaceous plant species richness

A total of 38 herbaceous plant species were identified in this study, of which nine were present in the seed-bank but absent in the vegetation survey. A total of 16 species were present in both the seed-bank and the vegetation and 13 species were found in the vegetation survey but absent in the seed-bank. The seed bank study revealed that the hedgerow transects had a higher mean species richness of herbaceous plant species than the woodland (Figure 4.3). Variation in the number of species per quadrat was lowest in the woodland vegetation and seed bank samples and highest in the seed bank on the North Eastern side of the hedgerow.

Figure 4.3 Comparison of the mean number of herbaceous plant species located in the vegetation and seed banks of the woodland and hedgerow transects (bar = SE)



A significant difference (Wilcoxon's test for matched pairs) was found between the number of species in the woodland and hedgerow seed-banks, vegetation and seed-bank on the south-western side of the hedgerow and vegetation and seed-bank in the north-eastern side of the hedgerow (Table 4.1). This analysis found that the numbers of species within the woodland vegetation and seed bank were not significantly different. No significant differences were found between each side of the hedgerow when the numbers of species in the vegetation or seed bank were compared.

The association between distance and species number was calculated for plant species presence within each woodland or hedgerow quadrat, using Spearman Rank Correlation Coefficient (Table 4.2).

Table 4.2 Spearman Rank Correlation Coefficients: between the number of herbaceous species and distance away from the woodland edge

	Woodland	Hedge NE	Hedge SW
Vegetation	- 0.32	-0.22	-0.43
Seed-bank	0.25	0.47	0.80 *

* = Significant at $p < 0.01$

A negative correlation indicates decreasing herbaceous plant diversity with increasing distance away from the woodland edge and a positive correlation indicates increasing herbaceous plant diversity with increasing distance away from the woodland edge. Species richness in the seed bank along the south-western side of the hedgerow correlated positively with distance ($p < 0.01$). However, another trend, not detected as significant in this analysis, may also be present and worthy of further investigation. A negative correlation was found for species richness along each of the vegetation transects, suggesting a decrease in species number away from the woodland edge into the woodland and out along the adjoining hedgerow. All samples from the seed bank showed a positive correlation, between distance and species richness, indicating increasing herbaceous plant species richness away into and away from woodland edge.

Table 4.1 Results of Wilcoxon test for matched pairs for the number of herbaceous plant species in each transect surveyed

	Woodland						Hedge NE						Hedge SW					
	Vegetation			Seed bank			Vegetation			Seed bank			Vegetation			Seed bank		
	n	T	p	n	T	p	n	T	p	n	T	p	n	T	p	n	T	p
Woodland vegetation				10	12.9	ns	9	21.5	ns				8	18.5	ns			
Woodland seed bank										9	1	<0.02				9	0	<0.02
Hedge NE vegetation										10	7.5	ns	8	13	ns			
Hedge NE seed bank																9	9	ns
Hedge SW vegetation																10	2	<0.02
Hedge SW seed bank																		

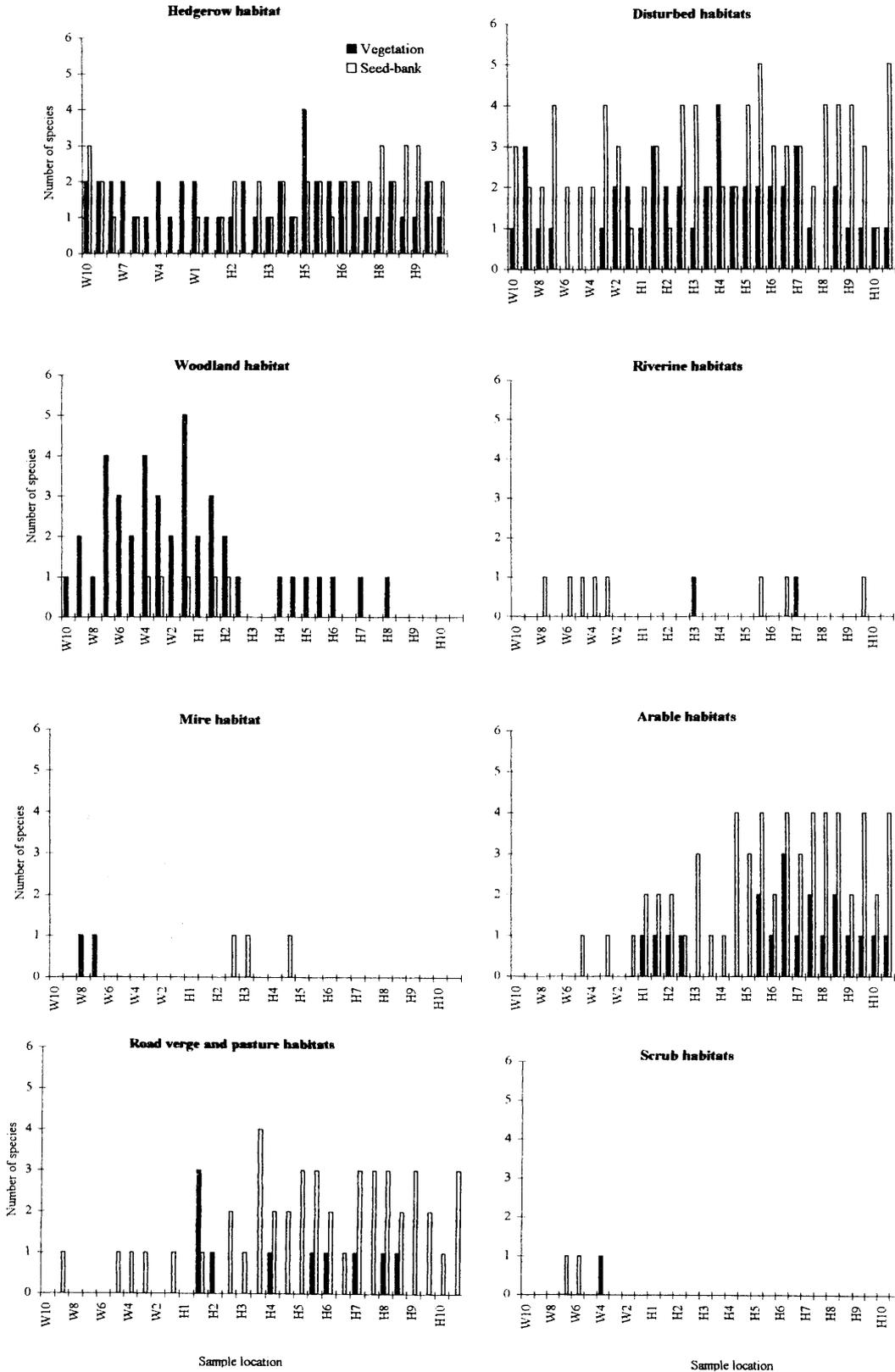
ns = non-significant

4.5.2 Spatial distribution of herbaceous plant species classified by habitat type.

The presence data for the herbaceous plant species found in both the seed bank and vegetation of the woodland and hedgerow transects are displayed in Appendix 4.1. The herbaceous plant species found in the vegetation and seed bank were grouped by habitat types, after Hodgson *et al.* (1995) (Figure 4.4). Plant species associated with habitats such as spoil heaps, quarries and scree were combined into one group and entitled “disturbed habitats”. Those species associated with roadside verges and pasture were also combined into a grassland group. The following observations are made:

- those species associated with the **hedgerow** habitat show a relatively even distribution across both the woodland and hedgerow vegetation, whereas the seed bank of this habitat type is more concentrated in the hedgerow transect (Figure 4.4).
- The species typical of **woodlands**, particularly in the seed bank, were confined to the woodland transect.
- Of the **mire** species, only two locations in the woodland transect were observed in the vegetation survey. Species from this habitat type were only found within the seed bank of the hedgerow transects.
- **Road verge** and **pasture**: the majority of species were found in the hedgerow seed bank, with some presence in the woodland. In the vegetation, a higher number of species were found in the hedgerow transects, closer to the woodland.
- Plant species associated with **disturbed** habitats occurred in the vegetation and seed banks of the woodland and hedgerow transects.
- **Riverine** species were present in the seed banks of the woodland and hedgerow, but in the vegetation were found only in the hedgerow.
- Species affiliated with **arable** land use are shown to have a distinct distribution along the woodland and hedgerow transects. Many more species were found in the hedgerow seed-bank than in the hedgerow vegetation. There is also an indication of arable species dispersing into the woodland seed bank.

Figure 4.4 Spatial distribution of the number of herbaceous plant species by habitat types.



- **Scrub** or developing woodland species were confined to the woodland vegetation and seed bank.

PCA was carried out on the number of species representing each habitat type in each quadrat location. Results showed that two groups of habitat types could be identified along the first axis, 53% of the variance was explained by the first axis; 90% of the variance was explained by the first four principal components (Table 4.3, Figure 4.5a). Arable, grassland and disturbed habitat type species were grouped together confirming the above analysis indicates similarity in spatial patterning and the number of species (Figure 4.4).

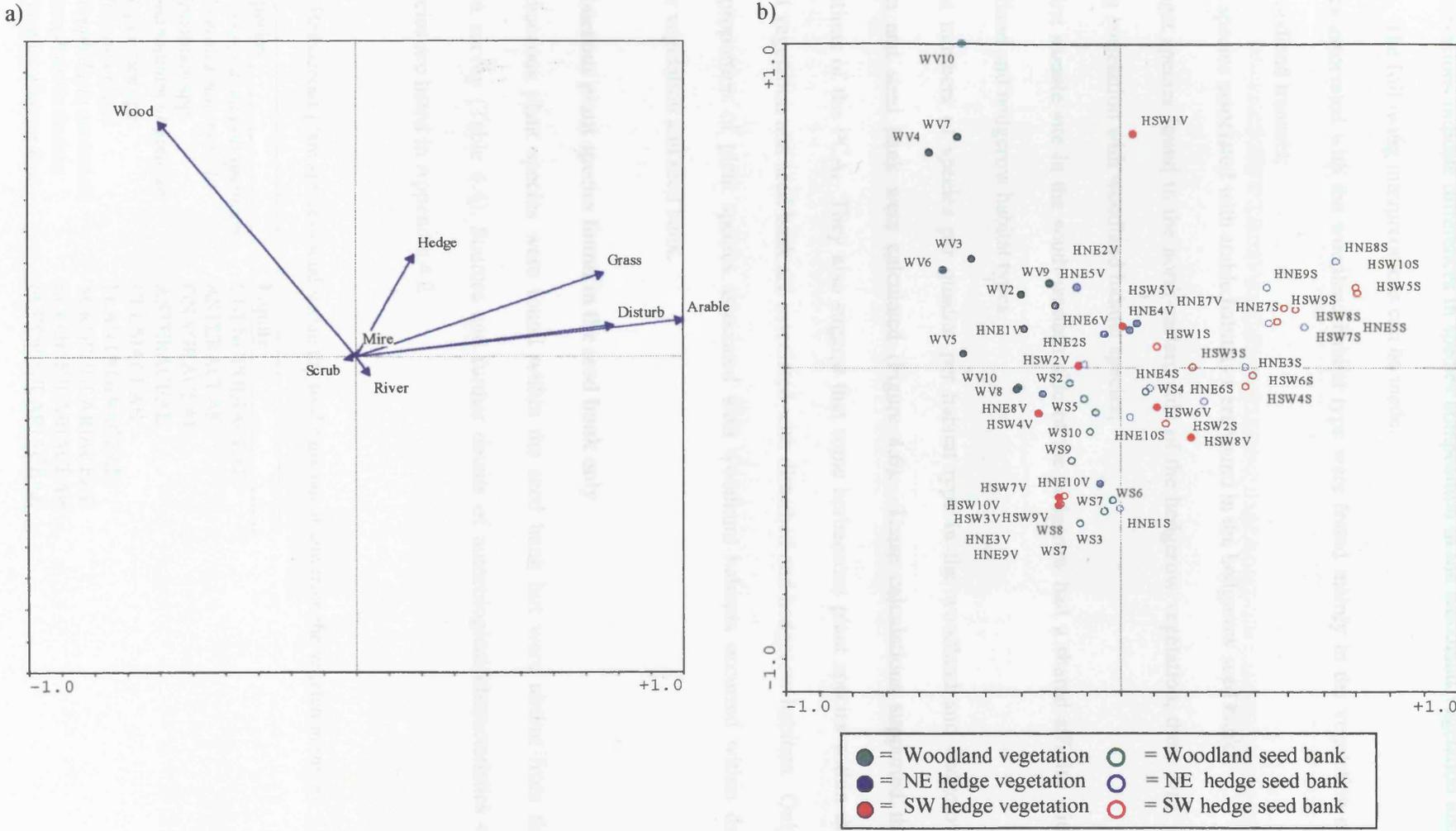
Table 4.3 Results of the PCA analysis for habitat type

PCA: Habitat type	% variance explained	Cumulative % of variance
PCA1	53	53
PCA2	15	68
PCA3	13	81
PCA4	9	90
Unexplained	10	100
Total sum of squares	422.37	
Total standard deviation	0.94	
Collinearity condition value	3.14	

The species associated with woodland and arable habitat types were the furthest apart, indicating that they were the most dissimilar habitat groups. Species associated with hedgerows were between these two extremes. Species associated with river, mire and scrub habitats are near to the centre of the diagram, adding to the explanatory power of this analysis, as stated in the methods section.

Arable, grassland, hedgerow and woodland habitat types were separated by the second, vertical, axis (Figure 4.5b). The woodland vegetation sites (filled circles) are seen to be located mainly on the left-hand side of the diagram; the seed samples (open circles) are grouped to the right hand side. The woodland vegetation sites also cluster in the top left quarter of the diagram, whereas the woodland seed bank samples sites are in the bottom left quarter.

Figure 4.5 PCA ordination of sample site locations with herbaceous plant species: associated with different habitat types



These observations indicate differences in species composition in the woodland vegetation and seed bank. The following interpretations can be made:

- species associated with the woodland habitat type were found mainly in the vegetation of the woodland transect;
- those species associated with arable habitats were found in the hedgerow seed bank;
- amongst species found in the north-eastern side of the hedgerow vegetation, there was a strong correlation with woodland habitat species;
- the first sample site in the south-western side of the hedgerow had a shared affinity with woodland and hedgerow habitat types.

The mean numbers of species per quadrat per habitat type in the woodland and hedgerow vegetation and seed bank were calculated (Figure 4.6). These calculations supported the interpretations of the PCA. They also suggest that some herbaceous plant species within the woodland vegetation and seed bank are associated with disturbed and hedgerow habitats. Only a small proportion of plant species associated with woodland habitats occurred within the hedgerow vegetation and seed bank.

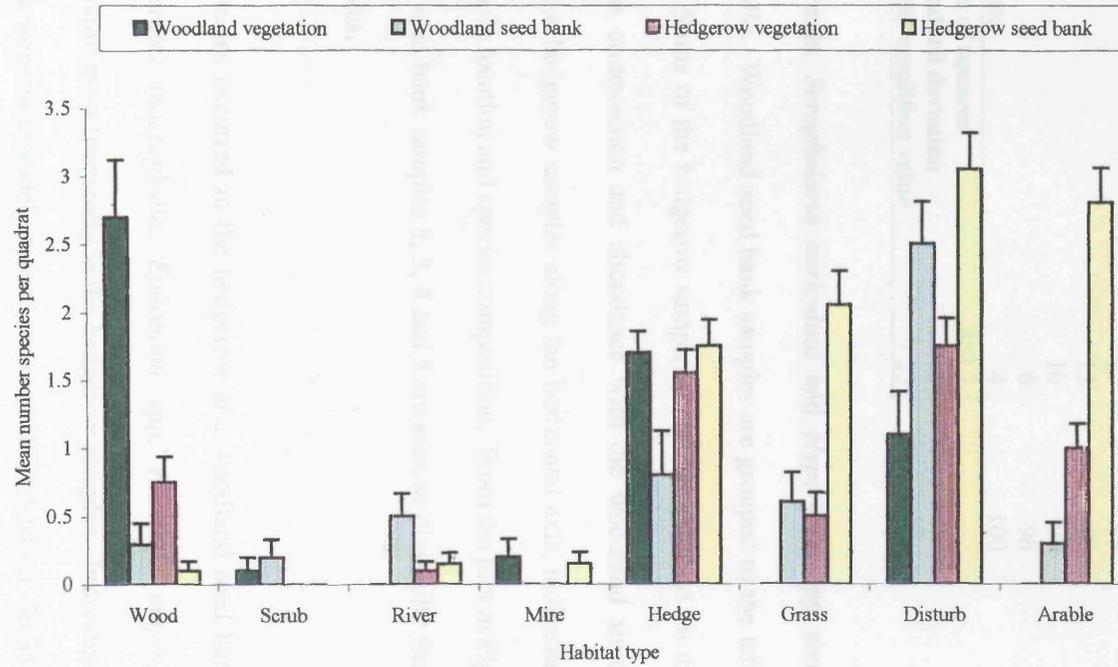
4.6 Herbaceous plant species found in the seed bank only

Nine herbaceous plant species were found within the seed bank but were absent from the vegetation survey (Table 4.4). Sources and further details of autecological characteristics of these species are listed in Appendix 4.2.

Table 4.4 Herbaceous plant species found within the seed bank but absent from the vegetation survey

Species	Family
<i>Chenopodium polyspermum</i>	CHENOPODIACEAE
<i>Cicerbita macrophylla</i>	ASTERACEAE
<i>Epilobium</i> spp.	ONAGRACEAE
<i>Gnaphalium uliginosum</i>	ASTERACEAE
<i>Hypericum</i> spp.	CLUSIACEAE
<i>Plantago major</i>	PLANTAGINACEAE
<i>Scrophularia auriculata</i>	SCROPHULARIACEAE
<i>Scrophularia nodosa</i>	SCROPHULARIACEAE
<i>Veronica chamaedrys</i>	SCROPHULARIACEAE

Figure 4.6 Mean number of species within each habitat type for vegetation and seed bank (Error bar = SE)



PCA separated *Veronica chamaedrys* along the horizontal axis from the other species found in the seed bank (67% of variance was explained by the first principal component and 96% explained by the first four principal components) (Table 4.5, Figure 4.7a).

Table 4.5 Results of the PCA analysis for herbaceous plant species found in the seed bank only

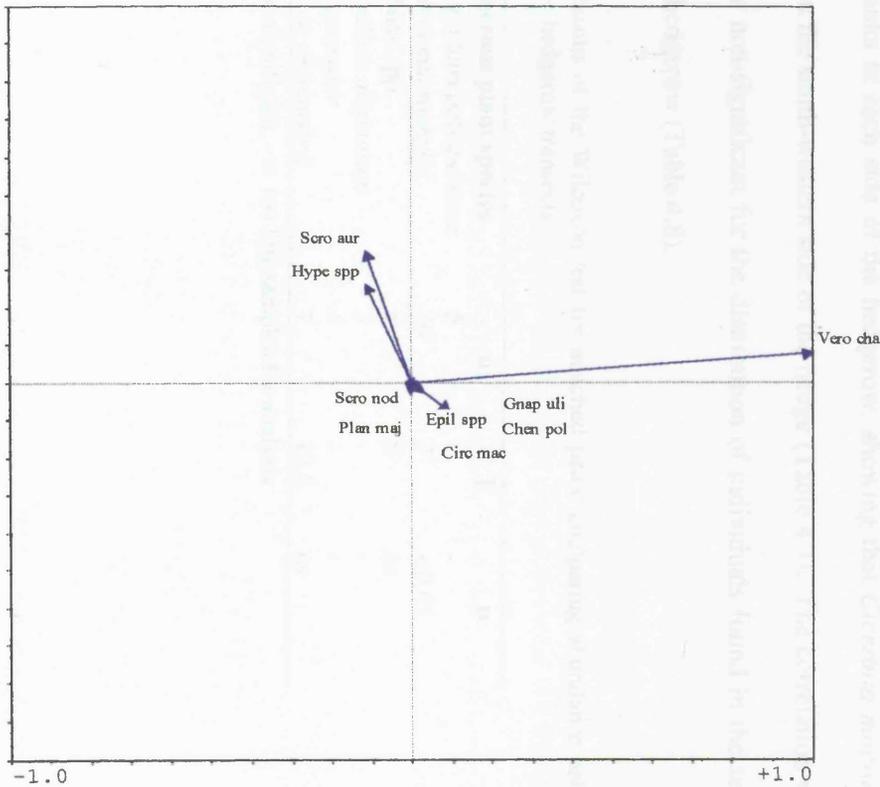
PC: seed bank only	% variance explained	Cumulative % variance
PC1	67	67
PC2	13	80
PC3	10	90
PC4	6	96
Unexplained	4	100
Total sum of squares	888.7	
Total standard deviation	1.81	
Collinearity condition value	7.33	

Along the second axis, *Scrophularia auriculata* and *Hypericum* spp were separated from *Cicerbita macrophylla*. Woodland seed bank samples are grouped to the left on the horizontal axis (Figure 4.7b). Some of the hedgerow samples were also grouped on this side, indicating similarity in species composition and abundance with the woodland sites. The PCA also separated some of the hedgerow samples along the horizontal axis, indicating the dissimilarity of these sites in sample location and species composition. From the plot in Figure 4.7b, the woodland seed bank samples 8, 3, 4 and 5 are seen as dissimilar from other woodland and hedgerow samples.

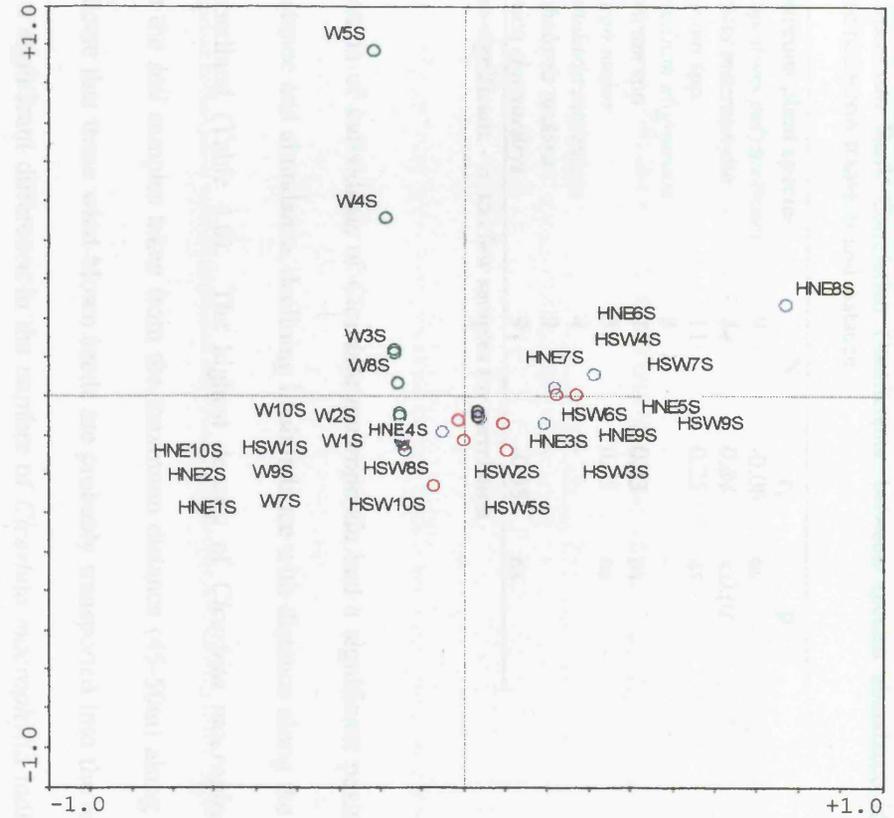
Four of the nine species occurred in the hedgerow and woodland seed banks (*Chenopodium polyspermum*, *Cicerbita macrophylla*, *Epilobium* spp, *Plantago major*). *Chenopodium polyspermum* was found most frequently in the hedgerow samples. Individuals arising from the woodland seed bank were more widely spaced, at intervals of 10-15m, 30-35m and with a peak in abundance at 45-50m from the woodland edge. No correlation between abundance and distance was found (Table 4.6).

Figure 4.7 PCA ordination of herbaceous plant species found exclusively in the seed bank

a)



b)



○ = Woodland seed bank ● = NE hedge seed bank ● = SW hedge seed bank

Table 4.6 Spearman Rank Correlation Coefficients: between species abundance in the combined woodland and hedgerow transects and distance

Herbaceous plant species	N	r _s	p
<i>Chenopodium polyspermum</i>	9	-0.06	ns
<i>Cicerbita macrophylla</i>	14	0.84	<0.01
<i>Epilobium</i> spp.	11	0.25	ns
<i>Gnaphalium uliginosum</i>	3	-	-
<i>Hypericum</i> spp.	7	0.43	ns
<i>Plantago major</i>	5	0.75	ns
<i>Scrophularia auriculata</i>	4	-	-
<i>Scrophularia nodosa</i>	2	-	-
<i>Veronica chamaedrys</i>	9	-0.35	ns

ns = non-significant, - = too few samples for correlation

The distribution of individuals of *Cicerbita macrophylla* had a significant positive correlation between distance and abundance, declining in abundance with distance along the hedgerow and into the woodland (Table 4.6). The highest density of *Cicerbita macrophylla* seeds was recorded in the soil samples taken from the maximum distance (45-50m) along the hedgerow. Results indicate that these wind-blown seeds are probably transported into the woodland edge. There was a significant difference in the number of *Cicerbita macrophylla* individuals within the seed banks in each side of the hedgerow, showing that *Cicerbita macrophylla* was more abundant on the south-western side of the hedge (Table 4.7). The correlation with distance was found to be non-significant for the distribution of individuals found in the seed bank on each side of the hedgerow (Table 4.8).

Table 4.7 Results of the Wilcoxon test for matched pairs: comparing abundance between NE and SW aspects of the hedgerow transects

Herbaceous plant species	n	T	p
<i>Chenopodium polyspermum</i>	5	-	-
<i>Cicerbita macrophylla</i>	10	7	<0.05
<i>Epilobium</i> spp.	8	8	ns
<i>Gnaphalium uliginosum</i>	3	-	-
<i>Plantago major</i>	4	-	-
<i>Veronica chamaedrys</i>	7	12.5	ns

ns = non-significant, - = too few samples for analysis

Table 4.8 Spearman Rank Correlation Coefficients: between species abundance in the NE and SW hedgerow transect and distance

Hedge transects Herbaceous plant species	NE			SW		
	n	r _s	p	n	r _s	p
<i>Chenopodium polyspermum</i>	3	-	-	4	-	-
<i>Cicerbita macrophylla</i>	5	0.8	ns	9	0.62	ns
<i>Epilobium</i> spp.	6	0.2	ns	6	0.31	ns
<i>Gnaphalium uliginosum</i>	1	-	-	2	-	-
<i>Plantago major</i>	1	-	-	3	-	-
<i>Veronica chamaedrys</i>	7	0.69	ns	9	-0.35	

ns = non-significant, - = too few samples for correlation

Individuals of *Epilobium* spp. were located in the hedgerow and woodland seed bank. This suggests that this species may be able to disperse into or from the woodland. The correlation analysis between distance and individuals abundance was non-significant.

The species only located in the woodland seed bank were *Scrophularia auriculata*, *S. nodosa* and *Hypericum* species. Each of these species is able to persist in the soil (Thompson *et al.* 1997). A concentration of seeds of these species was found in samples taken around 20-25m into the woodland (W5) (Figure 4.8).

Two species were recorded in the hedgerow seed bank only: *Veronica chamaedrys* and *Gnaphalium uliginosum* (Figure 4.9). No significant difference was found in the abundance of *Veronica chamaedrys* for each side of the hedgerow, or were there any correlation between abundance and distance. Seedlings of *Gnaphalium uliginosum* were not found in the woodland seed bank. Too few were located in the hedgerow seed bank for statistical analysis.

Figure 4.8 The spatial distribution of herbaceous plant species located in the seed bank only.

NB: Scales on Y axes varying according to abundance of each species

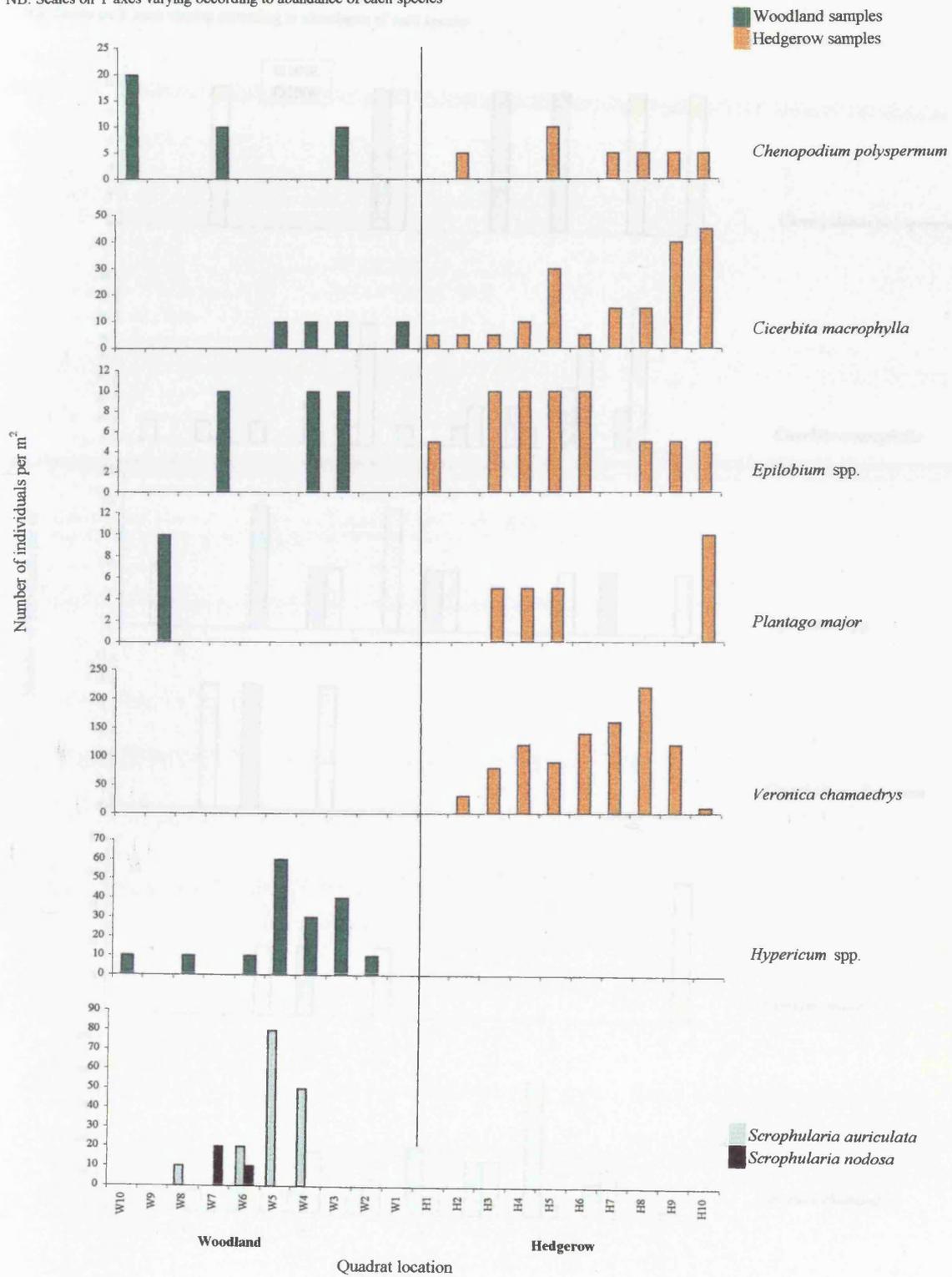
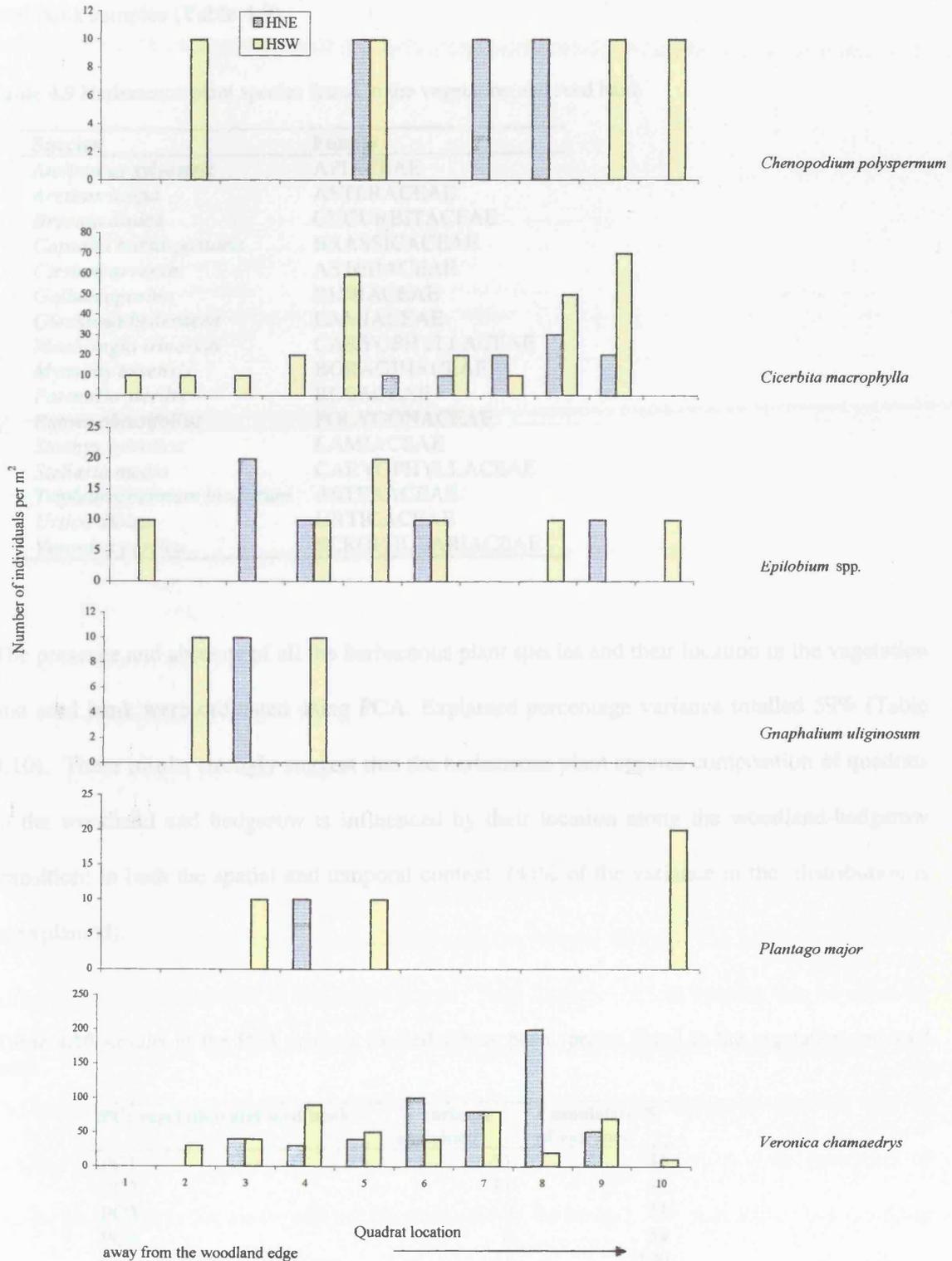


Figure 4.9 Spatial distribution of herbaceous plant species located in the seed bank only: hedgerow transect with aspect.

NB: Scales on Y axes varying according to abundance of each species



4.7 Herbaceous plant species found in both the vegetation survey and seed bank study.

4.7.1 Presence and abundance of herbaceous plant species.

Sixteen herbaceous plant species were found to be present in both the vegetation survey and the seed bank samples (Table 4.9).

Table 4.9 Herbaceous plant species found in the vegetation and seed bank

Species	Family
<i>Anthriscus sylvestris</i>	APIACEAE
<i>Arctium lappa</i>	ASTERACEAE
<i>Bryonia dioica</i>	CUCURBITACEAE
<i>Capsella bursa-pastoris</i>	BRASSICACEAE
<i>Cirsium arvense</i>	ASTERACEAE
<i>Galium aparine</i>	RUBIACEAE
<i>Glechoma hederacea</i>	LAMIACEAE
<i>Moehringia trinervia</i>	CARYOPHYLLACEAE
<i>Myosotis arvensis</i>	BORAGINACEAE
<i>Potentilla sterilis</i>	ROSACEAE
<i>Rumex obtusifolius</i>	POLYGONACEAE
<i>Stachys sylvatica</i>	LAMIACEAE
<i>Stellaria media</i>	CARYOPHYLLACEAE
<i>Tripleurospermum inodorum</i>	ASTERACEAE
<i>Urtica dioica</i>	URTICACEAE
<i>Veronica persica</i>	SCROPHULARIACEAE

The presence and absence of all the herbaceous plant species and their location in the vegetation and seed bank were ordinated using PCA. Explained percentage variance totalled 59% (Table 4.10). These results strongly suggest that the herbaceous plant species composition of quadrats in the woodland and hedgerow is influenced by their location along the woodland-hedgerow transition; in both the spatial and temporal context (41% of the variance in the distribution is unexplained).

Table 4.10 Results of the PCA analysis for herbaceous plant species found in the vegetation and seed bank

PC: vegetation and seed bank	% variance explained	Cumulative % of variance
PC1	31	31
PC2	11	42
PC3	9	51
PC4	8	59
Unexplained	41	100
Total sum of squares	153.82	
Total standard deviation	0.40	
Collinearity condition value	1.97	

Results show that 31% of the variance accounted for the separation along the first axis of *Glechoma hederacea*, *Moehringia trinervia* and *Potentilla sterilis* from the remaining species, especially *Stachys sylvatica* and *Capsella bursa-pastoris* (Figure 4.10a). Twelve herbaceous plant species were separated by 11% of the variance up the second vertical axis. These species fall into two groups (Table 4.11).

Table 4.11 Species divided by PCA2

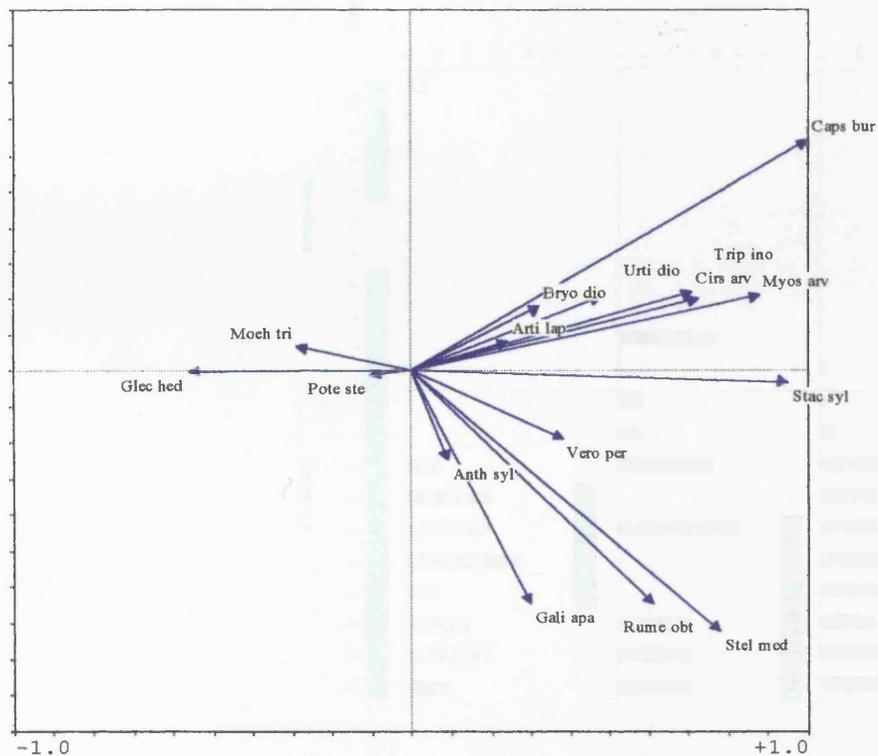
PC2 (a)	PC2 (b)
<i>Capsella bursa-pastoris</i>	<i>Stellaria media</i>
<i>Myosotis arvensis</i>	<i>Rumex obtusifolius</i>
<i>Tripleurosperum inodorum</i>	<i>Galium aparine</i>
<i>Cirsium arvense</i>	<i>Anthriscus sylvestris</i>
<i>Urtica dioica</i>	<i>Veronica persica</i>
<i>Bryonia dioica</i>	
<i>Articum lappa</i>	

Ordination of the sample sites shows that the woodland sites are separated by the horizontal axis (on the left-hand side of the plot, green closed circles = vegetation and green open circles = seed bank), and less strongly by the vertical axis (top section) (Figure 4.10b). Location of some of the hedgerow vegetation samples and a few hedgerow seed bank samples indicated a similarity in species composition with woodland sites. The majority of the hedgerow seed bank samples were separated from the woodland sites, on the right hand side of the plot.

In this study, individuals of *Anthriscus sylvestris* and *Bryonia dioica* were absent from the seed bank and vegetation present in the woodland samples (Figure 4.11a). The seeds of *Anthriscus sylvestris* were located near to the parent plants. Seed dispersal of this species may be aided by propulsive action as the wind moves the seed heads on the adult plant (See appendix 4.2b). Individuals of *Bryonia dioica* were found in the vegetation in each hedgerow transect (Figure 4.12a). Individuals located in the seed bank were not always located in close proximity to parent plants (up to 5m away, and the opposite side of the hedge). *Bryonia dioica* is a climbing herbaceous plant that could climb up and into the hedgerow, allowing seeds to drop off the

Figure 4.10 PCA ordination of herbaceous plant species located in the vegetation and seed bank

a)



b)

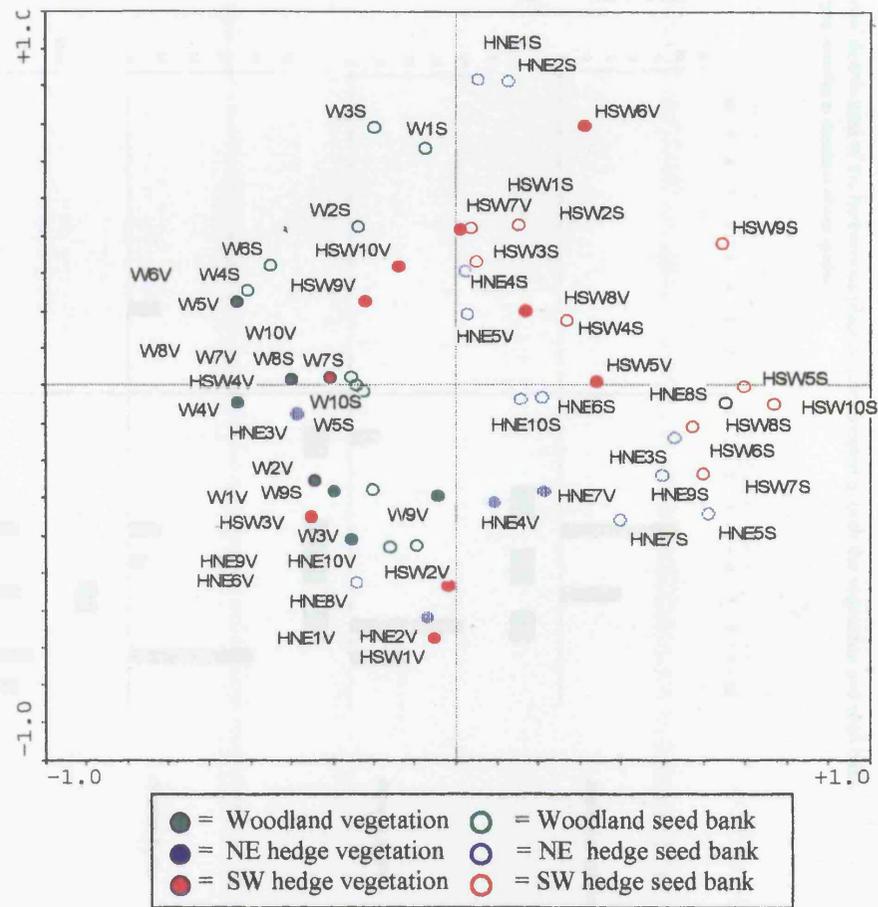


Figure 4.11a Spatial distribution of the herbaceous plant species located in both the vegetation and seed bank
 NB: Scales on Y axes varying according to abundance of each species

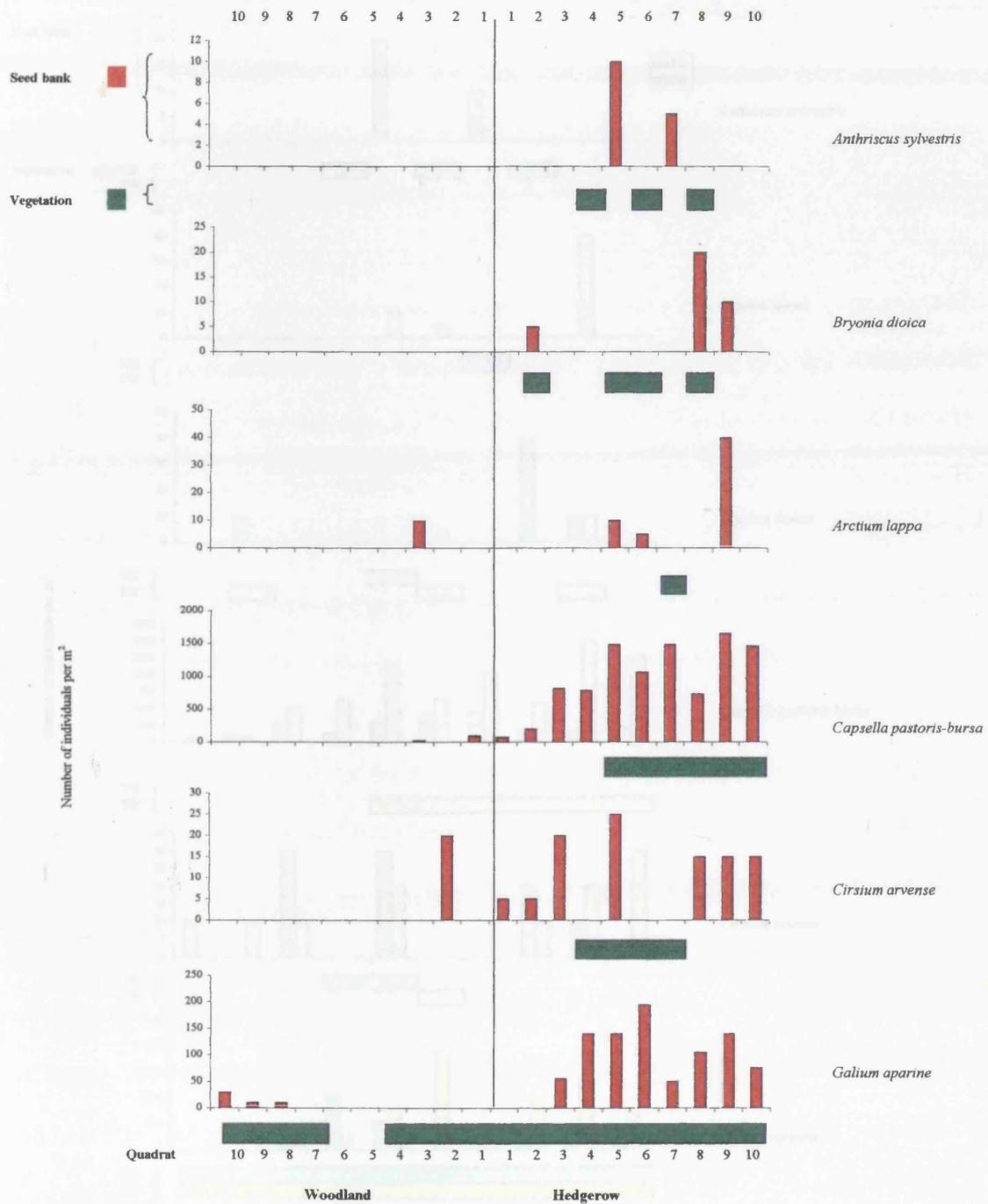
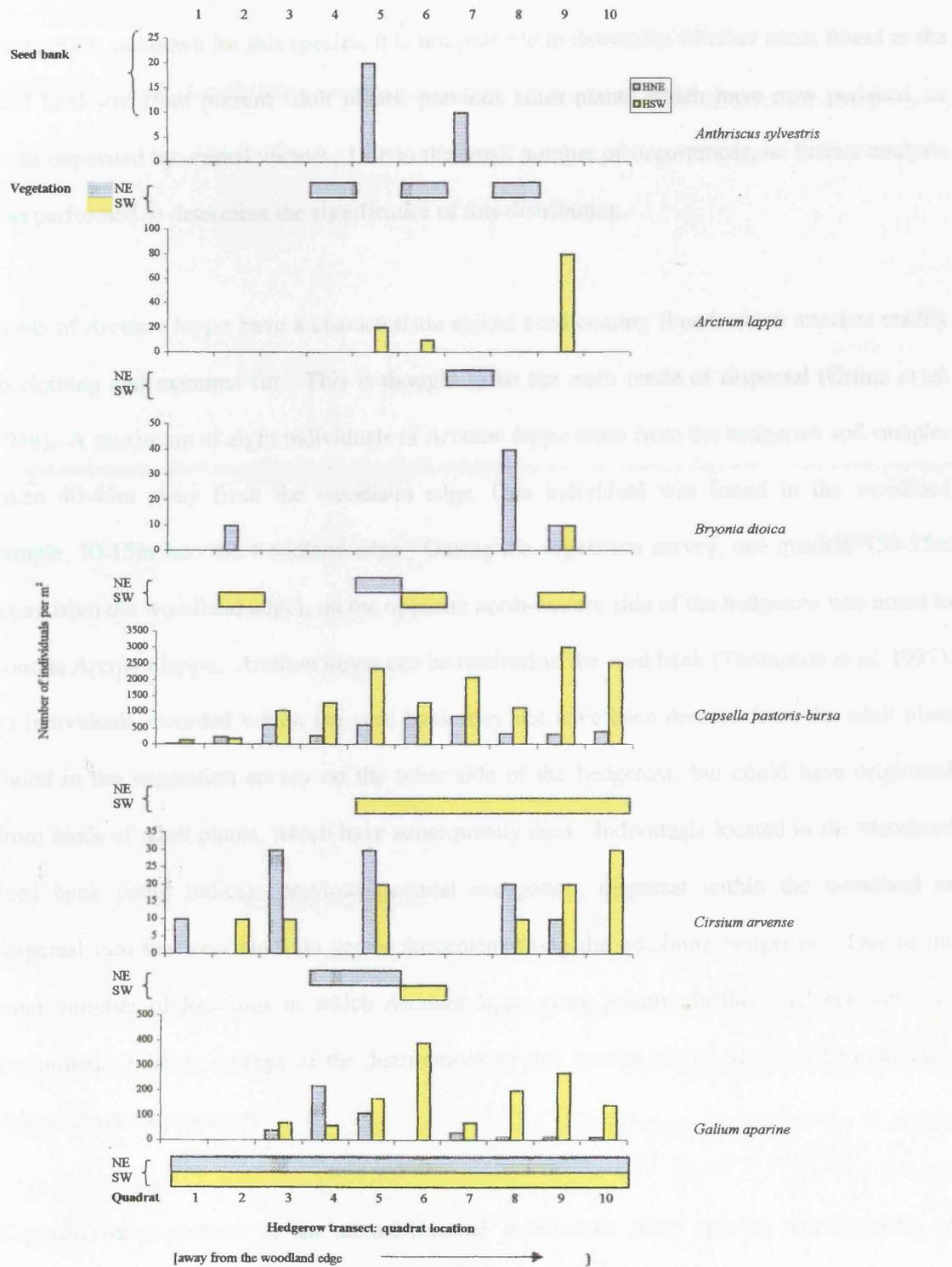


Figure 4.12a Spatial distribution of the herbaceous plant species located in both the vegetation and seed bank with hedgerow aspect
 NB: Scales on Y axes varying according to abundance of each species



parent plant on the opposite side of the hedgerow. This species produces fruits containing 3-6 seeds, which are thought to be dispersed by animal vectors (Appendix 4.2). As the seed bank longevity is unknown for this species, it is not possible to determine whether seeds found in the seed bank are from present adult plants, previous adult plants which have now perished, or seeds deposited by animal vectors. Due to the small number of occurrences, no further analysis was performed to determine the significance of this distribution.

Seeds of *Arctium lappa* have a characteristic spiked seed coating (burr) which attaches readily to clothing and mammal fur. This is thought to be the main mode of dispersal (Grime *et al.* 1988). A maximum of eight individuals of *Arctium lappa* arose from the hedgerow soil samples taken 40-45m away from the woodland edge. One individual was found in the woodland sample, 10-15m into the woodland edge. During the vegetation survey, one quadrat (30-35m away from the woodland edge), on the opposite north-eastern side of the hedgerow was noted to contain *Arctium lappa*. *Arctium lappa* can be retained in the seed bank (Thompson *et al.* 1997), so individuals recorded within the seed bank may not have been derived from the adult plant found in the vegetation survey on the other side of the hedgerow, but could have originated from seeds of adult plants, which have subsequently died. Individuals located in the woodland seed bank could indicate previous parental occupation, dispersal within the woodland or dispersal into the woodland via vector movement along the adjoining hedgerow. Due to the small number of locations in which *Arctium lappa* were present, further analyses were not performed. Further surveys of the distributions of this species would be needed to elucidate dispersal-vector processes.

Capsella bursa-pastoris is an annual-biennial herbaceous plant species, characteristic of cultivated or open bare ground (Stace 1991) and is often found on continuously disturbed land (Grime *et al.* 1988). *Capsella bursa-pastoris* was abundant within the hedgerow seed bank. Nine individuals were found in the first quadrat (0-5m) within the woodland, and two individuals 10-15m into the woodland. A highly significant correlation was found between the

abundance of *Capsella bursa-pastoris* and distance along the combined woodland and hedgerow transects (Table 4.12). A seed-shadow (extent of seed fall) is noted as tailing towards the woodland edge.

Table 4.12 Spearman Rank Correlation Coefficients: between species abundance in the combined woodland and hedgerow seed bank and distance

Herbaceous plant species	N	r_s	P
<i>Anthriscus sylvestris</i>	2	-	-
<i>Arctium lappa</i>	4	-	-
<i>Bryonia dioica</i>	4	-	-
<i>Capsella bursa-pastoris</i>	12	0.81	<0.01
<i>Cirsium arvense</i>	8	0.08	ns
<i>Galium aparine</i>	11	0.57	ns
<i>Glechoma hederacea</i>	3	-	-
<i>Moehringia trinervia</i>	5	-	-
<i>Myosotis arvensis</i>	9	-0.08	ns
<i>Potentilla sterilis</i>	1	-	-
<i>Rumex obtusifolius</i>	11	-0.11	ns
<i>Stachys sylvatica</i>	12	0.66	<0.05
<i>Stellaria media</i>	9	0.90	<0.01
<i>Tripleurospermum inodorum</i>	8	0.62	ns
<i>Urtica dioica</i>	19	0.30	ns
<i>Veronica persica</i>	5	-	-

ns = non-significant, - = too few samples for correlation

A maximum of 302 individuals (3005 seeds per m²) of *Capsella bursa-pastoris* was identified in the seed bank samples taken from the ninth quadrat on the south-western side of the hedgerow (40-45m from the woodland edge). *Capsella bursa-pastoris* was significantly more abundant in the seed bank on the south-western side of the hedgerow (Table 4.13). A Spearman Rank Correlation Coefficient was calculated between the abundance of *Capsella bursa-pastoris* in the seed bank and distance along each side of the hedgerow. A highly significant correlation was found along the south-western side of the hedgerow with distance away from the woodland edge (Table 4.14).

Cirsium arvense is common throughout the British Isles and is customarily found in grassland, hedgerows, arable, waste and rough ground (Stace 1991). It is noted as a competitive perennial and designated as a noxious weed by the Weeds Act 1959 (Grime *et al.* 1988). The spatial

distribution of *Cirsium arvense* in the seed bank, from this research suggests some encroachment of the seeds of this species into the woodland edge from the hedgerow vegetation.

Table 4.13 Results of the Wilcoxon test for matched pairs: comparing species abundance within the seed bank between the NE and SW aspects of the hedgerow transects

Herbaceous plant species	N	T	P
<i>Anthriscus sylvestris</i>	2	-	-
<i>Arctium lappa</i>	3	-	-
<i>Bryonia dioica</i>	4	-	-
<i>Capsella bursa-pastoris</i>	10	1	<0.02
<i>Cirsium arvense</i>	7	13	ns
<i>Galium aparine</i>	8	5	ns
<i>Moehringia trinervia</i>	3	-	-
<i>Myosotis arvensis</i>	9	11	ns
<i>Rumex obtusifolius</i>	9	11	ns
<i>Stachys sylvatica</i>	8	14.5	ns
<i>Stellaria media</i>	8	3.5	ns
<i>Tripleurospermum inodorum</i>	7	0	<0.02
<i>Urtica dioica</i>	10	7	<0.05
<i>Veronica persica</i>	5	-	-

ns = non-significant, - = too few samples for analysis

Table 4.14 Spearman Rank Correlation Coefficients: between species abundance in the NE and SW hedgerow transect and distance

Hedge transects Herbaceous plant species	NE			SW		
	n	r _s	P	n	r _s	P
<i>Anthriscus sylvestris</i>	2	-	-	0	-	-
<i>Arctium lappa</i>	0	-	-	3	-	-
<i>Bryonia dioica</i>	3	-	-	1	-	-
<i>Capsella bursa-pastoris</i>	10	0.43	ns	10	0.83	<0.01
<i>Cirsium arvense</i>	5	-0.1	ns	6	0.79	ns
<i>Galium aparine</i>	6	0.79	ns	8	0.46	ns
<i>Moehringia trinervia</i>	2	-	-	1	-	-
<i>Myosotis arvensis</i>	4	-	-	7	-0.34	ns
<i>Rumex obtusifolius</i>	6	-0.27	ns	7	-0.13	ns
<i>Stachys sylvatica</i>	9	0.49	ns	7	-0.06	ns
<i>Stellaria media</i>	7	0.87	<0.05	7	0.89	<0.05
<i>Tripleurospermum inodorum</i>	3	-	-	8	0.62	ns
<i>Urtica dioica</i>	10	-0.32	ns	10	-0.06	ns
<i>Veronica persica</i>	3	-	-	2	-	-

ns = non-significant, - = too few samples for correlation

(two individuals were found 5-10m into the woodland). There was, however, no significant correlation between the abundance of this species and distance from the woodland edge; nor was the abundance significantly different between the two sides of the hedgerow. It cannot be ruled out that the individuals found could have arisen during the seed bank study from

vegetative fragments within the soil samples, although it is very unlikely, given that the soils samples were sieved when prepared for germination.

No correlation was found between abundance of *Galium aparine* and distance along the woodland and hedgerow transition. The distribution pattern implies that the reproductive success of the plants in the hedgerow is far greater in the hedgerow than those close to, or within the woodland. Taylor (1999) points out that *Galium aparine* is particularly intolerant of nutrient-poor soils. In this study, this species was absent in the seed bank samples taken in the woodland edge vicinity, whilst plants were present in the vegetation. The results do not substantiate the cause of the absence of retained seeds. Conditions in the woodland edge may contribute to a reduced competitive ability or vitality. *Galium aparine* was present in all hedgerow quadrats in the vegetation survey. Among the data for the seed bank, no significant difference was found in the abundance of individuals between the two sides of the hedgerow. A correlation between abundance and distance was not found.

Glechoma hederacea (Figure 4.11b) was present in eight woodland quadrats in the vegetation survey but was absent in the hedgerow vegetation. Ten individuals were counted in the seed bank sample, all of which occurred within the woodland away from the woodland edge and the adjacent hedgerow. These results indicate a decline in the reproductive success of *Glechoma hederacea* towards the woodland edge. Further analyses were not performed, as there were too few occurrences.

Moehringia trinervia was found in four consecutive quadrats in the vegetation, spanning the woodland edge and the first hedgerow quadrat on both sides of the hedge (Figures 4.12b). In the seed bank, the majority of the individuals found were located 5-10m into the woodland edge. Germinating seeds were found in the hedgerow soils samples taken 0-5m from the woodland on the south-eastern side of the hedge and in the sample at a distance 5-10m on the

Figure 4.11b Spatial distribution of the herbaceous plant species located in both the vegetation and seed bank: continued
 NB: Scales on Y axes varying according to abundance of each species

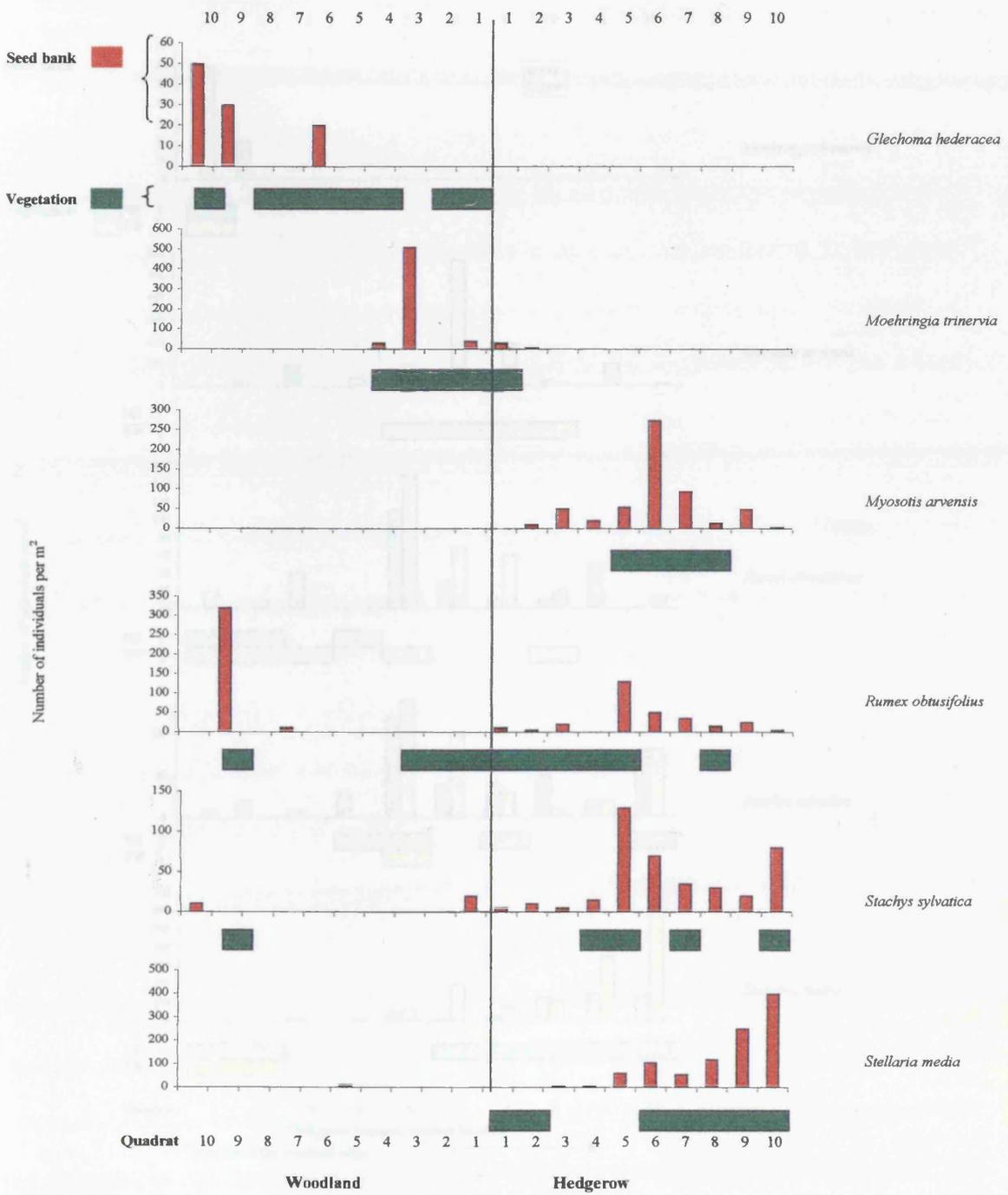
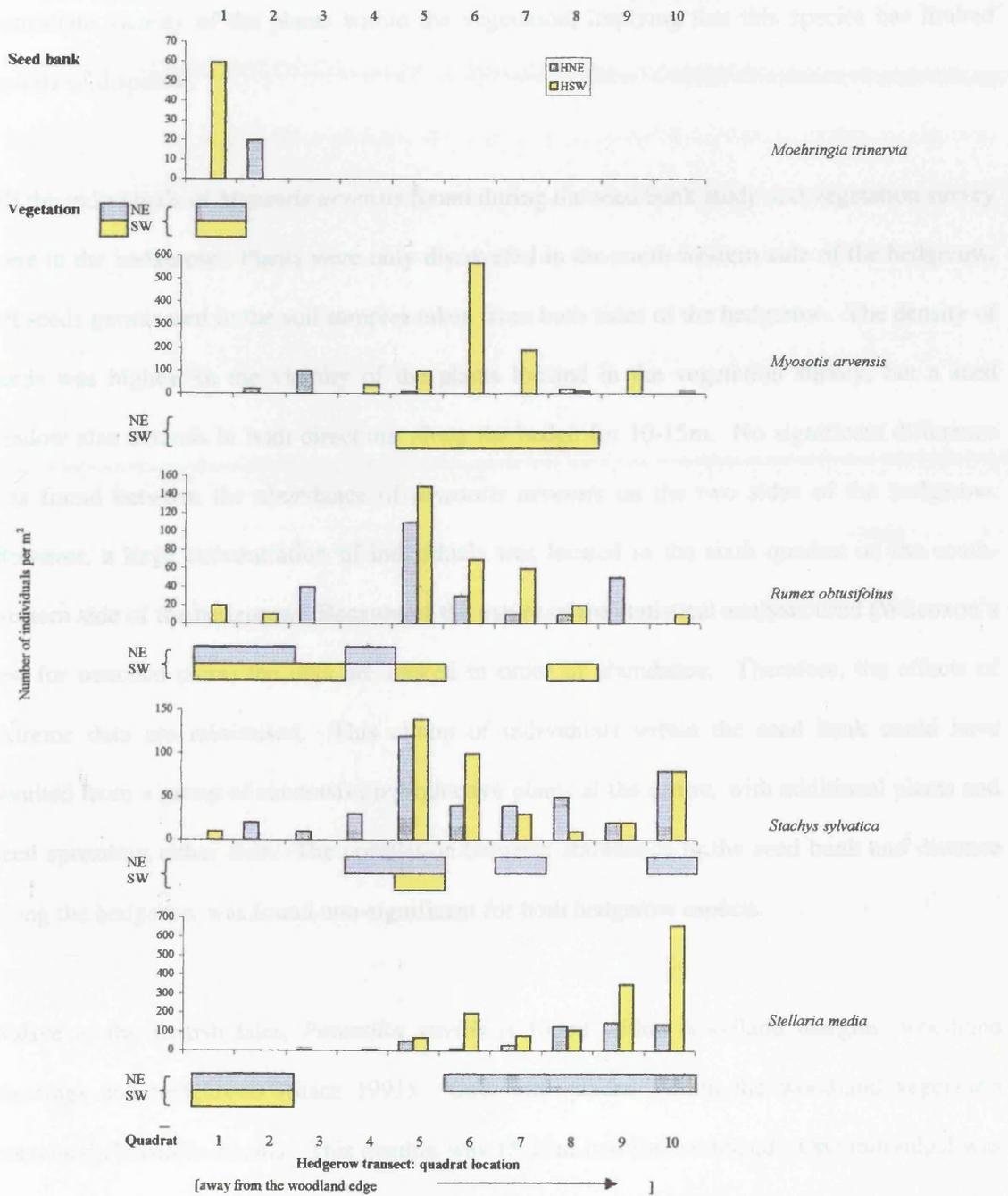


Figure 4.12b Spatial distribution of the herbaceous plant species located in both the vegetation and seed bank with hedgerow aspect: continued
 NB: Scales on Y axes varying according to abundance of each species



north western side. There was no significant association between abundance and distance away from the woodland margin. Distribution patterns suggest that seeds occurred within the immediate vicinity of the plants within the vegetation, implying that this species has limited powers of dispersal.

All the individuals of *Myosotis arvensis* found during the seed bank study and vegetation survey were in the hedgerow. Plants were only discovered in the south-western side of the hedgerow, yet seeds germinated in the soil samples taken from both sides of the hedgerow. The density of seeds was highest in the vicinity of the plants located in the vegetation survey, but a seed shadow also extends in both directions along the hedge for 10-15m. No significant difference was found between the abundance of *Myosotis arvensis* on the two sides of the hedgerow. However, a large concentration of individuals was located in the sixth quadrat on the south-western side of the hedgerow. Because of the nature of the statistical analysis used (Wilcoxon's test for matched pairs) the data are ranked in order of abundance. Therefore, the effects of extreme data are minimised. This clump of individuals within the seed bank could have resulted from a group of successful reproductive plants at the centre, with additional plants and seed spreading either side. The correlation between abundance in the seed bank and distance along the hedgerow was found non-significant for both hedgerow aspects.

Native to the British Isles, *Potentilla sterilis* is found within woodland margins, woodland clearings and hedgerows (Stace 1991). Only one quadrat within the woodland vegetation contained *Potentilla sterilis*. This quadrat was 15-20m into the woodland. One individual was also identified during the seed bank study: this came from the soil samples in the quadrat 20-25m into the woodland.

Rumex obtusifolius is a native perennial commonly found by roads and rivers, on waste and cultivated ground throughout the British Isles (Stace 1991). Sutton (1995) also regards *Rumex obtusifolius* as a plant common to field margins and hedgerows and it is noted as an agricultural

weed in the Weeds Act 1959 (Grime *et al.* 1988). In this study, *Rumex obtusifolius* was found in both the vegetation and seed bank within the woodland and along the hedgerow. The correlation between the number of *Rumex obtusifolius* individuals and distance along the woodland and hedgerow transect was non-significant. A large peak in abundance of individuals was detected in the woodland seed bank, 40-45m into the woodland. Although this species was discovered in the vegetation survey at the woodland edge, no individuals arose from the seed bank study in these locations. The abundance of individuals on the two sides of the hedgerow was not significantly different and no correlation between abundance and distance was found on either side of the hedge.

Stachys sylvatica, characteristic of hedgerows, road-verges, riverbanks, and the edge of woodland rides and floodplains (Grime *et al.* 1988), was more abundant in the hedgerow seed bank than within the woodland. A significant positive correlation was found with abundance within the seed bank and distance along the woodland and hedgerow transects. Results of a Wilcoxon test for matched pairs showed no significant difference between the abundance of individuals in seed banks when the two sides of the hedgerow were compared. Also, no correlation was found between abundance and distance along the two aspects of the hedgerow. In the vegetation survey, only one quadrat was found to contain *Stachys sylvatica*; this was located on the south-western side of the hedgerow. More quadrats were found to contain this species in the vegetation on the north-eastern side of the hedge. Although individuals located in the seed bank were concentrated around the locations where plants were present in the vegetation, a seed shadow is seen to extend towards and into the woodland edge, particularly on the north-eastern side of the hedgerow.

Stellaria media is a sprawling, much branched, annual herb (Stace 1991). Although primarily an arable weed it also occurs in a wide range of habitats typically associated with disturbance and high soil fertility (Grime *et al.* 1988). The abundance of *Stellaria media* in the seed bank was found to decline along the hedgerow, towards the woodland edge. This results in a highly

significant correlation with distance (Table 4.11). One individual was located in a sample taken 20-25m into the woodland. Comparison of the number of individuals, within the seed bank on the two sides of the hedgerow revealed no significant difference (Table 4.12). The majority of the individuals found in the seed bank were located further away from the woodland. A significant correlation was also between the abundance of this species in the seed bank and the distance away from the woodland, on both sides of the hedge (Table 4.13). The reduced abundance in the seed bank towards the woodland suggests intolerance to shading could contribute to the pattern of spatial distribution of this species.

Only one hedgerow quadrat was found to contain the herbaceous plant species *Tripleurospermum inodorum* in the vegetation survey; this was 25-20m away from the woodland edge (Quadrat 7), on the south-western side of the hedgerow (Figure 4.11c). This species was absent from the woodland sites. *Tripleurospermum inodorum* was significantly more abundant in the seed bank of the south-western side of the hedgerow than the north-eastern side (Figure 4.12c). There was no correlation between the number of individuals in the seed bank and distance along the combined woodland hedgerow transect, or between the abundance and distance along either side of the hedgerow.

Urtica dioica occurred in the woodland and hedgerow in both the vegetation survey and seed bank study. Stace (1991) describes this species as being typically associated with woodlands, fens and fertile cultivated ground. No significant association was found between the abundance of individuals found within the seed bank and distance for either side of the hedgerow or along the woodland and hedgerow transects combined. A significant difference was found between the abundance of *Urtica dioica* in the seed bank on opposing sides of the hedgerow, more individuals being identified on the south-western side. These results are consistent with the higher frequency of plants found on this side of the hedgerow during the vegetation survey.

Figure 4.11c Spatial distribution of the herbaceous plant species located in both the vegetation and seed bank: continued

NB: Scales on Y axes varying according to abundance of each species

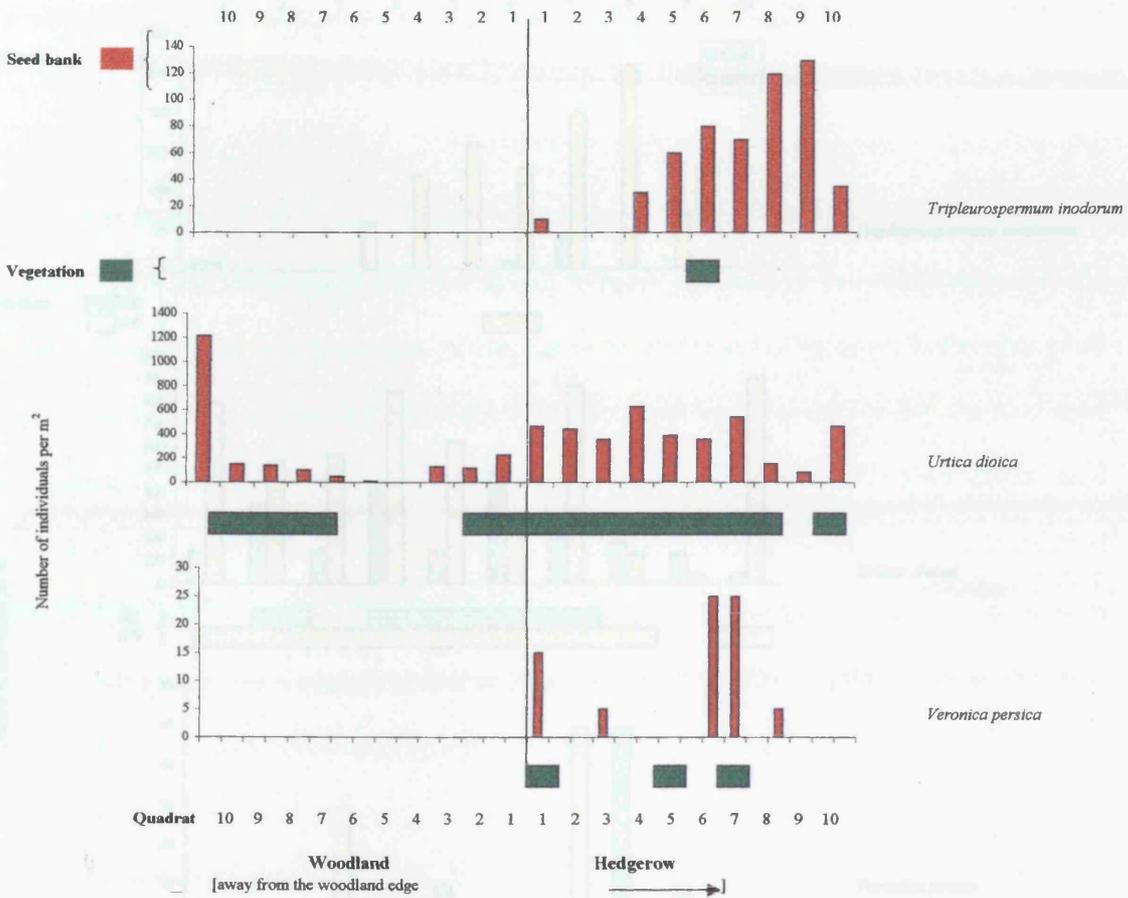
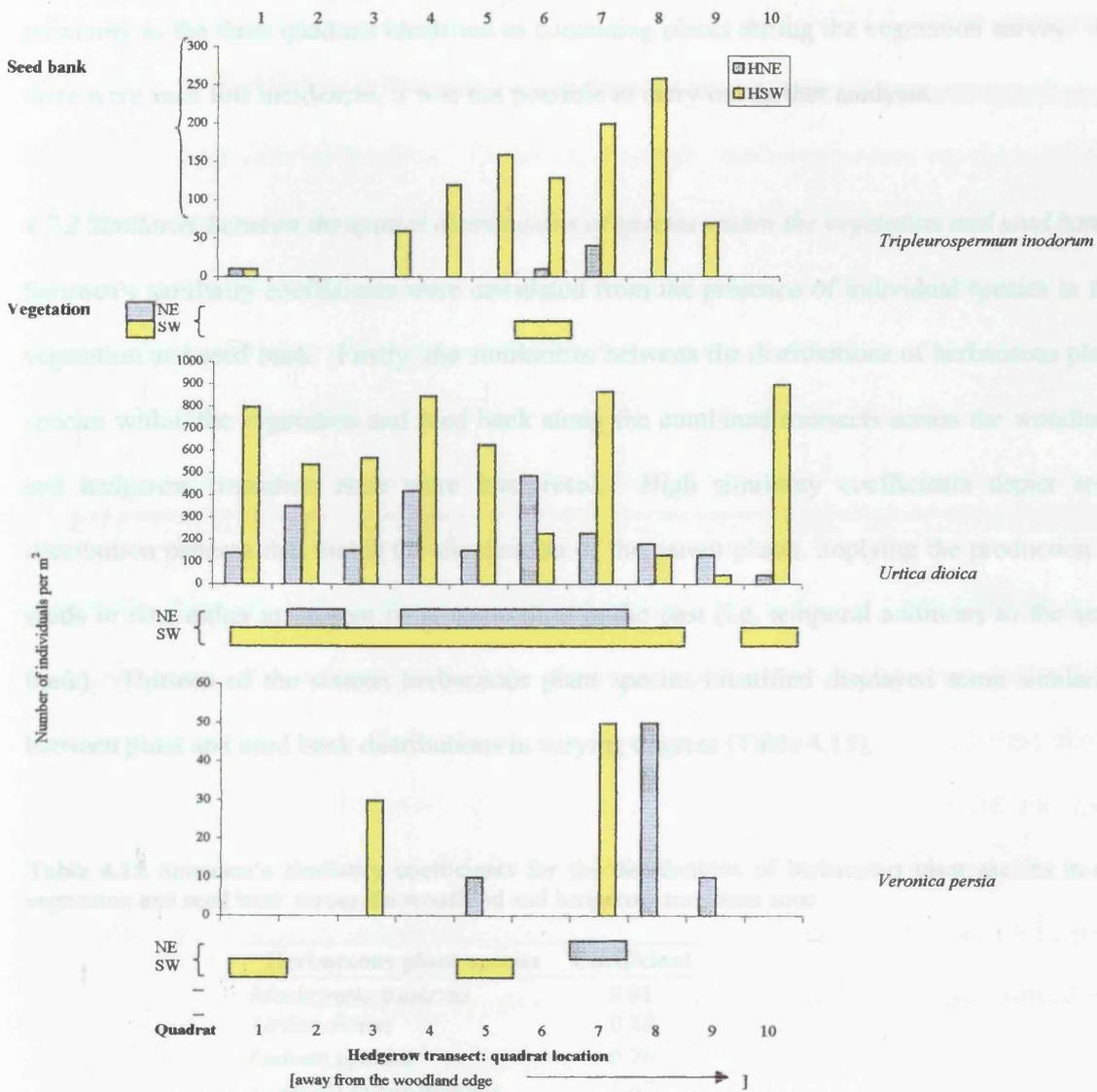


Figure 4.12c Spatial distribution of the herbaceous plant species located in both the vegetation and seed bank with hedgerow aspect: continued
 NB: Scales on Y axes varying according to abundance of each species



Veronica persica, a naturalised non-native species, (Stace 1991) was absent in the woodland seed bank and vegetation surveys. Those individuals found in the seed bank study were in close proximity to the three quadrats identified as containing plants during the vegetation survey. As there were such few incidences, it was not possible to carry out further analysis.

4.7.2 Similarity between the spatial distributions of species within the vegetation and seed bank.

Sørensen's similarity coefficients were calculated from the presence of individual species in the vegetation and seed bank. Firstly, the similarities between the distributions of herbaceous plant species within the vegetation and seed bank along the combined transects across the woodland and hedgerow transition zone were interpreted. High similarity coefficients depict seed distribution patterns that match the distribution of the parent plants, implying the production of seeds *in situ*, either at present or at some time in the past (i.e. temporal additions to the seed bank). Thirteen of the sixteen herbaceous plant species identified displayed some similarity between plant and seed bank distributions in varying degrees (Table 4.15).

Table 4.15 Sørensen's similarity coefficients for the distributions of herbaceous plant species in the vegetation and seed bank across the woodland and hedgerow transition zone

Herbaceous plant species	Coefficient
<i>Moehringia trinervia</i>	0.91
<i>Urtica dioica</i>	0.88
<i>Galium aparine</i>	0.76
<i>Capsella bursa-pastoris</i>	0.67
<i>Stellaria media</i>	0.63
<i>Myosotis arvensis</i>	0.62
<i>Bryonia dioica</i>	0.57
<i>Rumex obtusifolius</i>	0.50
<i>Veronica persica</i>	0.50
<i>Stachys sylvatica</i>	0.47
<i>Glechoma hederacea</i>	0.40
<i>Tripleurospermum inodorum</i>	0.20
<i>Cirsium arvense</i>	0.17
<i>Anthriscus sylvestris</i>	0.00
<i>Arctium lappa</i>	0.00
<i>Potentilla sterilis</i>	0.00

Nine species had 50% similarity or more. *Moehringia trinervia* and *Urtica dioica* had the highest coefficient values (0.91 and 0.88), indicating a high chance of finding seeds in the soil

near to the parent plants. Seven other species had coefficient values of 0.50 (*Galium aparine*, *Capsella bursa pastoris*, *Stellaria media*, *Myosotis arvensis*, *Bryonia dioica*, *Rumex obtusifolius*, and *Veronica persica*). Four species (*Moehringia trinervia*, *Galium aparine*, *Stellaria media* and *Myosotis arvensis*) were depicted in Appendix 4.2 as having short – intermediate seed bank persistency. Therefore, the high coefficient values for these species suggest that seed production and vitality of these species was sufficient to maintain individuals above and below the ground. Species with more persistent seed banks (*Capsella bursa pastoris*, *Rumex obtusifolius*) may reflect seed production over longer periods of time.

The previous section showed that the spatial distribution of some species was not always closely associated with seeds found within the seed bank. Species with low similarity values may indicate species with a) low vitality or b) high powers of seed dispersal. *Stachys sylvatica*, *Glechoma hederacea*, *Tripleurospermum inodorum* and *Cirsium arvense* had values below 0.50, indicating a reduced chance of finding seeds within the seed bank near to the parent plants. Both *Tripleurospermum inodorum* and *Cirsium arvense* produce seeds adapted for wind dispersal and are able to be retained within the seed bank. *Stachys sylvatica* and *Glechoma hederacea* are dispersed by animal vectors and have short to intermediate term seed persistency. Low similarity coefficient values for spatial distribution of these species may reflect the efficiency of dispersing away from the parent plant.

Anthriscus sylvestris, *Articum lappa* and *Potentilla sterilis* were found to have a percentage similarity coefficient of zero, as no corresponding locations were found in the vegetation and seed bank. The seeds of *Articum lappa* are able to persist within the seed bank and are also dispersed by animal vectors. The dispersal mode of *Anthriscus sylvestris*, as mentioned previously, is unknown, but is thought to disperse by wind-propulsion. This species is retained within the seed bank through short to intermediate periods and an explanation for the disparate distributions of the seeds within soil samples and adult plants is not apparent. *Potentilla sterilis* was only found on two occasions, once in the seed bank and the other in the vegetation. It is

vegetation. It is concluded therefore, within the location of study, that this species was displaying limited vitality, although it could persist within the plant community through vegetative reproduction, if conditions are unfavourable to seed production.

These results suggest that the use of similarity indices can aid interpretation of spatial data, indicating the relative positioning of plants in vegetation and distribution of seeds. This method may also indicate the efficient temporal and spatial dispersal strategies of plant species present within a plant community. In this instance, arrivals of long distance dispersers and remnant unproductive species have been identified.

4.8 Herbaceous plant species found in the woodland and hedgerow vegetation only.

Thirteen herbaceous plant species were identified during the vegetation survey but did not appear to be present in the seed bank (Table 4.16).

Table 4.16 Species present in the vegetation survey but absent in the seed bank

Species	Family
1. <i>Aegopodium podagraria</i>	APIACEAE
2. <i>Alliaria petiolata</i>	BRASSICACEAE
3. <i>Arum maculatum</i>	ARACEAE
4. <i>Circaea lutetiana</i>	ONAGRACEAE
5. <i>Galium mollugo</i>	RUBIACEAE
6. <i>Geranium molle</i>	GERANIACEAE
7. <i>Geum urbanum.</i>	ROSACEAE
8. <i>Hedera helix</i>	ARALIACEAE
9. <i>Heracleum sphondylium</i>	APIACEAE
10. <i>Hyacinthoides non-scripta</i>	LILIACEAE
11. <i>Mercurialis perennis</i>	EUPHORBIACEAE
12. <i>Primula vulgaris</i>	PRIMULACEAE
13. <i>Viola rivinianna</i>	VIOLACEAE

This could be due to one or a combination of the following factors:

1. germinating conditions within the greenhouse were not suitable for species with particular requirements (period of chilling, scarring, optimum temperatures etc.);
2. time of sampling meant that some species were missed (previous season's seeds have either germinated or failed to survive within the seed bank);

3. parent plants are at the limits of their ecological optimum and are not reproducing by seed.

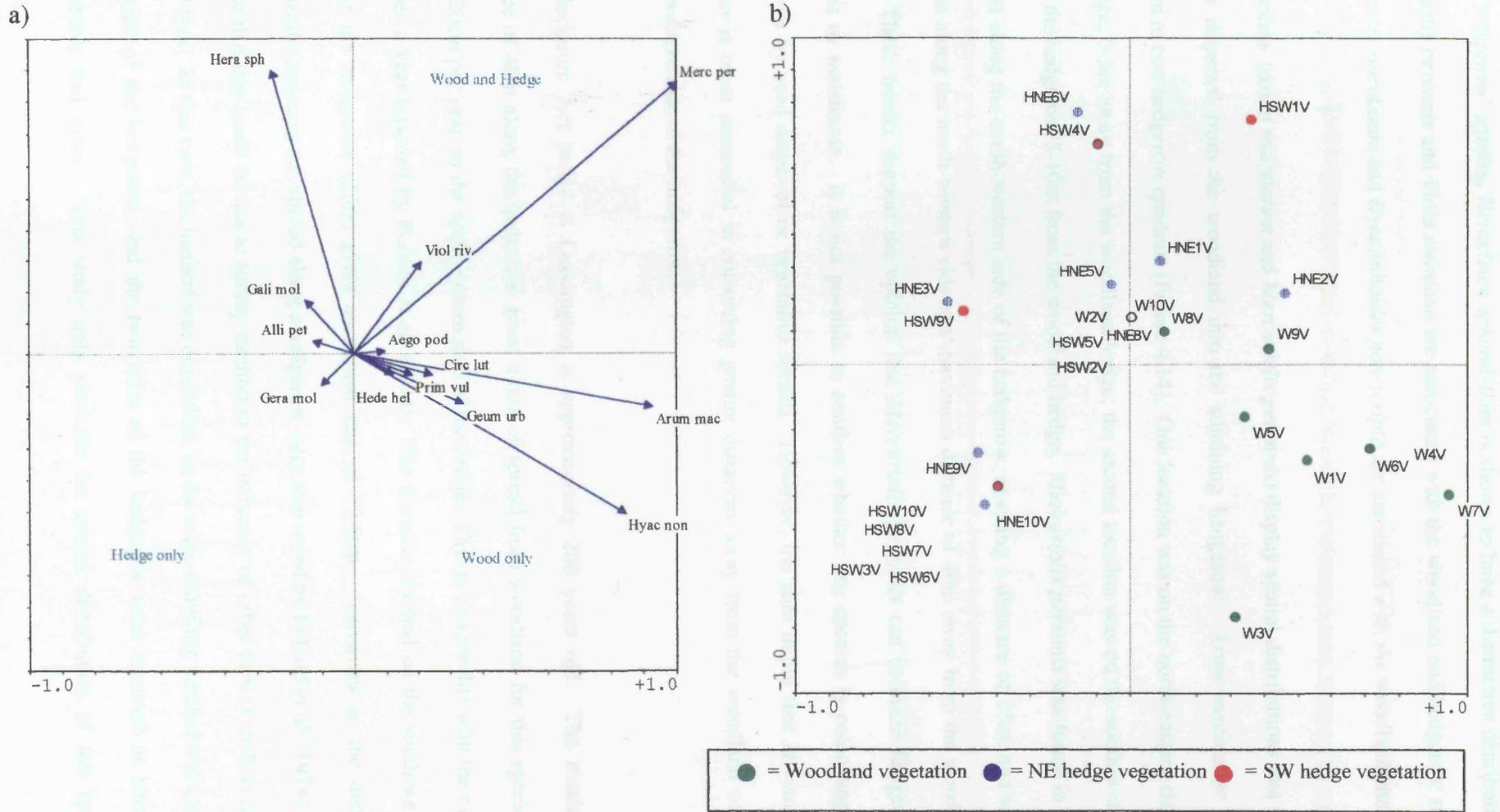
Of the thirteen species present as adults in the vegetation, but were absent within the seed bank, eleven species were noted as having transient seed-banks. The seeds of these species are not viable for long periods within the soil. Transient seeds germinate soon after release or survive in the soil through the winter and germinate in the following spring. These results suggest that the seed bank study did meet the germination requirements of most species within the study. If this was not the case, many more species in the vegetation would have been recorded as absent from the seed bank study, and those species would have varying persistency within the soil. However, seeds of *Primula vulgaris* were noted as having short-to-long term persistence within seed-banks and were absent in the seed bank study, possibly either because specialised germination requirements were not met, or because too few were present in the seed bank due to low productivity in the section of the woodland sampled.

The occurrences of the herbaceous plant species found in the vegetation only were ordinated with sample site locations using Principal Component Analysis (Figure 4.13 and Table 4.17). Twenty nine percent of the variance was explained by the first horizontal axis. Those species located in the hedgerow transects are on the left side, and those found only in the woodland and woodland and hedgerow sample sites are on the right hand side. The vertical axis separates the species found in both hedgerow and woodland from those in the woodland only (20% of the explained variance, 73% variance explained by the first four principal components).

Table 4.17 Results of the PCA for herbaceous plant species found in the vegetation only

PC: vegetation and seed bank	% variance explained	Culmulative % variance
PC1	29	29
PC2	20	49
PC3	13	62
PC4	11	73
Unexplained	27	100
Total sum of squares	37.34	
Total standard deviation	0.30	
Collinearity condition value	0.98	

Figure 4.13 PCA ordination of herbaceous plant species present in the vegetation only

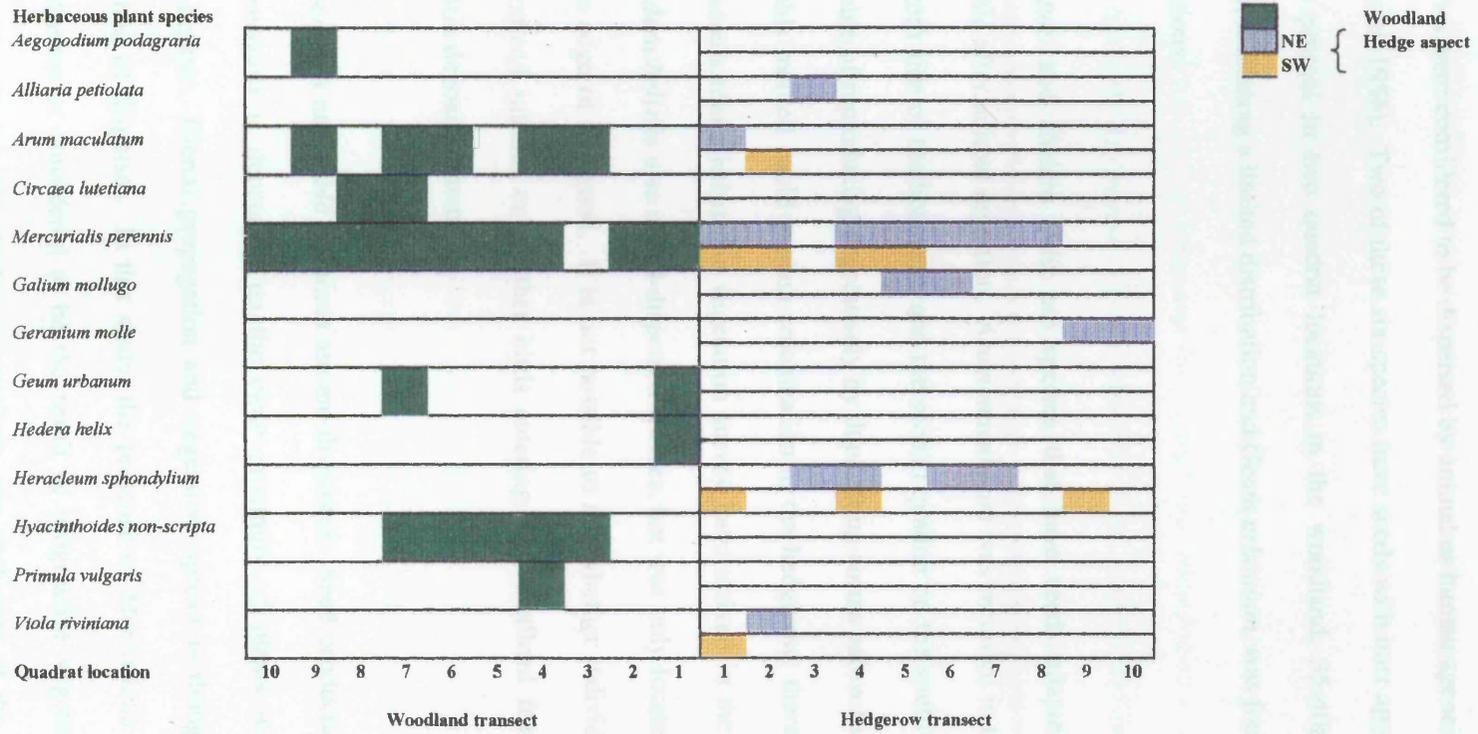


Of the 'hedgerow' species, *Heracleum sphondylium* is shown to have a distinctive distribution. *Mercurialis perennis* and *Viola riviniana* are associated with the woodland and hedgerow sites, while *Arum maculatum* and *Hyacinthoides non-scripta* are associated with the woodland sites.

Two species (*Arum maculatum* and *Mercurialis perennis*) display spatial distributions that may indicate dispersal from the woodland into the adjoining hedgerow. *Arum maculatum* was recorded in two hedgerow quadrats (Figure 4.14). One location was on the north-eastern side of the hedge, 0-5m away from the woodland hedge; the second location was on the south-western side of the hedgerow 5-10m from the woodland hedge. *Mercurialis perennis* was found in four quadrats along the south-western side of the hedgerow, reaching a distance of 25m, and seven quadrats along the north-western side to a maximum distance of 40m away from the woodland edge. These results support the opinion that *Mercurialis perennis* can colonize hedgerows adjacent to woodlands. It is not possible to confirm whether this species is colonizing the hedgerow by seed dispersal or vegetative spread. However, the data imply that *Mercurialis perennis* is more successful in colonizing greater distances away from the woodland on the north-western side of the hedgerow.

The Enclosure Act hedge at Geddington is approximately 200 years old. The maximum distance of 40m along the hedgerow gives a rate of spread from woodland for this species of about 20cm per year on the north-eastern side of the hedge. This is comparable with the rate of 8 inches a year reported by Pollard *et al.* (1974). The distance reached on the south-western side of the hedgerow (25m) gives an annual rate of 12.5cm. Variations in the distance *Mercurialis perennis* can spread along a hedgerow were also noted by Pollard *et al.* (1974), who suggest that this could be due to survey method or the influence of other factors such as aspect or soil type. In this case, the method was controlled, as the same sampling method was used on each side of the hedgerow, and the two sides of the hedgerow were assumed as being of comparable soil types. This study only provides the spatial distribution of this species

Figure 4.14 The spatial distribution of herbaceous plant species located in the vegetation survey only



from one transect. However, the results from this and the previous chapter suggest that aspect may influence the rate of spread of *Mercurialis perennis*.

Six of the species were considered to be dispersed by animal or human agencies (Hodgson *et al.* 1995, Grime *et al.* 1988). Two of these six species have seeds with burr appendages. *Circaea lutetiana*, was present in two quadrat locations in the woodland, 35-40m away from the woodland edge, indicating a limited distribution and *Geum urbanum*, was found in two separate woodland locations.

Arum maculatum and *Hedera helix* are species that have seeds adapted to dispersal by remaining viable after animal ingestion. *Arum maculatum* was recorded in the first quadrat on the north-western side of the hedgerow and the second quadrat on the south-eastern side. This species is capable of reproducing vegetatively by duplicating corms below the soil surface. It is unlikely that this method could explain colonization in the hedgerow; therefore it is proposed that the individuals identified in the vegetation survey have arrived in the hedgerow by bird dispersal. *Hedera helix* is also a bird-dispersed species, but was only located in one woodland quadrat, at the edge of the wood. It is not possible to say whether individuals had dispersed from the woodland interior or whether birds entering the woodland from the surrounding landscape matrix deposited them.

Mercurialis perennis and *Viola riviniana* are ant-dispersed. Seed production of the dioecious *Mercurialis perennis* is dependent on the close proximity of plants with separate sexual reproductive organs. Clonal propagation and vegetative spread is thought to be the more common method of dispersal. In this study, the presence of *Mercurialis perennis* along the adjoining hedgerow is considered to be the result of progressive vegetative spread. *Viola riviniana* was identified in two hedgerow quadrats, one each side of the hedge immediately adjacent to the woodland edge, but was not found within the woodland.

Four species (*Alliaria petiolata*, *Heracleum sphondylium*, *Hyacinthoides non-scripta* and *Primula vulgaris*) are noted as having seeds released from fruit capsules and are further dispersed by wind. *Alliaria petiolata* was recorded in only one hedgerow quadrat and was absent within the seed bank. These results indicate that this species had limited seed production, seed dispersal, and/or colonization within the hedgerow. *Heracleum sphondylium* was located in six places, three quadrats on each side of the hedgerow. This species was found nearer to the woodland edge on the south-western side of the hedgerow. Although successful in the hedgerow habitat, there was no indication that *Heracleum sphondylium* is dispersing into the woodland. *Hyacinthoides non-scripta* occurred in five consecutive quadrats within the woodland vegetation. It was absent in the vegetation near the woodland edge and the adjoining hedgerow. This species has the capacity to maintain a population by reproducing vegetatively. However, in this study it is not possible to verify whether seed production or vegetative propagation was maintaining the population. It would be necessary to monitor the population over a period of time to determine reproductive and colonization success of this species. As mentioned previously, *Primula vulgaris* was found isolated in one woodland quadrat. It is suggested that this species is struggling to maintain a presence, neither spreading vegetatively nor via seed dispersal in this particular woodland location.

Two species were autochorous: *Geranium molle* was found only on the north-eastern side of the hedgerow, 40-50m away from the woodland edge but *Aegopodium podagraria* was also found in only one location, 40-45m into the woodland. The adaptive mode of seed dispersal for *Galium mollugo* was not established from the literature research. This species was present in the north-western side of the hedgerow, 20-30m away from the woodland edge.

4.9 Similarity between herbaceous species distribution in the woodland and hedgerow transects.

4.9.1 Comparison across the woodland/hedgerow transition zone

A comparison was made between the distribution of herbaceous plant species distribution across the woodland and hedgerow transition. This was achieved by comparing the presence of each species in the first woodland quadrat with the combined first hedgerow quadrats, the second woodland quadrats with the second hedgerow quadrats, and so on, using the Sørensen's similarity coefficient. A high coefficient would indicate continuity in plant distribution across the environmental gradient, while a low value would indicate discontinuity. Similarities were examined for the distribution of all the herbaceous plant species within the seed bank and in the vegetation in each case (Table 4.18). Twelve herbaceous plant species were found to display a degree of continuity across the woodland/hedgerow transition. For four species, this distribution was found within the seed bank and vegetation. *Urtica dioica* displayed the highest similarity coefficients.

Table 4.18 Sørensen's similarity coefficients of herbaceous plant species across the woodland-hedgerow transition (comparison between species location along the transects)

Herbaceous plant species	Similarity Coefficients	
	Seed bank	Vegetation
<i>Urtica dioica</i>	0.95	0.75
<i>Galium aparine</i>	0.55	0.89
<i>Rumex obtusifolius</i>	0.36	0.6
<i>Moehringia trinervia</i>	0.40	0.33
<i>Stachys sylvatica</i>	0.33	0
<i>Circebita macrophylla</i>	0.57	-
<i>Chenopodium polyspermum</i>	0.44	-
<i>Epilobium spp.</i>	0.36	-
<i>Capsella pastoris-bursa</i>	0.33	-
<i>Cirsium arvense</i>	0.25	-
<i>Stellaria media</i>	0.22	-
<i>Mercurialis perennis</i>	-	0.88

The seed banks of *Galium aparine* and *Rumex obtusifolius* were less widely distributed than the adult plants in the vegetation across the woodland/hedgerow transition. The degree of similarity in the distribution of *Moehringia trinervia* in both the vegetation and seed bank reflects the

positions in which individuals were found: across the woodland edge and immediately into the hedgerow. *Stachys sylvatica* was found in both the seed bank and the vegetation, but this analysis suggests that the distributions of seeds and adult plants were not highly associated with each other across the woodland/hedgerow transition.

Similarity coefficients of six species were restricted to the distribution of seeds within the seed bank. *Circebita macrophylla* and *Chenopodium polyspermum* were found to have similarity coefficients of 0.57 and 0.44 respectively, reflecting the distribution of these species across the transition zone. *Stellaria media* showed the lowest similarity coefficient (0.22) in distributions between the woodland and hedgerow transects. The woodland herbaceous species, *Mercurialis perennis* was located in the vegetation only and had a similarity coefficient of 0.88, depicting a high continuity across the woodland-hedgerow transition.

4.9.2 Comparison between hedgerow aspect

In the sections 4.6-8, the distribution of some of the herbaceous plant species were different in the two hedgerow transects. A Sørensen's similarity coefficient was calculated for each species on each side of the hedgerow. Quadrats on the north-eastern side of the hedge were then compared with the equivalent quadrat on the south-western side. Species with coefficient values of 1.00 is equivalent to identical distributions on each side of the hedgerow irrespective of aspect; lower coefficient values depict increasing dissimilarity between the two hedgerow aspects (Table 4.19).

In total, seventeen herbaceous plant species were identified in each hedgerow transect. Ten species were present in the seed bank and vegetation. Similarity coefficients for *Urtica dioica* and *Galium aparine* indicate that the distribution of these species was not influenced by hedgerow aspect. The seed bank of *Rumex obtusifolius*, *Stellaria media* and *Stachys sylvatica* showed a greater similarity between the hedgerow aspects than the presence of the adult plants. The species *Capsella bursa-pastoris*, *Cirsium arvense*, *Tripleurospermum inodorum*, *Byronia*

dioica and *Myosotis arvensis* each have a degree of similarity in distribution in the seed bank, but adult plants, present in the vegetation were not found to have this association. The distribution of *Moehringia trinervia* was found to be dissimilar in the seed bank, but individuals in the vegetation corresponded exactly on each side of the hedgerow.

Table 4.19 Sørensen's similarity coefficients of herbaceous plant species: between hedgerow aspects

Herbaceous plant species	Similarity Coefficients	
	Seed bank	Vegetation
<i>Urtica dioica</i>	1.00	0.71
<i>Galium aparine</i>	0.93	1.00
<i>Rumex obtusifolius</i>	0.62	0.50
<i>Stellaria media</i>	0.86	0.44
<i>Stachys sylvatica</i>	0.75	0.40
<i>Capsella pastoris-bursa</i>	1.00	0
<i>Cirsium arvense</i>	0.73	0
<i>Tripleurospermum inodorum</i>	0.60	0
<i>Bryonia dioica</i>	0.50	0
<i>Myosotis arvensis</i>	0.36	0
<i>Moehringia trinervia</i>	0	1.00
<i>Veronica chamaedrys</i>	0.88	-
<i>Circebita macrophylla</i>	0.62	-
<i>Epilobium spp.</i>	0.40	-
<i>Chenopodium polyspermum</i>	0.29	-
<i>Mercurialis perennis</i>	-	0.73
<i>Heracleum sphondylium</i>	-	0.29

Four species were absent in the hedgerow vegetation. Of these species, *Veronica chamaedrys* and *Circebita macrophylla* were found to have the highest similarity coefficient values, indicating a similar distribution each side of the hedgerow. *Mercurialis perennis* and *Heracleum sphondylium* were absent in the seed bank study. *Mercurialis perennis* was found to have a similarity coefficient value of 0.73, whereas *Heracleum sphondylium* was found to have a lower value of 0.29.

4.10 Summary of results

4.10.1 Herbaceous plant species in the seed bank only

Among the herbaceous plant species found only in the seed bank, no evidence was found to

demonstrate dispersal of “woodland” herbaceous plant species from the woodland into the hedgerow seed bank. Seeds of each of the three herbaceous plants species restricted to the woodland seed bank are released from capsules and dispersed by the wind (Table 4.20). Within the woodland and hedgerow seed banks, species were mainly wind-dispersed, although *Plantago major* produces seeds that become mucilaginous when wet and are then carried in mud on the feet of humans, birds and mammals or on agricultural machinery.

Seven of the nine species are able to persist within the seed bank indeterminately. Species that were recorded in the seed bank may possibly reflect past disturbances within the study site, by lying dormant until future unpredictable disturbance events occur. Alternatively, presence in the seed bank could be the result of seed influx from surrounding disturbed habitats. This study suggests that seeds of disturbed habitats are dispersing into the woodland from surrounding agricultural landscape. Nevertheless, the results do not show whether species found in the seed bank are distributed evenly across the landscape or concentrated within the hedgerow. It is feasible that wind currents could carry seed into the hedgerow, where they are trapped in existing vegetation. All of these species can be called opportunistic species. However, this strategy does not guarantee colonization success either in the woodland or hedgerow habitats.

4.10.2 Herbaceous plant species located in the vegetation and seed bank

Species present in the both the seed bank and vegetation are representative of species maintaining populations both above and below ground (Table 4.21). Seed bank and dispersal strategies were investigated to examine relationships with spatial distribution and colonization potential. Eight species were regarded as being able to produce seeds that are retained in the seed bank for short to intermediate terms. Seven species are able to persist in the seed bank. *Galium aparine* was the only species positively identified as having a transient seed bank. This species could be considered fully reproductive if there were a high abundance of individuals in both the vegetation and seed bank, reflecting most recent seed input. In this study, seeds of this

Table 4.20 Summary of results: herbaceous plant species located in the seed bank only

Herbaceous plant species	Common Habitat	Dispersal mode	Vegetative spread	Seed bank type	r_s : Distance wood/hedge	Hedge Aspect abundance
Woodland						
<i>Hypericum</i> spp.	Disturbed	Wind: capsule	Rhizomes	2-3	-	-
<i>Scrophularia auriculata</i>	Riverine	Wind: capsule	None	2-3	-	-
<i>Scrophularia nodosa</i>	Scrub	Wind: capsule	None	2-3	-	-
Hedgerow						
<i>Gnaphalium uliginosum</i>	Mire	Wind: plume	None	2-3	-	-
<i>Veronica chamaedrys</i>	Pasture	Wind: capsule	Stolons	1-2	-	-
Woodland & hedgerow						
<i>Chenopodium polyspermum</i>	Disturbed	Autochore?	None	2-3	-	-
<i>Cicerbita macrophylla</i>	Disturbed	Wind: plume?	None?	2-3?	0.84, $p < 0.01$	$P < 0.05$: SW
<i>Epilobium</i> spp.	Disturbed/ Mire	Wind: plume	Stolons	2	-	-
<i>Plantago major</i>	Path	Animal: muc	None	2-3	-	-

Table 4.21 Summary of herbaceous plants species found in the seed bank study and vegetation survey

Species in seed bank	Species in vegetation	Common habitat	Dispersal mode	Vegetative spread	Seed bank types	r_s : Distance wood/hedge	Hedge Aspect abundance	r_s : Distance Hedge Aspect
<i>Glechoma hederacea</i>	Woodland	Hedge	?	Stolons	1-2	-	-	-
<i>Potentilla sterilis</i>	Woodland	Pasture	?	Stolons	1-2	-	-	-
<i>Galium aparine</i>	H & W	Hedge	Animal-burr	None	1	-	-	-
<i>Moehringia trinervia</i>	H & W	Wood	Animal-ant	None	1-2	-	-	-
<i>Rumex obtusifolius</i>	H & W	Disturbed	Animal-bur?	Limited	2-3	-	-	-
<i>Stachys sylvatica</i>	H & W	Hedge	Animal-bur?	Rhizomes	1-2	0.66, $p < 0.05$	-	-
<i>Urtica dioica</i>	H & W	Disturbed	Animal?	Rhizome	2	-	$P < 0.05$: SW	-
<i>Anthriscus sylvestris</i>	Hedgerow	Road-verge	?	None	1-2	-	-	-
<i>Bryonia dioica</i>	Hedgerow	Hedge?	Animal-ingested?	?	?	-	-	-
<i>Myosotis arvensis</i>	Hedgerow	Arable	Animal?	None	2	-	-	-
<i>Tripleurospermum inodorum</i>	Hedgerow	Arable	Animal	None	3	-	$P < 0.02$: SW	-
<i>Veronica persica</i>	Hedgerow	Arable	Animal-ant	Limited	2-3	-	-	-
<i>Articum lappa</i>	Hedgerow	River bank	Animal-burr	None	3	-	-	-
<i>Capsella bursa-pastoris</i>	Hedgerow	Arable	Animal-mucilaginous	None	3	0.81, $p < 0.01$	$P < 0.02$: SW	0.83, $p < 0.01$
<i>Cirsium arvense</i>	Hedgerow	Disturbed	Wind plumed	Roots	1-3	-	-	-
<i>Stellaria media</i>	Hedgerow	Arable	Animal-ingested?	Limited	2-3	0.90, $p < 0.01$	-	SW = 0.86 $p < 0.05$ NE = 0.89 $p < 0.05$

species found within the seed bank varied along the environmental gradient crossing the woodland and hedgerow transition.

Two species were restricted to the woodland vegetation and seed bank (*Potentilla sterilis* and *Glechoma hederacea*). Each is regarded as transient or short-term persistent within the seed bank. Both are able to produce creeping stolons. Nine herbaceous plants species were located in both the woodland and hedgerow seed banks and vegetation. All except one were classified as being dispersed by animal or human agencies. *Galium aparine* was found widely distributed among the vegetation within the woodland and hedgerow, although fewer seeds were found within the seed bank at the woodland edge. *Moehringia trinervia* was limited within the seed bank to the immediate vicinity of the plants found in the vegetation. Four species (*Capsella bursa-pastoris*, *Galium aparine*, *Stachys sylvatica*, *Stellaria media*) displayed a significant correlation between abundance and distance along the woodland and hedgerow transect; each decreasing in abundance along the hedgerow towards the woodland.

Five species (*Anthriscus sylvestris*, *Bryonia dioica*, *Myosotis arvensis*, *Tripleurospermum inodorum* and *Veronica perscia*) were restricted to hedgerow seed bank and vegetation. With the exception of *Anthriscus sylvestris*, all these species are dispersed by animal or human agencies and were found to have extended seed shadows. *Tripleurospermum inodorum* was found to be significantly more abundant on the south-western side of the hedgerow.

The herbaceous plant species: *Capsella bursa-pastoris*, *Galium aparine*, *Stellaria media* and *Urtica dioica*, demonstrated a significant difference in abundance with hedgerow aspect. Each of these species was more abundant on the south-western side of the hedgerow. Two of these species (*Capsella bursa-pastoris* and *Stellaria media*) also displayed a significant correlation with distance.

In total, ten species were shown to display extended seed shadows (Table 4.22).

Table 4.22 Number of species with extended or limited seed shadows and dispersal strategies

Seed shadow Dispersal mode	Limited	Extended	Correlation with distance
Animal-adhesive	1		
Animal-burr		3	2
Animal-ant-	2	1	
Animal-igested	1	1	1
Animal?		2	1
Wind-plumed		1	
Unknown	2	1	
Total	6	10	4

Eight of these were species with seeds that are animal-dispersed, one is wind-dispersed and another species has an unknown dispersal mode. Within this group, three species with seeds disperse by attachment of burred appendages; the abundance of two of these significantly correlated with distance. Seed shadows were not found to extend from the woodland vegetation into the adjoining hedgerow, possibly indicating that no detectable dispersal of woodland plants into the adjoining hedge existed.

Extended seed shadows were found within the hedgerow and into the woodland edge. Four species (*Arctium lappa*, *Capsella bursa-pastoris*, *Cirsium arvense*, *Stellaria media*) were present in both the woodland and hedgerow seed banks but were absent in the woodland vegetation. These species show an ability to disperse seeds into the woodland, but may have either the inability or opportunity to establish within the woodland. These results indicate that some movement of seeds had occurred within the woodland-hedgerow transition zone, by both wind and animal dispersal vectors.

4.10.3 Herbaceous plant species located in the vegetation only.

The majority (85%) of species found only within the vegetation survey were species producing seeds that are transient within the seed bank. Therefore, colonization success of these species is dependent upon spatial processes, rather than temporal seed bank strategies. Within this group, dispersal strategies were less defined: six species were considered as being dispersed by animal

or human vectors and four are wind dispersed. The largest percentage of species represented the woodland habitat type, along with species associated with disturbed ground, river and mire. Two species gave indication of dispersal from the woodland into the adjoining hedgerow (*Mercurialis perennis* and *Arum maculatum*). *Arum maculatum* was found just outside the woodland edge. For *Mercurialis perennis*, colonization was found to occur along the hedgerow at a maximum distance of 40m (20cm per annum) away from the woodland edge, on the north-eastern side of the hedgerow, and 25m (12.5cm per annum) away from the woodland edge, on the south-western side of the hedgerow. Each of these species is animal-dispersed and is capable of vegetative propagation.

Chapter 5: Immigration, colonization and establishment of woody plant species in three Experimental Hawthorn Hedgerows under three differing management regimes.

5.1 Introduction

The investigation in Chapter Three suggests that some woody plant species were dispersing from woodland into adjoining Enclosure hedgerows. However, the spatial patterns of shrub species colonizing the adjoining hedgerows did not provide conclusive evidence that immigration was occurring directly from the neighbouring woodland. This could have been because dispersal of shrub species, in particular, may occur at a larger scale than the project design could detect. As indicated in Chapter Two, spatial and temporal processes influencing the distribution of woody plant species immigrating, colonizing and establishing in hedgerows needs further examination.

The majority of shrub species in Britain bear fruits, which are attractive to birds as a potential food source (Stiles 1980). In turn, birds disperse seeds of many woody plant species (Snow and Snow 1988). A positive feedback system occurs, in which the colonization of woody plant species and bird behaviour is interdependent (McDonnell and Stiles 1983, Forman and Baudry 1984). The availability of bird dispersers, the proximity of seed sources, and bird behaviour all contribute to successful immigration into hedgerows. Mammals may also play a part in the dissemination of fruits and seeds, but their contribution is not examined in this thesis.

The effect of hedgerow management on the success of woody species colonizing and establishing in hedgerows has also to be fully investigated. Variation in the physical structure of hedgerows that may result in conditions that support colonization by woody plant species (facilitation), may be detrimental to their survival and establishment (inhibition) or have little or no effect (tolerance).

5.2 Study site

The Experimental Hawthorn Hedgerows (EHH) examined in this study are located at the Institute of Terrestrial Ecology (ITE) (now Centre for Ecology and Hydrology CEH) Experimental Station, Monks Wood, Abbots Ripton, Cambridgeshire (Figure 5.1) (OS TF35116). The EHH at Monks Wood were part of a project, directed by Dr Norman Moore, that aimed to evaluate the effects of various types of management on hedgerow structure and composition, and to assess the colonization of plants and invertebrates (Sparks pers. com. 1997).

Monks Wood National Nature Reserve (NNR) lies on the north-western edge of the Hawthorn Hedge Field (HHF) (Figure 5.2). The south-eastern boundary of the field is believed to have originated in the eleventh century. Historical evidence revealed that the Countess Judith, niece of William the Conqueror, ordered the formation of this boundary (Pollard *et al.* 1974). “Judith’s Hedge”, as it is now known, contains a diverse woodland relict community. However, a section of this boundary seems to be of more recent origin (post-Enclosure period 1791-1835) (Pollard *et al.* 1974). The boundary running parallel down the western side of the Hawthorn Hedge Field (Saul’s Lane) is part of a green lane that enters the NNR. The eastern boundary of the field is of uncertain origin. It consists of planted trees and shrubs and a fenceline that borders residential buildings within the Experimental Station which were built during the 1960s. Further historical information for the HHF is given in Appendix 5.1.

The EHH were set out in March 1962. Saplings of *Crataegus monogyna* were planted in double rows (18 inches (45.7cm) apart) at 50yd (45.7m) intervals, starting 50yds from Saul’s Lane and 30yds (27.4m) from Monks Wood NNR (for planting details see Appendix 5.2). Eight hedgerows were planted; a ninth hedgerow consisting mainly of leftover saplings was considered too short to be incorporated into the experimental design (see Appendix 5.3).

Figure 5.1 Location of Institute of Terrestrial Ecology Research Station, Monks Wood, Abbots Ripton, near Huntingdon, Cambridgeshire. Inset: map displaying the location of Cambridgeshire in the East of England.

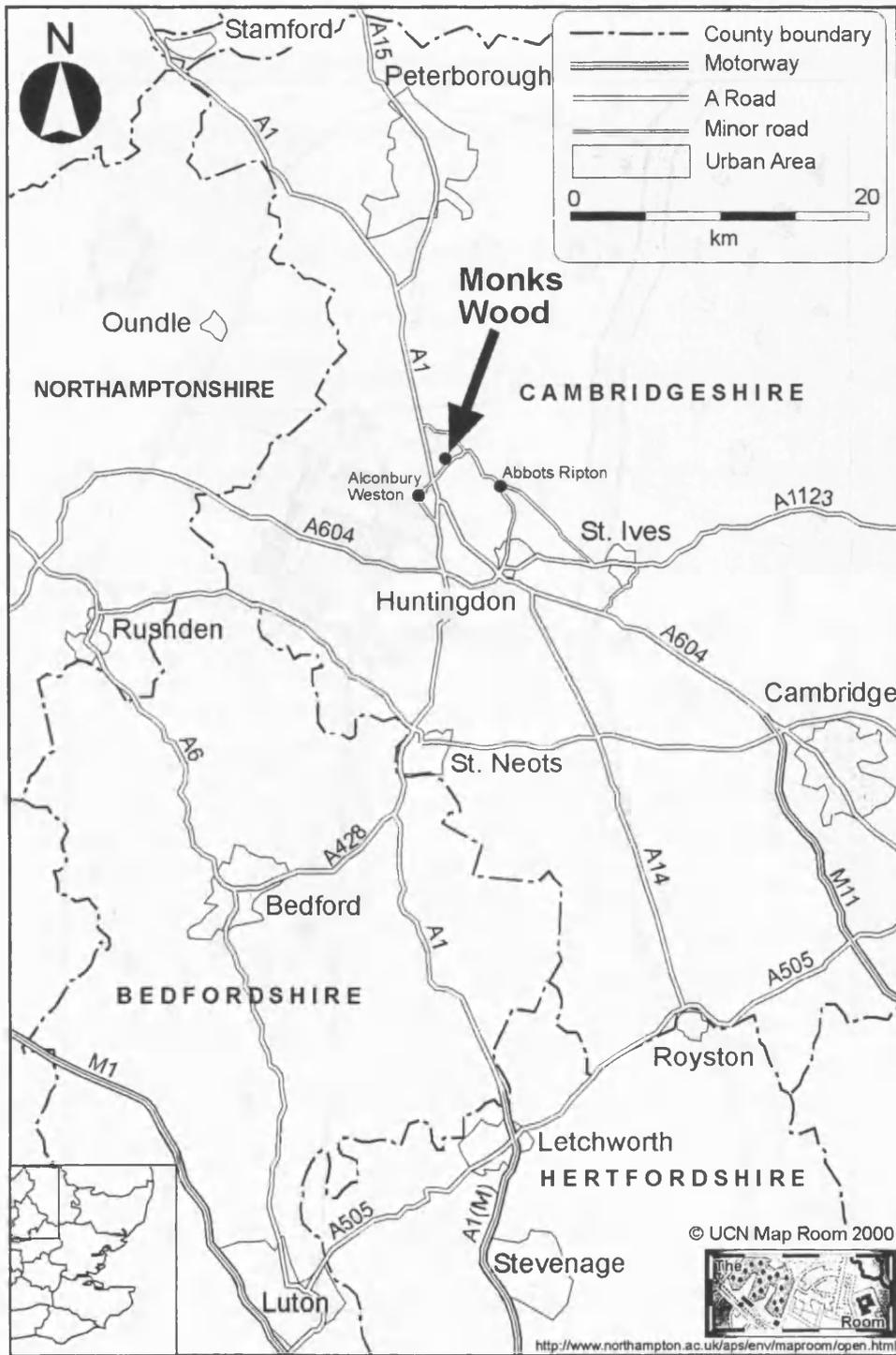
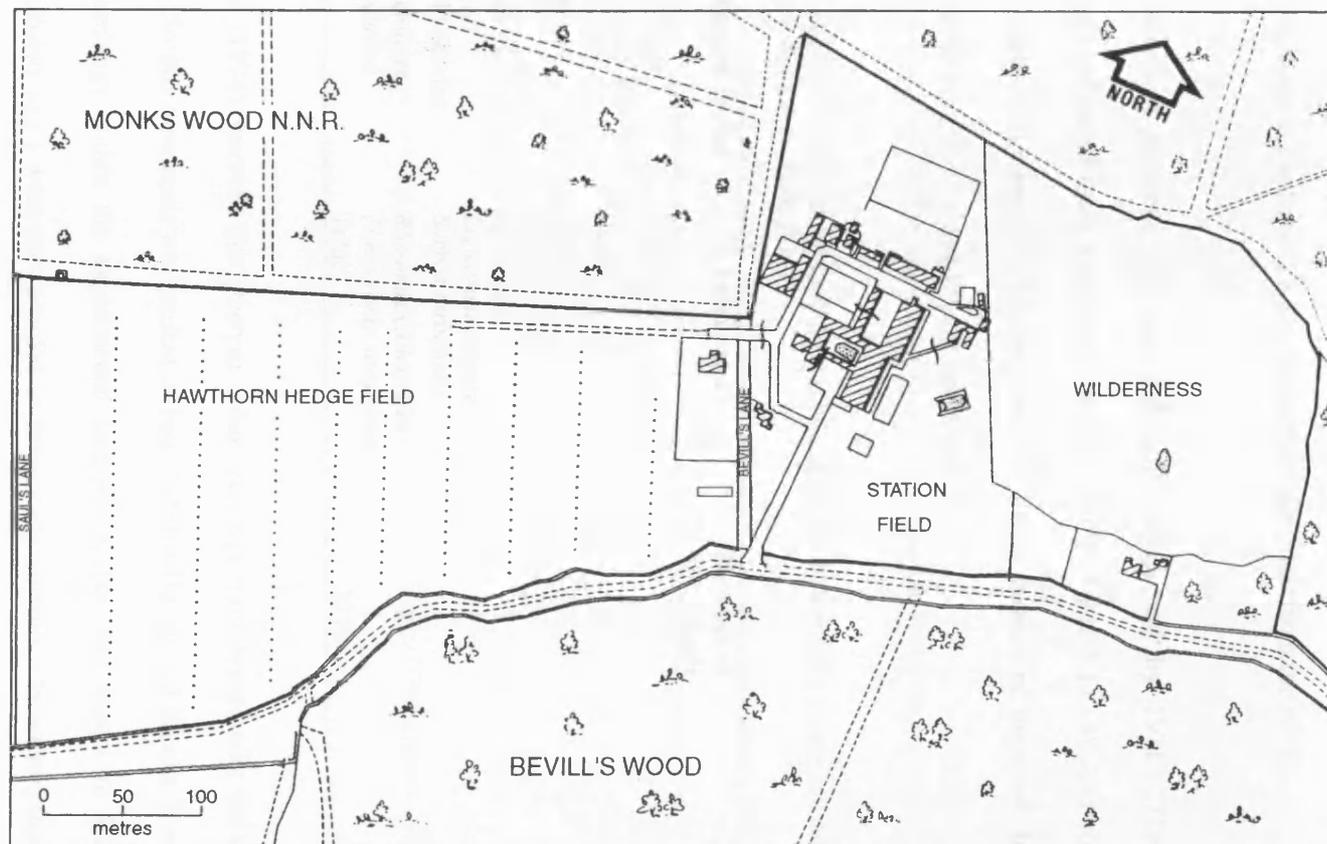


Figure 5.2 Experimental Hawthorn Hedge Field adjacent to Monks Wood National Nature Reserve (from Steele and Welch 1973).



In the early phase of development, the growth of the new hedgerows was retarded through grazing by rabbits (*Oryctolagus cuniculanus*), hares (*Lepus europaeus*) and several species of deer (Pollard pers. com. 1997). A perimeter fence was erected to exclude grazers and browsers between 1965 and 1972, although this measure was never fully effective. The fence ran along Judith's Hedge, but it did not exclude animals visiting the HHF from the NNR.

In 1969, researchers recorded 180 new individual plants and by 1971, 2719 additional individuals had colonized these hedgerows (Pollard 1973) (Table 5.1). Pollard observed that many of the earlier colonists were characterised by strong powers of dispersal; berries from shrubs were more frequently found in later invasions.

Table 5.1 Numbers of individuals of seedling shrubs and trees colonizing the young hawthorn hedges at Monks Wood (1969-1971) (Pollard 1973)

English names	Latin names	Number of individuals
Dog Rose	<i>Rosa canina</i>	1417
Common Hawthorn	<i>Crataegus monogyna</i>	920
Blackthorn	<i>Prunus spinosa</i>	161
Ash	<i>Fraxinus excelsior</i>	152
Oak	<i>Quercus robur</i>	51
Field Maple	<i>Acer campestre</i>	7
Privet	<i>Ligustrum vulgare</i>	5
Wild Service	<i>Sorbus torminalis</i>	3
Buckthorn	<i>Rhamnus catharticus</i>	2
Dogwood	<i>Thelycrania sanguinea</i>	1
	Total	2719

Pollard *et al.* (1974) observed that *Quercus robur* seedlings were dying under the shade of the hedgerows. *Sorbus torminalis* was present in both Judith's Hedge and Monks Wood, and was found as seedlings within the experimental hedgerows, but was absent in later surveys. Brambles (*Rubus* agg.) were not recorded in these early surveys. However, the absence of other climbing species such as Black Bryony (*Tamus communis*), Hedge Bindweed (*Calystegia sepium*), and Ivy (*Hedera helix*) was noted.

By 1974, the experimental hedgerows were fruiting and attracting many birds (thrushes (*Turdus*

spp.) in particular) and small mammals were also thought to be acting as agents of dispersal for potential incoming plant species. The researchers suggested that the initial flush of seedlings entering these hedgerows would be a short phase in the developmental stages of the experiment (Pollard *et al.* 1974). Immigrating woody plant species would colonize more successfully during the early stages of hedgerow development. Once the hawthorn plants had grown to form a hedge, they would enforce a competitive influence on colonizing individuals.

5.3 Methods

5.3.1 Experimental Hawthorn Hedgerows

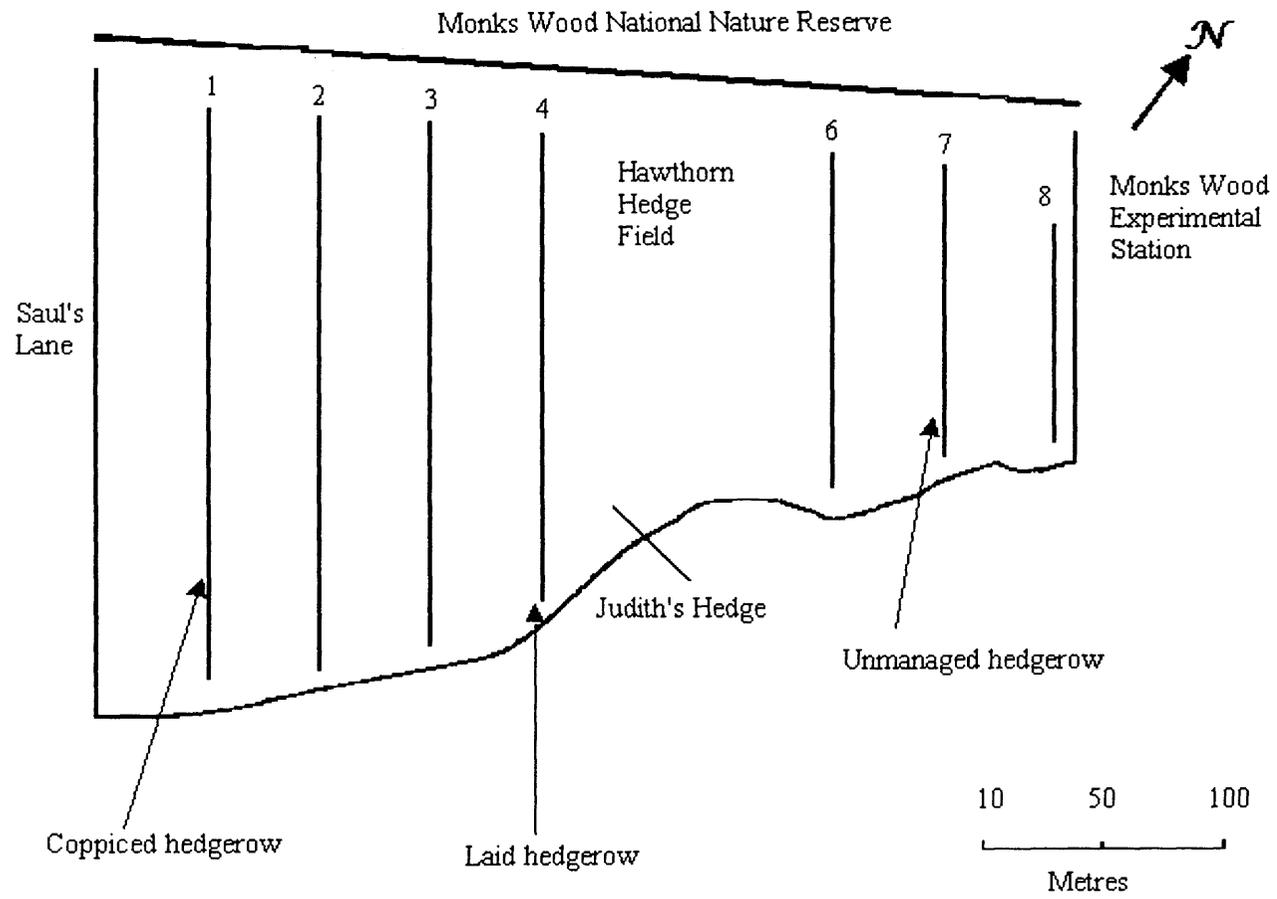
Several events had altered the EHH since their planting in 1962; two of the EHH were removed to make way for other experiments within the Experimental Hawthorn Hedge Field. The experimental hedgerows had grown into lines of tall shrubs. In 1990, a new management regime was initiated (Table 5.2). Three of the remaining seven EHH were chosen for this research, Hedges 1, 4 and 8, as they represented three contrasting management regimes (Figure 5.3). Replication of each hedgerow type was not possible, as the more recent managements of the remaining EHH were too varied.

Table 5.2 Recent management strategies for the Experimental Hawthorn Hedgerows (1990-96) (Tim Sparks pers.com.)

Hedge No.	Recent Management Strategies
Hedge 1	Coppiced in 1990/91 with sections trimmed in 1996
Hedge 2	Divided into 12 sections with: unmanaged, coppiced, laid replicates 1990/91, trimmed 1996
Hedge 3	Unmanaged until 1996, with sections cut down to 1 - 1.5 metres
Hedge 4	Traditional hedge laying 1990/91, with sections trimmed in 1996
Hedge 5	Hedge removed
Hedge 6	Hedge removed
Hedge 7	As Hedge 4
Hedge 8	Uncut since 1975, although the Monks Wood end was trimmed, because of the close proximity to the Meteorological Station
Hedge 9	Similar to Hedge 8 with a section trimmed near the Meteorological Station.

Hedge 1 - The Coppiced Hedge is located nearest to Saul's Lane. This is the longest of the remaining EHH (247m in length). Several large gaps along its length are presumed to be the

Figure 5.3 The Experimental Hawthorn Hedgerows



result of regeneration failure after coppicing in 1990 (Sparks pers. com. 1997). In 1996, the year preceding this study, this hedgerow was trimmed at regular intervals along its length with a mechanical hedge trimmer. The physical effect of this trimming was still evident at the time of survey.

Hedge 4 – The Laid Hedge was chosen from the two laid EHH because of its accessibility on both sides (204m in length). In 1996, sections of the hedge were trimmed but, due to rapid re-growth, these sections were indistinguishable from the rest at the time of survey.

Hedge 8 – An Unmanaged Hedge was the longer of the two unmanaged hedgerows (128m in length). Along the first 46m of Hedge 8 (from the Monks Wood end), thick multiple stems at the hedgerow base provided evidence of the first coppicing event of 1969. Apart from the initial coppicing management, this hedgerow has not received any formal management in the past thirty years.

5.3.2 Sampling strategy

In previous surveys carried out by Monks Wood staff, two researchers surveyed both sides of each hedgerow simultaneously, recording woody plant species colonizing the EHH. When an individual was identified, the following details were recorded:

- species;
- height of each individual plant;
- distance along the hedge;
- distance out from the hedge (within 1 metre of the hedge bottom).

Replication of this method was attempted for this study. After the initial few hours, it was concluded that this method was too time-consuming and labour intensive. An alternative method was developed that produced comparable data. Data were recorded in each 1m quadrat, along the length of each hedgerow. The census included:

- the identification of each species;
- the number of individuals in the three size-classes (see below).

Each side of the three hedgerows was surveyed separately. Counting all individuals in every quadrat along the length of the hedgerow ensured that the sampling was consistent with previous data sets collected by staff at Monks Wood. A full census of woody plant species within each of the hedgerow survey was compiled. The census aimed to provide reasonable estimates of the abundance and distributions of the woody plant populations found within the planted hedgerows.

It is acknowledged that some woody plant species are capable of reproducing vegetatively. Thus for the purpose of this study, it was assumed that stems seen above the ground were individuals. Care was taken not to misidentify small individuals: for example, leaves of *Prunus spinosa* can vary in size and shape in young, rapidly growing stems. The *Rubus* aggregate group was not identified down to species level, but observations in the field suggest that there were at least three different variants within the hedgerows.

Although changes were made to the method of collecting data in this thesis (see above), the three size-class categories used by previous researchers were retained. In unpublished records located at Monks Wood, individuals for each species were grouped into three size-classes:

- Size-class 1 = under 10cm high
- Size-class 2 = over 10cm and under 30cm in height
- Size-class 3 = over 30 cm high.

The grouping of woody plant species size-classes are justified here as follows:

- a) **Size-class 1** = individual stems measuring <10cm high. Individuals in this size-class are not referred to as seedlings *per se*. Some individuals identified were obviously older, bearing woody stems with some indication of damaged by browsing animals. Browsing or other forms of predation will affect the growth and development of young plants. In some cases, where browsing had been intense, individuals appeared as miniature coppice growths. Evidence of browsing has implications for classifying individuals into size-classes. In addition, some species of woody plant are known to reproduce vegetatively, producing

suckering stems. Nevertheless, this size-class will largely contain individuals that have dispersed into the hedgerow and are in the initial phase of colonizing the hedgerow. The success or failure of these individuals is determined by pressures of grazing or the ability to gain resources for further growth under competitive conditions. For this study, this size-class will be referred to as the **Colonization Phase** in the process of hedgerow development.

- b) **Size-class 2** = individuals measuring between 10cm and 30cm in height. It was presumed that these individuals had succeeded in the initial colonizing phase and were striving to survive under predatory and competitive pressures within the hedgerow base. This group of individuals is termed as being in the **Survivorship Phase**.
- c) **Size-class 3** = individuals measured >30cm in height. This size-class represents those individuals that have grown to a height that can potentially become incorporated into the hedgerow itself. These individuals have succeeded to continue growing under stressful conditions and have begun the **Establishment Phase**.

5.3.3 A survey of the vegetation boundaries surrounding the EHH

This survey aimed to assess, in a semi-quantitative fashion, the relative abundance of the woody plant species in the boundaries of the HHF. The boundaries of the field were walked; no attempt was made to measure distances. The relative abundance of individuals of each woody plant species was assessed by approximation, counting where possible and converting the results into a DAFOR abundance system (Dominant = Highest occurrences, Abundant = >50 individuals, Frequent = 11–50 individuals, Occasional = 2–10 individuals, Rare = 1 individual).

5.3.4 Assessment of bird disperser availability

Data were made available by research staff at the research station, where birds have been regularly recorded in the HHF in systematic surveys (for species list see Appendix 5.4). Bird preferences for woody plant species' seeds and fruits were gathered from a variety of literature sources (Woodruffe-Peacock 1918, Ridley 1930, Snow and Snow 1988, Sørensen 1981).

5.3.5 Autecological comparison

The life histories of each woody plant species within the seed source boundaries were compared by using the data from The Comparative Plant Ecology Electronic Database (Hodgson *et al.* 1995). Where relevant information was unavailable, other floras were explored for data (Nicholson *et al.* 1960, McClintock and Fitter 1965, Vedel and Lange 1960, Stokoe 1970, Phillips 1977, Clapham *et al.* 1987, Snow and Snow 1988, Stace 1991). For additional autecological information see Appendix 5.5.

5.4 Analysis

The analyses of spatial pattern in the distribution of immigrants, and colonization and establishment success of individual plants are divided into the following sections:

- an analysis of the spatial distribution of additional woody plant species located in the three EHH;
- an assessment of woody plant seed source availability and the development of a model to assess immigration potential of bird-dispersed woody plant species;
- the examination of the spatial characteristics in the distribution of individual woody plant species and the presentation of a devised model to interpret the distributions of these species;
- a comparison of past data, from previous researchers, with these recent data to investigate the survivorship and establishment of previous colonizers.

To aid the reader, the methods for these analyses and rationales for the two models will be presented within the relevant sections that follow.

5.5 Spatial patterns of woody plant species diversity in the colonization, survivorship and establishment phases

This section examines the spatial distribution of additional plant species in each size-class and quadrat location. A maximum of five woody plant species per quadrat was found in the colonization phase on the western side of Hedge 8 (the unmanaged hedge) (Table 5.3). Three

climbing species in the colonization phase were found in quadrats on the western side of the layered experimental hedgerow (Hedge 4) and each aspect of the unmanaged hedgerow (Table 5.4). A maximum of three woody tree and shrubs species was found within quadrats on the western side of Hedge 8 (Table 5.5).

5.5.1 Visual comparison

The total number of woody tree, shrub and climbing species identified in each size-class are displayed in Appendix 5.6. The distribution of number of woody plant species and climbers (Figure 5.4), climbing species (Figure 5.5) and woody tree and shrub species (Figure 5.6) per quadrat were mapped by quadrat location. Direct comparison between these three diagrams shows that firstly, when all the woody plant species are examined the spatial patterns of woody species richness along each experimental hedgerow are complex (Figure 5.4). When separated, the climbing species are shown to produce much of the 'background noise' in species richness distribution (Figure 5.5). A separate plot of tree and shrub species reveals an underlying spatial pattern of species richness (Figure 5.6). The patterns of spatial distribution of tree and shrub species appear similar in each experimental hedgerow: with more species appearing to be entering the experimental hedgerows at the ends nearest to Judith's Hedge. In particular, the tree and shrub species found colonizing (Size-class 1) each experimental hedgerow display similar patterns of distribution, although quadrats appear to be more frequently occupied along the entire length of the unmanaged hedgerow (Hedge 8).

The number of species surviving (Size-class 2) within the coppiced (Hedge 1) and laid (Hedge 4) hedgerows, display similar distributions to the colonists. However, fewer sites are occupied by the established individuals (Size-class 3).

Table 5.3 Descriptive statistics for the number of woody plant species

		Colonization					Survivorship					Establishment				
		Max	Mean	Mode	SE	S ²	Max	Mean	Mode	SE	S ²	Max	Mean	Mode	SE	S ²
Hedge 1	West	4	1.33	1	0.06	0.94	4	0.18	2	0.06	0.81	3	1.20	1	0.06	0.76
	East	4	1.47	2	0.06	0.75	4	1.56	2	0.05	0.73	4	1.22	1	0.05	0.63
Hedge 4	West	4	1.65	2	0.05	0.55	4	1.73	2	0.05	0.55	3	1.30	1	0.05	0.54
	East	4	1.40	1	0.06	0.62	4	1.24	1	0.05	0.57	2	0.71	1	0.04	0.38
Hedge 8	West	5	2.03	2	0.07	0.71	3	1.02	1	0.06	0.47	3	0.95	1	0.07	0.61
	East	4	1.64	2	0.06	0.48	2	0.91	1	0.05	0.36	3	0.80	1	0.06	0.48

Table 5.4 Descriptive statistics for the number of woody climbing species

		Colonization					Survivorship					Establishment				
		Max	Mean	Mode	SE	S ²	Max	Mean	Mode	SE	S ²	Max	Mean	Mode	SE	S ²
Hedge 1	West	2	1.37	2	0.05	0.61	2	1.51	2	0.04	0.46	2	1.12	1	0.05	0.22
	East	2	1.34	2	0.05	0.52	2	1.43	2	0.04	0.47	2	1.14	1	0.04	0.12
Hedge 4	West	3	1.44	2	0.04	0.38	2	1.55	2	0.04	0.36	2	1.25	1	0.05	0.16
	East	2	1.24	1	0.04	0.40	3	1.12	1	0.04	0.38	2	0.70	1	0.04	0.14
Hedge 8	West	3	1.72	2	0.05	0.35	2	0.96	1	0.05	0.37	2	0.90	1	0.07	0.05
	East	3	1.42	1	0.05	0.39	2	0.84	1	0.05	0.30	2	0.80	1	0.06	0.05

Table 5.5 Descriptive statistics for the number of tree and shrub species

		Colonization					Survivorship					Establishment				
		Max	Mean	Mode	SE	S ²	Max	Mean	Mode	SE	S ²	Max	Mean	Mode	SE	S ²
Hedge 1	West	2	0.19	0	0.03	0.20	2	0.24	0	0.03	0.22	1	0.09	0	0.02	0.08
	East	2	0.13	0	0.02	0.13	2	0.14	0	0.02	0.13	2	0.07	0	0.02	0.09
Hedge 4	West	2	0.21	0	0.03	0.22	2	0.18	0	0.03	0.16	1	0.05	0	0.02	0.05
	East	2	0.16	0	0.03	0.63	2	0.12	0	0.03	0.14	1	0.01	0	0.01	0.01
Hedge 8	West	3	0.31	0	0.05	0.34	1	0.05	0	0.02	0.05	1	0.06	0	0.02	0.05
	East	1	0.22	0	0.04	0.17	1	0.05	0	0.02	0.05	1	0.01	0	0.01	0.01

Figure 5.4 Spatial pattern of the total number of additional woody plant species

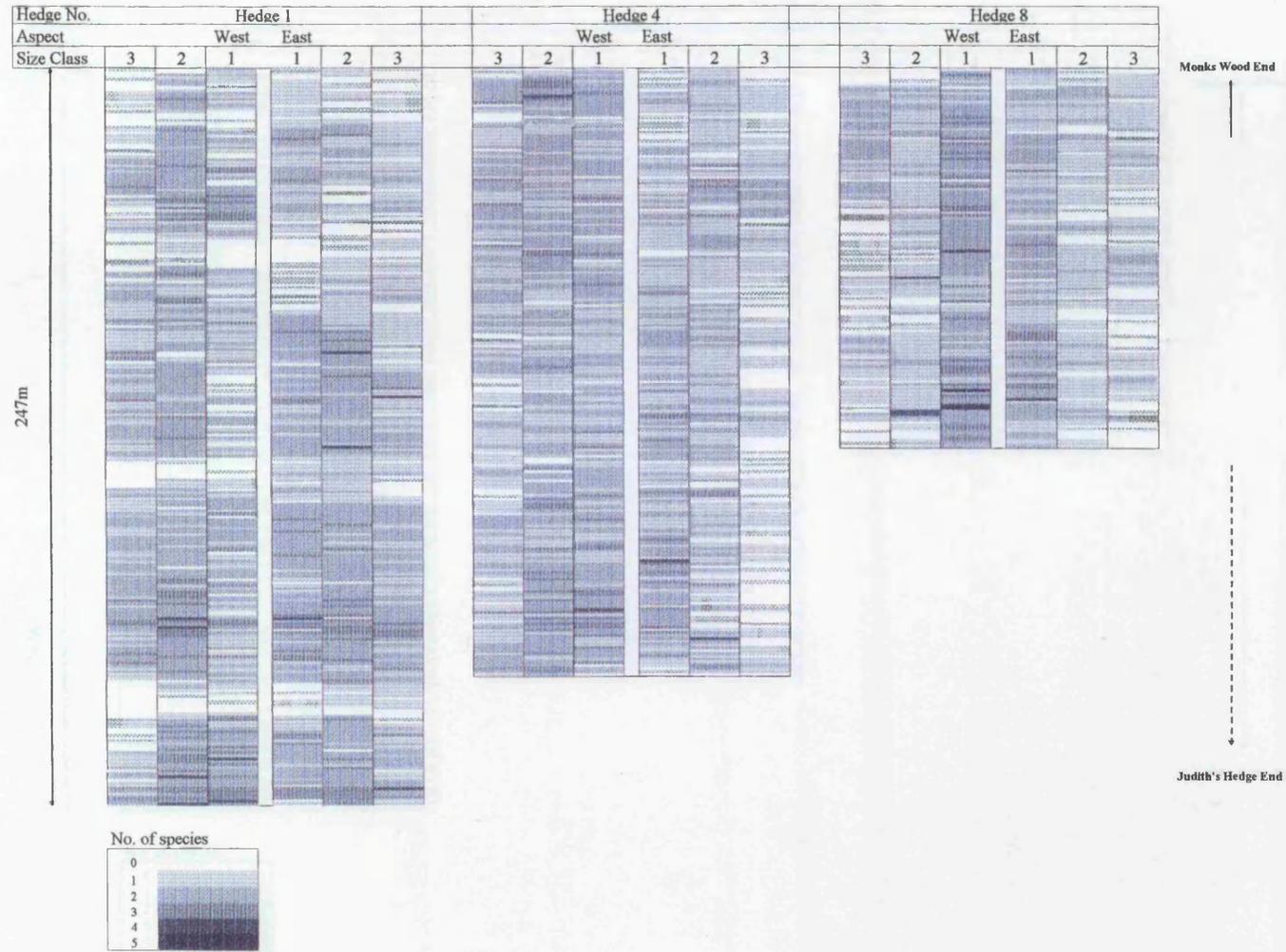
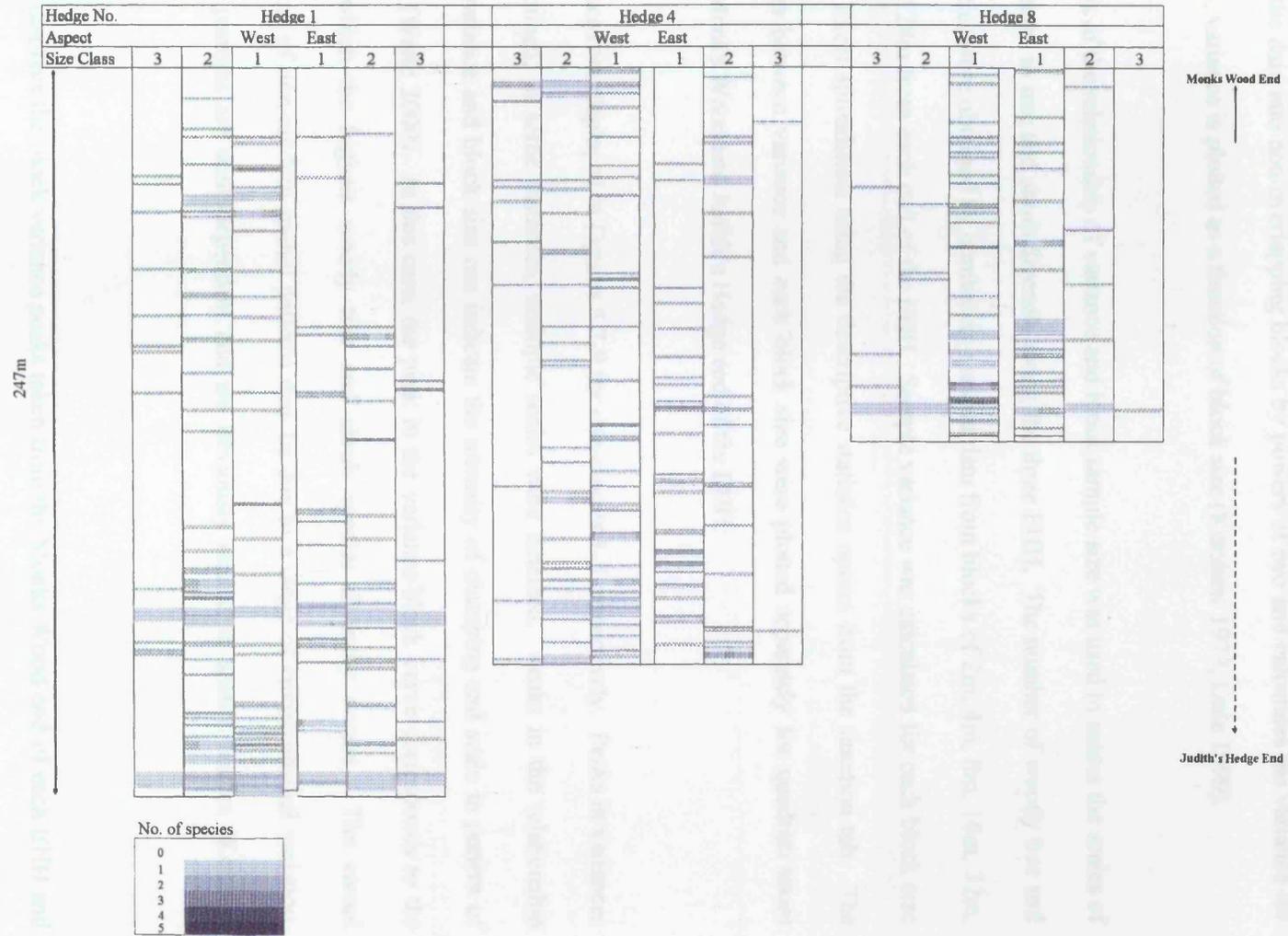


Figure 5.5 Spatial pattern of the number of woody climbing species



Figure 5.6 Spatial pattern of the number of tree and shrub species



5.5.2 *Detection of pattern and scale*

A method of analysing contiguous quadrat data was devised by Greig-Smith (1952), modified by Kershaw (1957), and is generally referred to as Blocked Quadrat Variance (BQV). BQV combines the data into non-overlapping blocks by powers of two and calculates the variance for each block; variance is plotted as a function of block size (Kershaw 1973, Dale 1999).

An analysis of the relationship of variance and block sample size was used to assess the scales of spatial patterns in tree and shrub diversity along the three EHH. The number of woody tree and shrub species were obtained by combining quadrat data from blocks of 2m, 4m, 8m, 16m, 32m, 64m, and 128m from each end of the EHH. Sample variance was calculated for each block size within an Excel spreadsheet using the descriptive statistics option from the function tab. The relationship between variance and each block size were plotted separately for quadrats taken from the Monks Wood and Judith's Hedge end of the EHH.

The variances are displayed in Figures 5.7-9 for size-classes 1-3 respectively. Peaks in variances were examined; in some instances, multiple scales were detected. Peaks in the relationship between variance and block size can indicate the intensity of clumping and scale in pattern of clumping (Waite 2000). In this case, the peak in the variance-block curve corresponds to the scale at which the highest woody tree and shrub species diversity occurs. The causal mechanisms of non-random spatial patterns may be due to a range of environmental variation, but some patterns are scale-dependent and are obviously related to spatial factors (Kershaw 1973).

Table 5.6 displays the block variance peaks taken from the Monks Wood end of each EHH and Table 5.7 shows the block variance peaks from Judith's Hedge end. Dark coloured blocks represent the strongest peak in variance; the lighter shaded blocks indicate additional peaks in variance and reflect multiple scales in pattern. A comparison of these two tables of block

Figure 5.7 Sample variance / block size graphs for number of woody tree and shrub species in the colonization phase a) from Monks Wood end, b) from Judith's Hedge end.

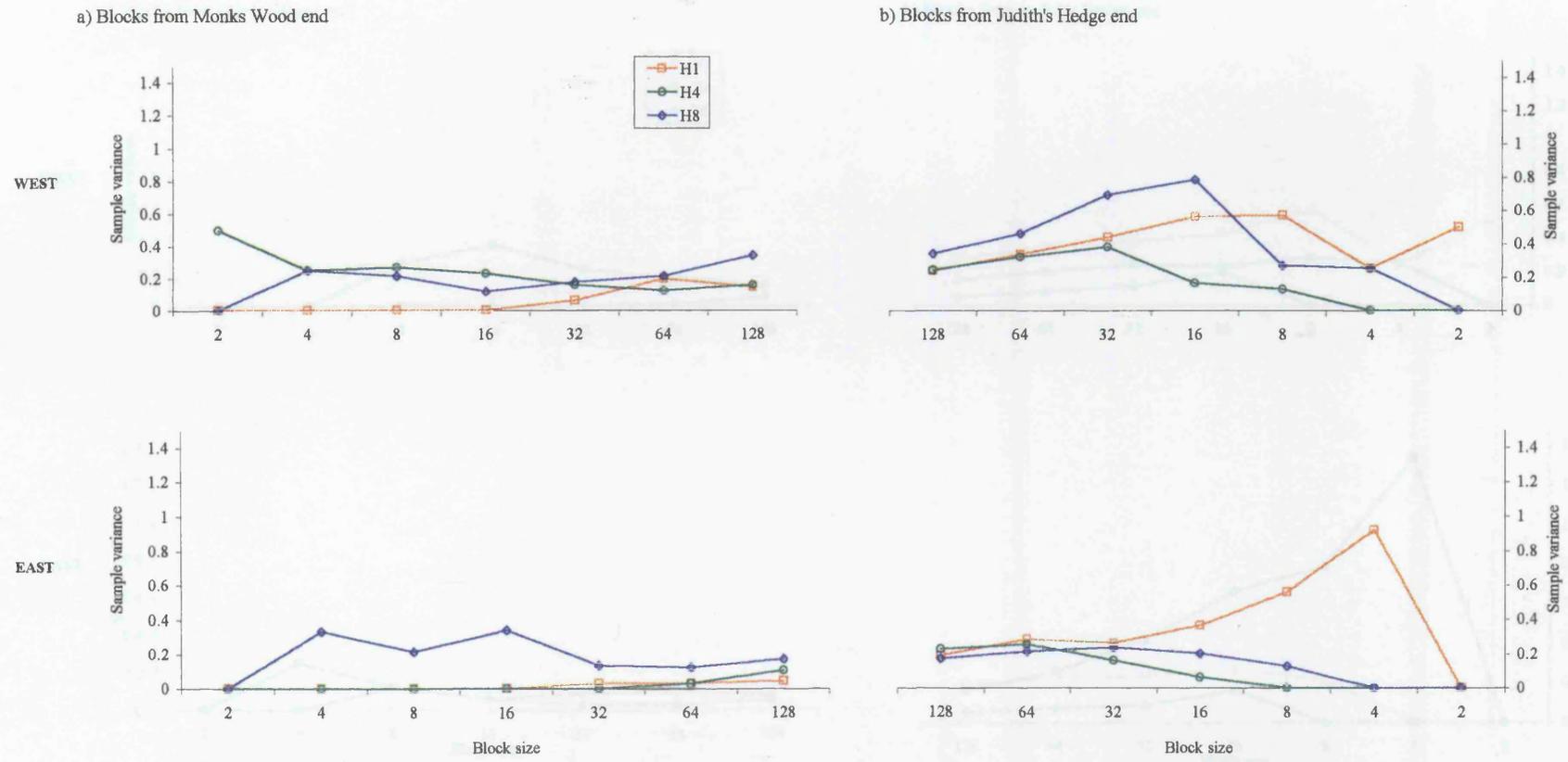


Figure 5.8 Sample variance / block size graphs for number of woody tree and shrub species in the survivorship phase a) from Monks Wood end, b) from Judith's Hedge end.

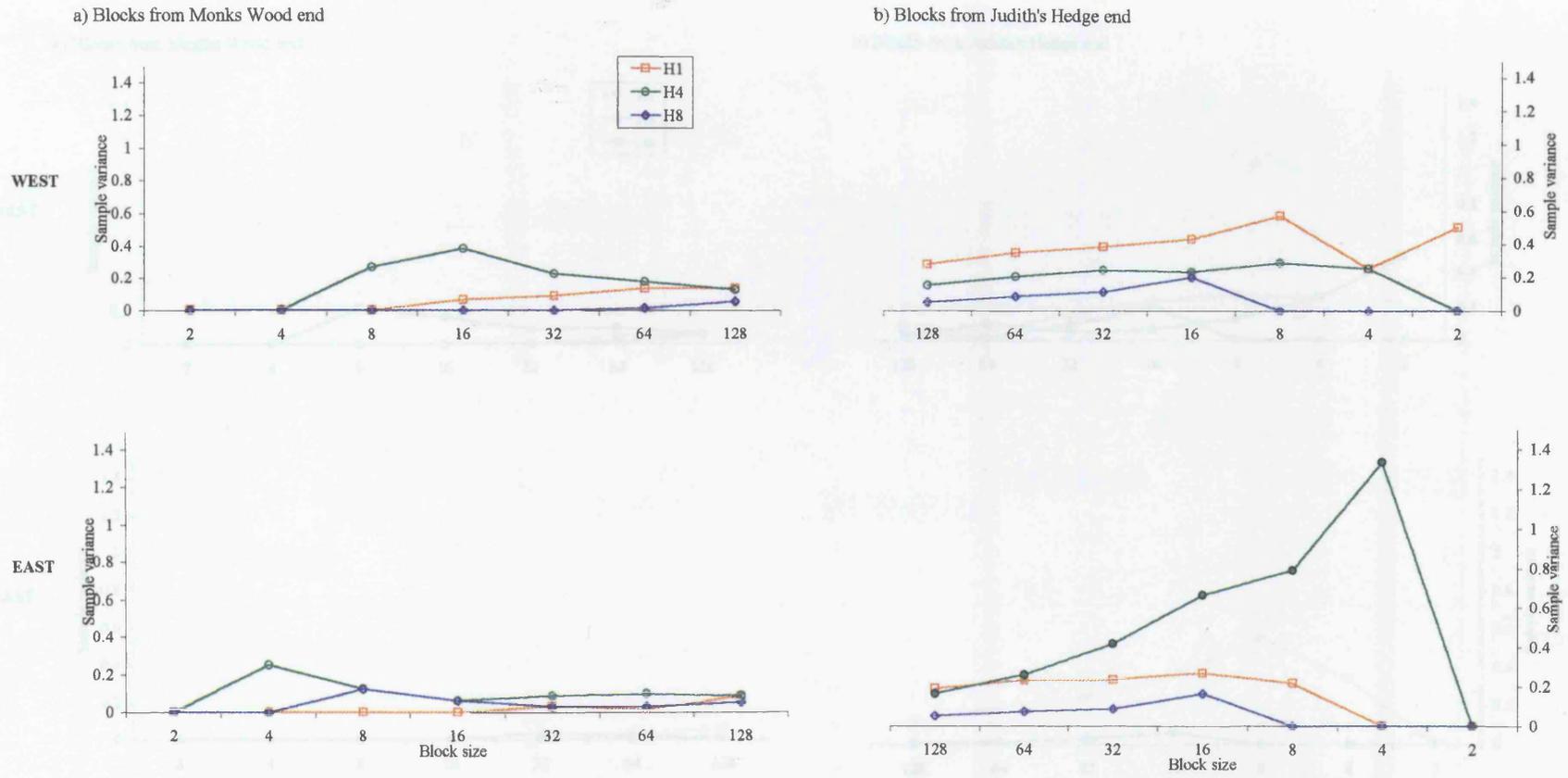


Figure 5.9 Sample variance / block size graphs for number of woody tree and shrub species in the establishment phase a) from Monks Wood end, b) from Judith's Hedge end.

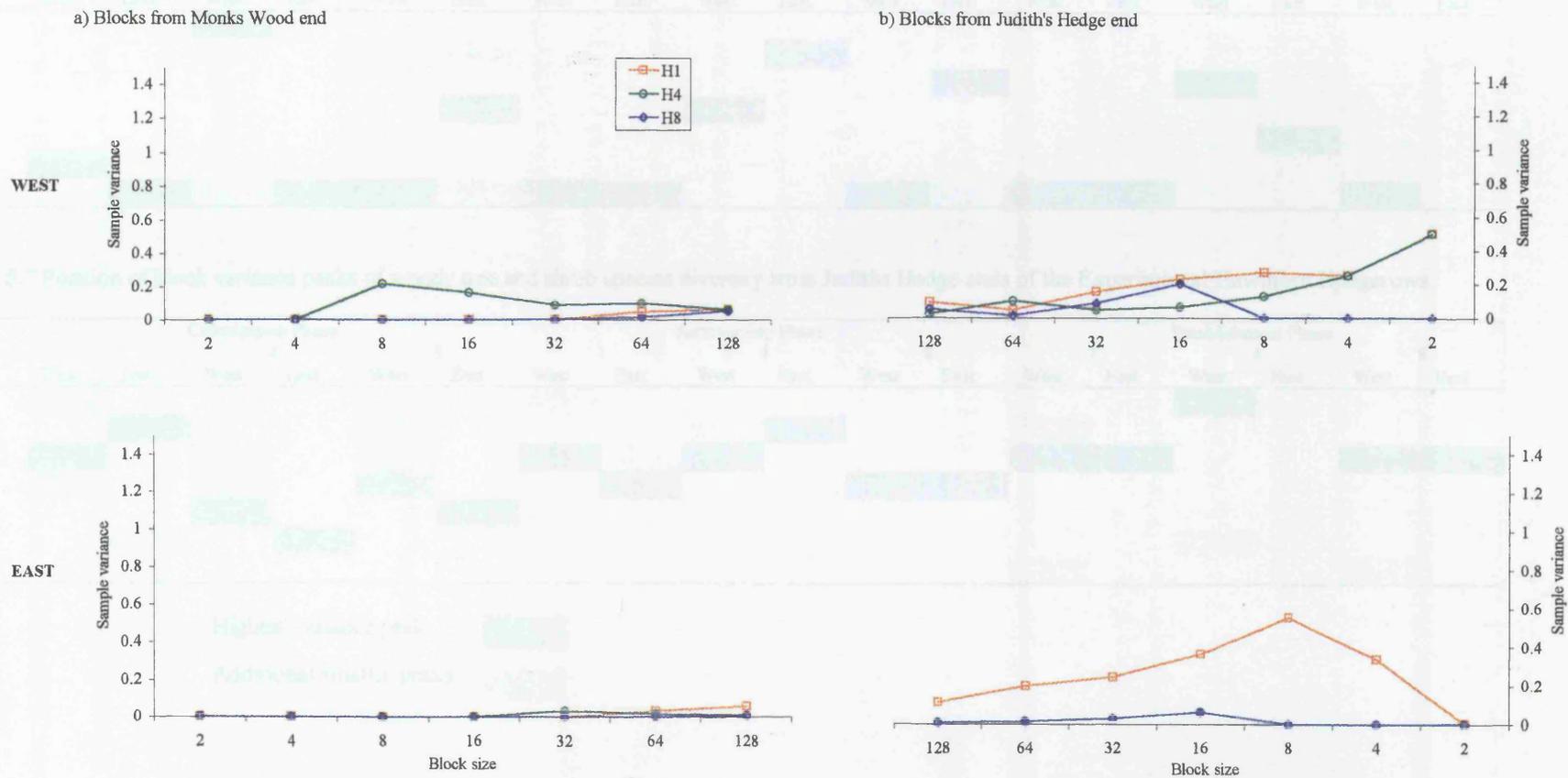


Table 5.6 Position of block variance peaks of woody tree and shrub species diversity from Monks wood ends of the Experimental Hawthorn Hedgerows.

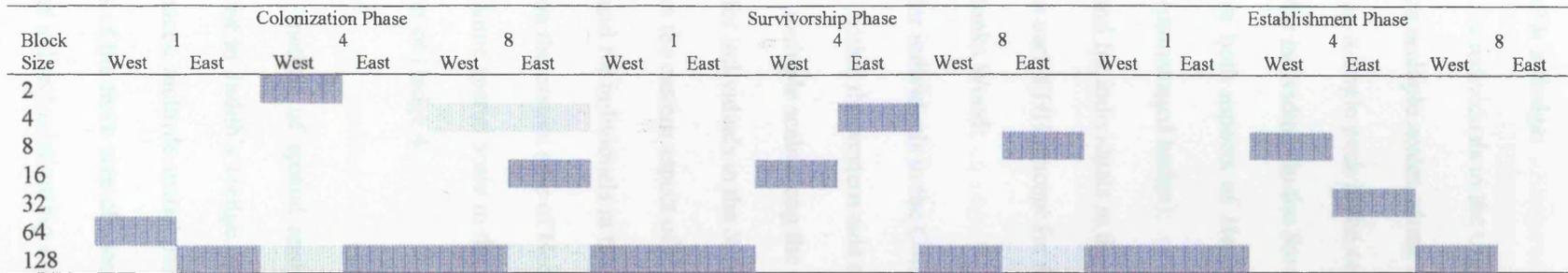
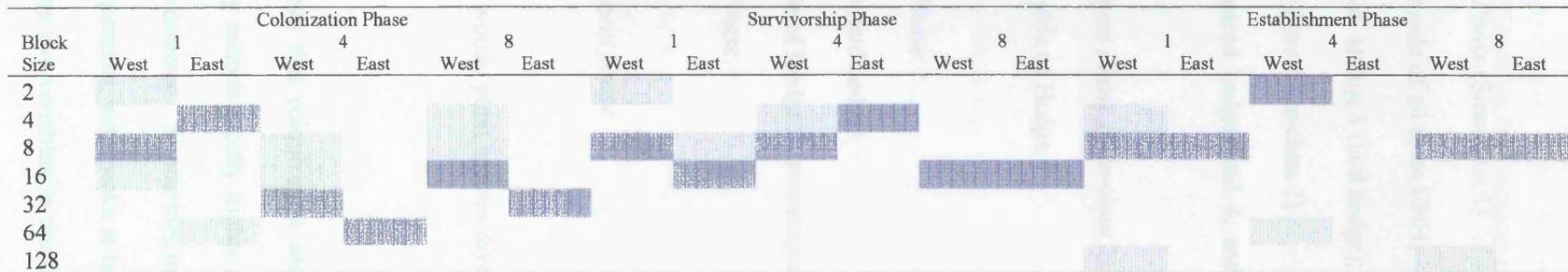


Table 5.7 Position of block variance peaks of woody tree and shrub species diversity from Judiths Hedge ends of the Experimental Hawthorn Hedgerows.



Highest variance peak 
 Additional smaller peaks 

variance peaks, demonstrate variability in scales of pattern and indicates that higher woody tree and shrub species diversity is occurring closest to

1) Judith's Hedge:

- a) for individuals in the *Colonization Phase* (Size-class 1)
 - as multiple scales, along the western side of all three EHH;
 - as a single peak in the eastern side of Hedge 4 (laid hedge);
- b) for individuals in the *Survivorship Phase* (Size-class 2)
 - in both aspects of Hedges 1 (coppiced hedge) and 4, and the western side of Hedge 8 (unmanaged hedge);
- c) and for individuals in the *Establishment Phase* (Size-class 3)
 - in each EHH, except for the eastern side of Hedge 4

2) Monks Wood:

- a) for individuals in the *Colonization Phase*
 - within the western side of Hedge 4 (laid hedge)
 - multiple scale along the eastern side of Hedge 8 (unmanaged hedge)
- b) for individuals in the *Survivorship Phase*
 - in the eastern aspect of Hedge 8
- c) and for individuals in the *Establishment phase*
 - on the eastern side of Hedge 4.

The same spatial scale in the pattern of woody plant species diversity was located on the eastern aspect of Hedge 4.

This method of spatial analysis suggests that colonization success in the EHH was greatest nearest to Judith's Hedge, and possibly reflects locally higher rates of immigration. In some instances, multiple spatial patterns were detected. Similarities in pattern were also discovered in each of the three size-classes. Similar patterns, with peaks at the same block size, suggest that either a direct relationship exists between two variables, in this case tree and shrub diversity and

distance from either Judith's Hedge or Monks Wood NNR, or the operation of some common unknown factor (Waite 2000). However, some disparities were detected in the spatial patterns between hedgerow management and hedgerow aspect. Results from this section have shown that complex spatial patterns exist within the distributions of the tree and shrub species, in the three experimental hedgerows at Monks Wood. Complexities are probably due to interactive processes during immigration, colonization, survivorship and establishment. Differences are seen in the distribution of species in response to different hedgerow management regimes could reflect differences in the microenvironment. Similarities viewed could be due to spatial patterns in predation or dispersal vector movement.

The analysis used above does have disadvantages. The precision of block-size-variance decreases with block size and estimates of block-size-variance are not independent and cannot be tested statistically for significance (Waite 2000). However, this form of analysis is simple to use and gives an indication of spatial pattern for the purposes of this thesis. Waite (2000) states the given the inherent statistical problems associated with contiguous quadrat sampling and analysis, procedures based on the analysis of variance of blocked data should be treated as descriptive or explanatory. Despite these short-comings, Bouxin (1991) considers contiguous sampling to be the most effective method in the detection of spatial pattern.

5.6 The assessment of available woody plant seed sources and immigration potential

5.6.1 Woody plant species composition of boundaries that surround the Hawthorn Hedge Field.

During the boundary survey of Monks Wood, undertaken as part of the present study, nineteen woody plant species were identified (Table 5.8). Twenty-four woody plant species were identified by Steel (1973) within Monks Wood NNR. Seven of these previously recorded species absent from this survey have distinct associations with specific topographical, hydrological and edaphic associations within Monks Wood NNR (Steel 1973). Pollard *et al.* (1974) had detected *Viburnum opulus* and *Acer pseudoplatanus* along Judith's Hedge. These

two species were also not recorded in this present survey.

Table 5.8 Woody species composition of potential seed sources around the EHH field.

Field boundary	(Steel 1973)	(Pollard <i>et al.</i> 1974)	Boundary survey 1997				
	Monks Wood (NNR)	Judith's Hedge	Monks wood edge survey	Judith's Hedge survey	Saul's Lane	Stock-ing Close	Fence- line
Climbers							
<i>Clematis vitalba</i>	✓	UR		✓			
<i>Lonicera periclymenum</i>	✓	✓	✓	✓	✓		✓
<i>Rubus</i> agg.	✓	UR	✓	✓	✓	✓	✓
<i>Rosa canina</i>	✓	✓	✓	✓	✓	✓	✓
Total No. of climbers	4	2	3	4	3	2	3
Shrubs							
<i>Cornus sanguinea</i>	✓	✓	✓	✓	✓	✓	
<i>Corylus avellana</i>	✓	✓	✓	✓			✓
<i>Crateagus laevigata</i>	✓	✓	✓	✓			
<i>Crataegus monogyna</i>	✓	✓	✓	✓	✓	✓	✓
<i>Euonymus europaeus</i>		✓	✓	✓	✓		✓
<i>Ligustrum vulgare</i>	✓	✓	✓	✓	✓		
<i>Prunus spinosa</i>	✓	✓	✓	✓	✓	✓	✓
<i>Rhamnus catharticus</i>	✓	✓		✓			
<i>Salix caprea</i>	✓						
<i>Salix cinerea</i>	✓						
<i>Sambucus nigra</i>	✓	✓	✓	✓	✓		
<i>Symphoricarpos alba</i>			✓				
<i>Viburnum opulus</i>		✓					
<i>Viburnum lantana</i>		✓	✓	✓			
Total No. of shrub spp.	10	11	10	10	6	3	4
Trees							
<i>Acer campestre</i>	✓	✓	✓	✓			
<i>Acer pseudoplatanus</i>		✓					
<i>Betula pendula</i>	✓						
<i>Betula pubescens</i>	✓						
<i>Carpinus betulus</i>	✓						
<i>Fagus sylvatica</i>						✓	
<i>Fraxinus excelsior</i>	✓	✓	✓	✓	✓		✓
<i>Populus tremula</i>	✓						
<i>Quercus robur</i>	✓	✓	✓	✓	✓	✓	✓
<i>Malus sylvestris</i>	✓		✓				
<i>Salix alba</i>		✓		✓			
<i>Sorbus torminalis</i>	✓	✓		✓			
<i>Ulmus minor-</i> <i>carpinifolia</i>	✓						
Total No. of tree spp.	10	6	4	5	2	2	2
Total No. of woody spp. /without climbers	20	17	14	15	8	5	6
Total No. of woody spp.	24	19-22	17	19	11	7	9

✓ = recorded, UR = unrecorded

5.6.2 Dispersal, seed-bank, and regeneration strategies of potential seed sources.

The dispersal modes for the woody plant species located in the boundaries surrounding the HHH are listed Table 5.9.

Table 5.9 The life history characteristics of woody plant species surrounding the EHH (after Hodgson *et al.* 1995, * other literature sources; see Section 5.3.3)

		Mode of dispersal	Seed-bank	Regeneration Strategy
Climbers	<i>Clematis vitalba</i> *	Anemochore-plumed	Unkown	Unkown
	<i>Lonicera periclymenum</i>	Endozoochore	Transient	Vegetative & seed
	<i>Rosa canina</i>	Endozoochore	Transient	Vegetative & seed
	<i>Rubus</i> agg.	Endozoochore	Persistent	Vegetative, seed & seed bank
Shrubs	<i>Cornus sanguinea</i> *			Vegetative & seed
	<i>Corylus avellana</i>	Dyszoochore	Transient	Vegetative & seed
	<i>Crataegus laevigata</i>	Endozoochore?	Transient?	Seed only?
	<i>Crataegus monogyna</i>	Endozoochore	Transient	Seed only
	<i>Euonymus europaeus</i>	Endozoochore/ Myrmecochorre	Transient	Seed only
	<i>Ligustrum vulgare</i>	Endozoochore	Transient	Vegetative & seed
	<i>Prunus spinosa</i>	Endozoochore	Transient	Vegetative & seed
	<i>Rhamnus catharticus</i> *	Endozoochore		
	<i>Sambucus nigra</i>	Endozoochore	Persistent	Seed & seed bank
	<i>Symphoricarpus alba</i> *	Endozoochore		Vegetative & seed
	<i>Viburnum lantana</i> *	Endozoochore		
	<i>Acer campestre</i>	Anemochore-winged	Transient	Wide spread dispersal
	<i>Fagus sylvatica</i>	Dyszoochore	Transient	Wide spread dispersal
Trees	<i>Fraxinus excelsior</i>	Anemochore-winged	Transient	Seed only
	<i>Malus sylvestris</i>	Endozoochore	Transient	Seed only
	<i>Quercus robur</i>	Dyszoochore	Transient	Seed only
	<i>Salix alba</i>	Anemochore-plumed	Transient	Seed only
	<i>Sorbus torminalis</i> *			Vegetative & Wide spread dispersal

? = *Crataegus monogyna* and *C. laevigata* – bird disperser reference for *Crataegus* spp. only (Snow and Snow 1988)

Four woody plant species were listed as having seeds adapted for wind-dispersal: *Clematis vitalba* (a climbing species with numerous light plumed seeds), *Salix alba* (a tree species with small numerous light weight seeds), and *Acer campestre* and *Fraxinus excelsior* (which have larger seeds with winged appendages). Three species of climbers (*Lonicera periclymenum*, *Rosa canina*, and *Rubus* agg.), and nine species of shrub (*Crataegus laevigata*, *C. monogyna*, *Euonymus europaeus*, *Ligustrum vulgare*, *Prunus spinosa*, *Rhamnus catharticus*, *Sambucus nigra*, *Symphoricarpus alba* and *Viburnum lantana*), were noted as being dispersed by animal vectors after ingestion. Three tree species and one shrub species produce nuts, which attract mammals and birds that tend to cache food reserves.

Two woody plant species have persistent seed-banks: *Rubus* agg. and *Sambucus nigra*. The remaining species were all characterised as having transient or short-term seed-banks or were unknown. Nine woody plant species (*Lonicera periclymenum*, *Rosa canina*, *Rubus* agg., *Cornus sanguinea*, *Corylus avellana*, *Ligustrum vulgare*, *Prunus spinosa*, *Salix alba* and *Sorbus*

torminalis) were assessed as being capable of reproducing vegetatively.

5.6.3 Seed source abundance in the surrounding boundaries

The relative abundance of each woody plant species was converted into a DAFOR system (Table 5.10). *Rubus* agg. were too numerous to count and were classified as the dominant climbing species in each boundary surrounding the Hawthorn Hedge Field. *Rosa canina* was abundant in both Judith's Hedge and along the edge of Monks Wood (NNR). *Prunus spinosa* was the most dominant shrub in three of the four boundaries of the experimental field and the most prolific colonist along the fenceline. *Crataegus monogyna* and *Cornus sanguinea* were also abundant.

Table 5.10 Relative abundance of woody plant species surrounding the EHH field (1997)

Boundary	Monks Wood edge	Judith's Hedge	Saul's Lane	Stocking Close	Fence -line
Climbers					
<i>Clematis vitalba</i>		F			
<i>Lonicera periclymenum</i>	F	O	R		O
<i>Rubus</i> agg.	D	D	D	D	D
<i>Rosa canina</i>	A	A	F	F	F
Shrubs					
<i>Cornus sanguinea</i>	A	A	F	R	
<i>Corylus avellana</i>	O	F			R
<i>Crataegus laevigata</i>	R	O			
<i>Crataegus monogyna</i>	A	A	A	D	F
<i>Euonymus europaeus</i>	O	F	R		O
<i>Ligustrum vulgare</i>	F	F			
<i>Prunus spinosa</i>	D	D	D	R	D
<i>Rhamnus catharticus</i>		R			
<i>Sambucus nigra</i>	R	R	R		
<i>Symphoricarpos alba</i>	A				
<i>Viburnum lantana</i>	O	O			
Trees					
<i>Acer campestre</i>	F	F			
<i>Fagus sylvatica</i>				D	
<i>Fraxinus excelsior</i>	A	D	O		O
<i>Quercus robur</i>	D	F	O	O	D
<i>Malus sylvestris</i>					
<i>Salix alba</i>		R			
<i>Sorbus torminalis</i>	R	R			

Dominant = Highest occurrences, Abundant = >50 individuals, Frequent = 11–50 individuals, Occasional = 2–10 individuals, Rare = 1 individual

5.6.4 Bird dispersal vector availability

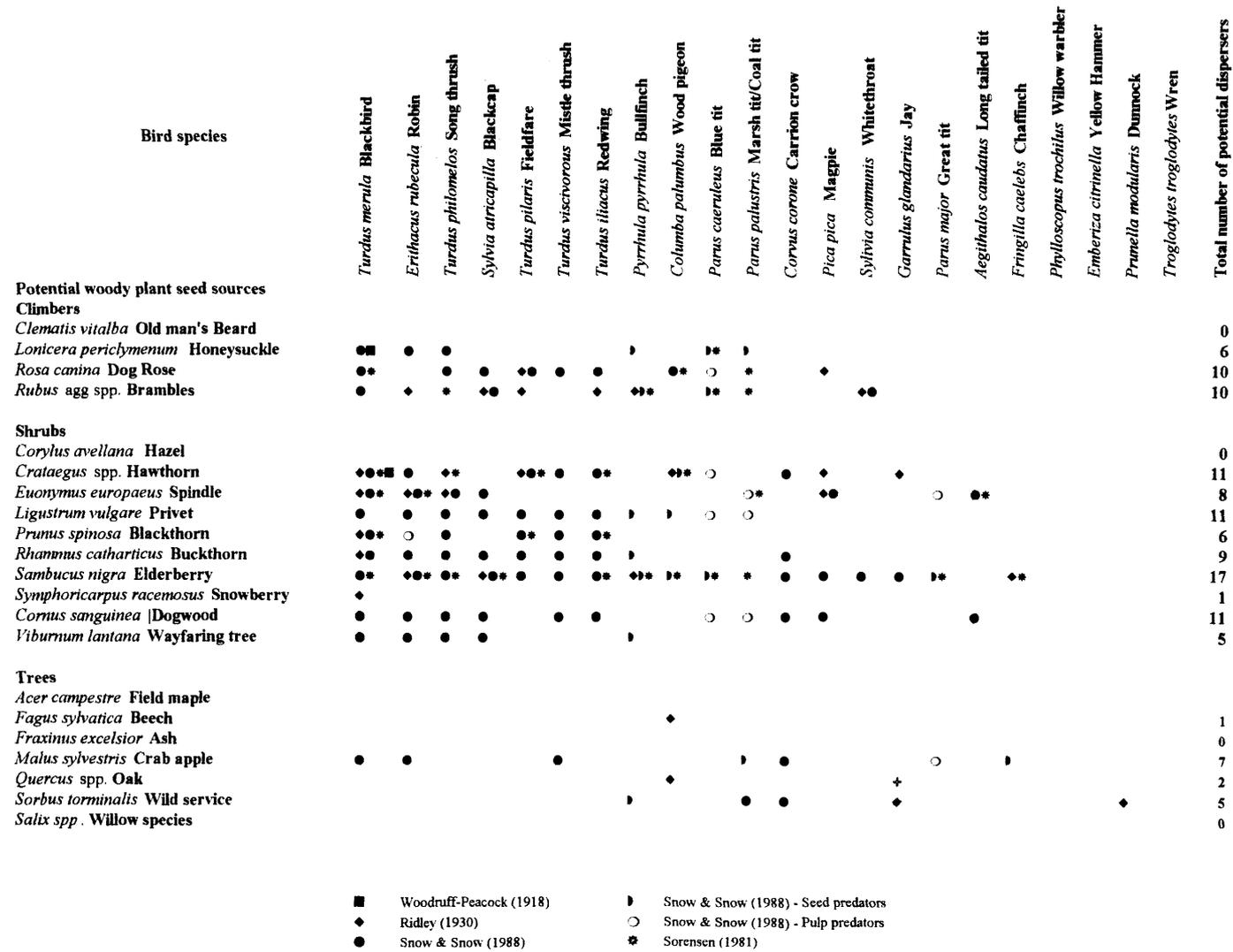
Figure 5.10 displays bird fruit preferences for woody plant species located in the Hawthorn Hedge Field and potential seed sources in the surrounding boundaries. This figure was formulated from:

- data on woody plant species present within the surrounding boundaries collected from this survey;
- bird data made available by researchers at the research station;
- bird fruit and seed preferences gathered from literature sources.

The number of potential bird dispersers for each woody plant species was estimated. Some bird species identified were mainly insectivorous and thus have little potential for woody-plant-species-dispersal. Finches and other bird species may act as seed predators, as they tend to destroy seeds during the ingestion process (Snow and Snow 1988). However, these species may accidentally drop seeds whilst feeding.

A maximum of ten possible bird dispersers was documented for the climbing woody plant species *Rubus* agg. and *Rosa canina*. Six potential dispersers were found for *Lonicera periclymenum*. Of the shrub species, *Sambucus nigra* has the maximum number of seventeen potential bird dispersers. Eleven potential bird dispersers were identified for *Cornus sanguinea*, *Ligustrum vulgare* and the *Crataegus* species combined. The number of potential bird dispersers decreases numerically for *Rhamnus catharticus*, *Euonymus europaeus*, *Prunus spinosa* and *Viburnum lantana*, respectively. No bird dispersers are listed for *Corylus avellana*. *Malus sylvestris* has the highest potential of dispersal by birds among the tree species; the efficiency of these dispersers may be dependent upon bird behaviour and size. Smaller birds will be unable to carry whole fruits away from the parent plant, whereas larger birds such as *Corvus corone* may pick-up fruits and carry them away. *Sorbus torminalis* was estimated as having five potential bird dispersers and *Quercus* spp as having two. *Fagus sylvatica* has only one potential bird disperser.

Figure 5.10 Bird fruit preferences for potential seed sources around the Experimental Hawthorn Hedgerows



■ Woodruff-Peacock (1918) ▷ Snow & Snow (1988) - Seed predators
 ◆ Ridley (1930) ○ Snow & Snow (1988) - Pulp predators
 ● Snow & Snow (1988) ✱ Sorensen (1981)

5.6.5 A scoring system to assess seed source and immigration potential.

A scoring system was devised to evaluate the immigration potential of each woody plant species in the EHH surveyed by estimating the potential contribution of seed source abundance in the boundaries surrounding the HHF and bird disperser availability.

The scoring system was as follows:

1. **Boundary score** = a rank relative abundance score was assigned to each species according to their DAFOR values within each of the surrounding boundaries of the Hawthorn Hedge Field (Table 5.11): Dominant = 5, Abundant = 4, Frequent = 3, Occasional = 2, Rare = 1
2. **Seed Source Score** = sum of boundary scores (Table 5.11);

The seed source score allocates a value for the potential contribution of seeds from the surrounding boundaries. However, the resulting scores exclude potential seed sources outside the surveyed area, and thus interpretation needs some degree of care. The scores reflect relative seed source availability within the boundaries immediately surrounding the HHF.

Table 5.11 Seed source scoring system

Boundary Scores Woody plant species	Monks Wood edge	Judith's Hedge	Sauls Lane	Stockin g Close	Seed Source Score
Climbers					
<i>Clematis vitalba</i>	-	F=3	-	-	3
<i>Lonicera periclymenum</i>	F=3	O=2	F=3	-	8
<i>Rubus</i> agg.	D=5	D=5	D=5	D=5	20
<i>Rosa canina</i>	A=4	A=4	F=3	F=3	14
Shrubs					
<i>Cornus sanguinea</i>	A = 4	A = 4	F = 3	R = 1	12
<i>Corylus avellana</i>	O=2	F=3	-	-	5
<i>Crataegus laevigata</i>	R=1	O=2	-	-	3
<i>Crataegus monogyna</i>	A=4	A=4	A=4	D=5	17
<i>Euonymus europaeus</i>	O=2	F=3	R=1	-	6
<i>Ligustrum vulgare</i>	F=3	F=3	-	-	6
<i>Prunus spinosa</i>	D=5	D=5	D=5	R=1	16
<i>Rhamnus catharticus</i>	-	R=1	-	-	1
<i>Sambucus nigra</i>	R=1	R=1	R=1	-	3
<i>Symphoricarpos alba</i>	A=4	-	-	-	4
<i>Viburnum lantana</i>	O=2	O=2	-	-	4
Trees					
<i>Acer campestre</i>	F=3	F=3	-	-	6
<i>Fagus sylvatica</i>	-	-	-	D=5	5
<i>Quercus robur</i>	D=5	F=3	O=2	O=2	12
<i>Malus sylvestris</i>	R=1	R=1	-	-	2
<i>Salix alba</i>	-	R=1	-	-	1
<i>Sorbus torminalis</i>	R=1	R=1	-	-	2

Rubus agg. were estimated as having the highest seed source score amongst all the woody plant species. Of the shrub species, scores for *Crataegus monogyna*, *Prunus spinosa* and *Cornus sanguinae* were indicated as the most abundant seed sources. *Quercus robur* is considered to have the highest potential tree seed source.

3. **Immigration score** = seed source score multiplied by number of potential bird dispersers.

This scoring system aims to quantify the contribution of potential seed source abundance to the immigration process. The number of potential bird species available and their fruit/seed preferences may bias the selection and quantity of seed immigration. The multiplication of the seed source score by the number of available bird dispersers (Figure 5.10) aimed to weigh the scoring system in favour of selected woody plant species with long distance dispersal strategies (Table 5.12).

Table 5.12 Immigration Scores (excluding wind dispersed spp)

Woody plant species	Number of potential bird dispersers	Seed Source Score	Potential Immigration Score
Climbers			
<i>Rubus</i> agg.	10	20	200
<i>Rosa canina</i>	10	14	140
<i>Lonicera periclymenum</i>	6	8	48
Shrubs			
<i>Crataegus monogyna</i>	11	17	187
<i>Cornus sanguinea</i>	11	12	132
<i>Prunus spinosa</i>	6	16	96
<i>Ligustrum vulgare</i>	11	6	66
<i>Sambucus nigra</i>	17	3	51
<i>Euonymus europaeus</i>	8	6	48
<i>Crataegus laevigata</i>	11?	3	33
<i>Viburnum lantana</i>	5	4	20
<i>Rhamnus catharticus</i>	9	1	9
<i>Corylus avellana</i>	0	5	5
<i>Symphoricarpus alba</i>	1	4	4
Trees			
<i>Malus sylvestris</i>	7	2	14
<i>Quercus robur</i>	0	12	12
<i>Sorbus torminalis</i>	5	2	10
<i>Fagus sylvatica</i>	0	5	5

? = *Crataegus monogyna* and *C. laevigata* – bird disperser reference for *Crataegus* spp. only (Snow and Snow 1988)

The results for the climbing species were similar to those calculated from seed sources

previously, with *Rubus* agg. attaining the highest score (score 200), but the inclusion of available bird dispersers alters the seed immigration potential of some of the shrub and tree species. *Crataegus monogyna* was still found to have the highest immigration potential (score 187). *Cornus sanguinea* have the second highest immigration scores (score 132), followed by *Prunus spinosa* (score 96), *Ligustrum vulgare* (score 66) and *Sambucus nigra* (score 51). Although *Corylus avellana* was found to have relatively good seed source availability, immigration is not attributed to the available bird dispersers. Mammalian dispersal is more likely, in this case, as the hard outer casing of the 'Hazel nut' would be less attractive to bird and is more likely to be preyed upon by animals. The potential contribution of mammalian dispersal for immigration potential is not considered in this assessment.

5.6.6 Prediction of immigration success and patterns of colonization

To provide a predictive tool, the immigration scores are divided into degrees of immigration potential (Table 5.13).

Table 5.13 Predicted immigration potential of woody plant species in the surrounding boundaries of the EHH field

Immigration score	Immigration potential	Climbing species	Shrub species	Tree species
Score >100	High	<i>Rubus</i> agg <i>Rosa canina</i>	<i>Crataegus monogyna</i> <i>Cornus sanguinea</i>	
Score 50-99	Moderate		<i>Prunus spinosa</i> <i>Ligustrum vulgare</i> <i>Sambucus nigra</i>	
Score 10-49	Low	<i>Lonicera periclymenum</i>	<i>Euonymus europaeus</i> <i>Viburnum lantana</i> <i>Crataegus laevigata</i>	<i>Quercus robur</i> <i>Malus sylvestris</i> <i>Sorbus torminalis</i>
Score <10	Very low		<i>Corylus avellana</i> <i>Rhamnus catharticus</i> <i>Symphoricarpos alba</i>	<i>Fagus sylvatica</i>

Of the climbing species, *Rubus* agg. were dominant in all the surrounding boundaries of the experimental field. By assessing the availability of number of potential bird dispersers, it can be predicted that there is a high possibility of this group of species colonizing the EHH. *Rosa canina* is also thought to have a high potential to disperse from the surrounding boundaries.

Lonicera periclymenum was assessed as having low immigration potential (scored 48).

The shrub species *Crataegus monogyna* and *Cornus sanguinea*, were assessed as having high immigration potential (scored >100). *Prunus spinosa*, *Ligustrum vulgare* and *Sambucus nigra* were considered as having a moderate immigration potential. Although bird dispersers were available for *Viburnum lantana*, *Crataegus laevigata* and *Euonymus europaeus*, the immigration potential for these species was predicted as low. This prediction reflects the low seed source abundance. The remaining shrub species, *Corylus avellana*, *Symphoricarpos alba* and *Rhamnus catharticus* were either found rarely or had few or no potential bird dispersers. These were regarded as having limited dispersal potential.

Three tree species had diaspores adapted for wind-dispersal (*Acer campestre*, *Fraxinus excelsior*, and *Salix alba*). Of the remaining tree species found in the surrounding boundaries, *Quercus robur*, *Malus sylvestris* and *Sorbus torminalis* was noted as having a low immigration potential and *Fagus sylvatica* was assessed as being very low with rare chance dispersal (scored 5).

5.6.7 Comparison of predicted immigration potential and colonization success

The presence of *Crataegus monogyna* is excluded in the following analyses as the majority of individuals present in the EHH would have derived from the original planted stock. Three climbing woody plant species were found in each of the three hedgerows surveyed: *Lonicera periclymenum*, *Rosa canina* and *Rubus* agg.. A maximum of nine woody tree and shrub species were recorded in the smallest size category (Size-class 1 – the colonizing phase) in Hedge 4. With the exception of *Sambucus nigra* and *Viburnum lantana*, all other woody shrub and tree species were represented in at least one transect of each hedgerow surveyed.

A **Colonization success score** for each woody plant species was assessed by the summed

presence in each size-class in each of the three EHH. For example, a species located in two hedgerows, and present in two size-classes would score the colonization success of four (Table 5.14).

Table 5.14 Comparison of woody plant species dispersal potential with actual presence in the three EHH

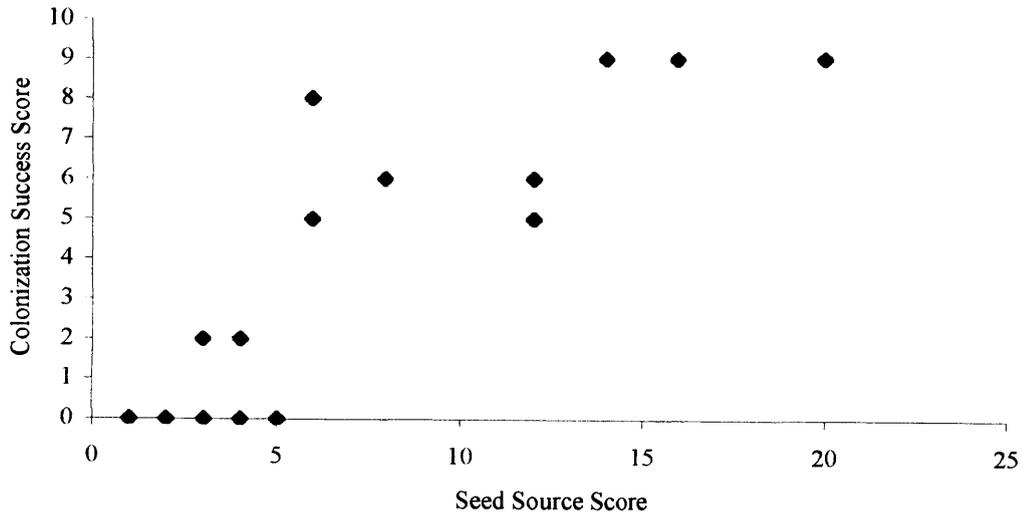
Woody plant species	Potential immigration score	Size-class present in each hedge			Colonization Success Score
		Hedge 1	Hedge 4	Hedge 8	
Climbers					
<i>Rubus</i> agg.	200	1,2,3	1,2,3	1,2,3	9
<i>Rosa canina</i>	140	1,2,3	1,2,3	1,2,3	9
<i>Lonicera periclymenum</i>	48	3	1,2	1,2,3	6
Shrubs					
<i>Prunus spinosa</i>	96	1,2,3	1,2,3	1,2,3	9
<i>Euonymus europaeus</i>	48	1,2,3	1,2,3	1,2	8
<i>Cornus sanguinea</i>	132	1,2,3	1,2	1	6
<i>Ligustrum vulgare</i>	66	1	1	1,2,3	5
<i>Viburnum lantana</i>	20	1	1	-	2
<i>Sambucus nigra</i>	51	-	1,2	-	2
<i>Crataegus laevigata</i>	33	-	-	-	
<i>Rhamnus catharticus</i>	9	-	-	-	
<i>Corylus avellana</i>	5	-	-	-	
<i>Symphoricarpos alba</i>	4	-	-	-	
Tree species					
<i>Quercus robur</i>	12	1,2	1,2	1	5
<i>Fagus sylvatica</i>	5	-	-	-	
<i>Malus sylvestris</i>	14	-	-	-	
<i>Sorbus torminalis</i>	10	-	-	-	
<i>Fraxinus excelsior</i>	? (wind)	1,2	1,2,3	1,2	

The colonization success scores were correlated with the seed source scores and immigration potential scores (Figure 5.11). A significant positive non-parametric correlation was found for seed source (Spearman rank correlation coefficients $n=17$, $r_s = 0.871$, $p<0.01$ two-tailed test), and immigration potential scores ($n=17$, $r_s = 0.848$, $p<0.01$ two-tailed test) with the colonization success scores. These results shows a strong correlation between colonization success and the seed source scoring system and when immigration potential values included the possible contribution of bird seed dispersers.

To test the scoring systems further, the total number of individuals found in the colonization phase, in each of the EHH were combined to obtain the total abundance of individuals (Table 5.15).

Figure 5.11 Correlation between woody plant species colonization success scores and seed source and immigration potential scores within three Experimental Hawthorn Hedgerows

a)



b)

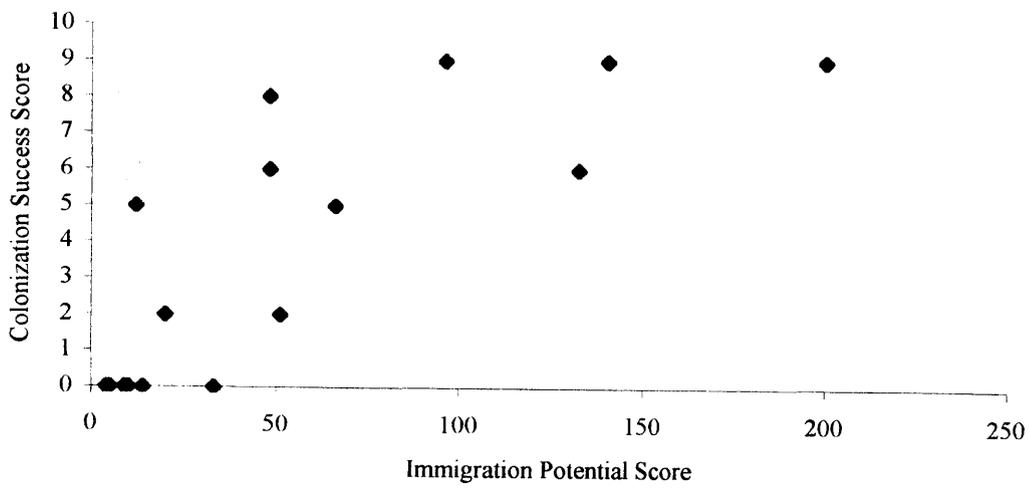


Table 5.15 Total abundance of woody plant species found colonizing the three EHH

Hedge No.	Hedge 1	Hedge 4	Hedge 8	Total abundance
Climbing species				
<i>Rubus</i> agg. spp.	987	1021	762	2770
<i>Rosa canina</i>	587	350	296	1233
<i>Lonicera periclymenum</i>	0	3	20	23
Tree and shrub species				
<i>Prunus spinosa</i>	46	29	70	145
<i>Cornus sanguinea</i>	72	18	4	94
<i>Euonymus europaeus</i>	37	37	4	78
<i>Ligustrum vulgare</i>	2	5	19	26
<i>Quercus robur</i>	4	2	4	10
<i>Fraxinus excelsior</i>	2	2	3	7
<i>Viburnum lantana</i>	1	1	0	2
<i>Sambucus nigra</i>	0	1	0	1

A Kruskal-Wallis test found the difference between the number of individuals (woody tree and shrub species) in each experimental hedgerow ($n = 11$, $N = 33$, $df. = 2$, $K = 0.03$) was non-significant. This suggested that the three types of hedgerow management might not play an important role in determining the abundance of colonizing individuals. The abundance values for each species in each experimental hedgerow were summed to give a total abundance value for each species and used to correlate with the seed source, immigration potential and colonization success scores (Table 5.16).

Table 5.16 Scoring system results with total abundance and abundance ranking

	Seed source scores	Immigration scores	Colonization success scores	Total abundance
<i>Rubus</i> agg. Spp.	20	200	9	2770
<i>Rosa canina</i>	14	140	9	1233
<i>Prunus spinosa</i>	16	96	9	145
<i>Cornus sanguinea</i>	12	132	6	94
<i>Euonymus europaeus</i>	6	48	8	78
<i>Ligustrum vulgare</i>	6	66	5	26
<i>Lonicera periclymenum</i>	8	48	6	23
<i>Quercus robur</i>	12	12	5	10
<i>Viburnum lantana</i>	4	20	2	2
<i>Sambucus nigra</i>	3	51	2	1

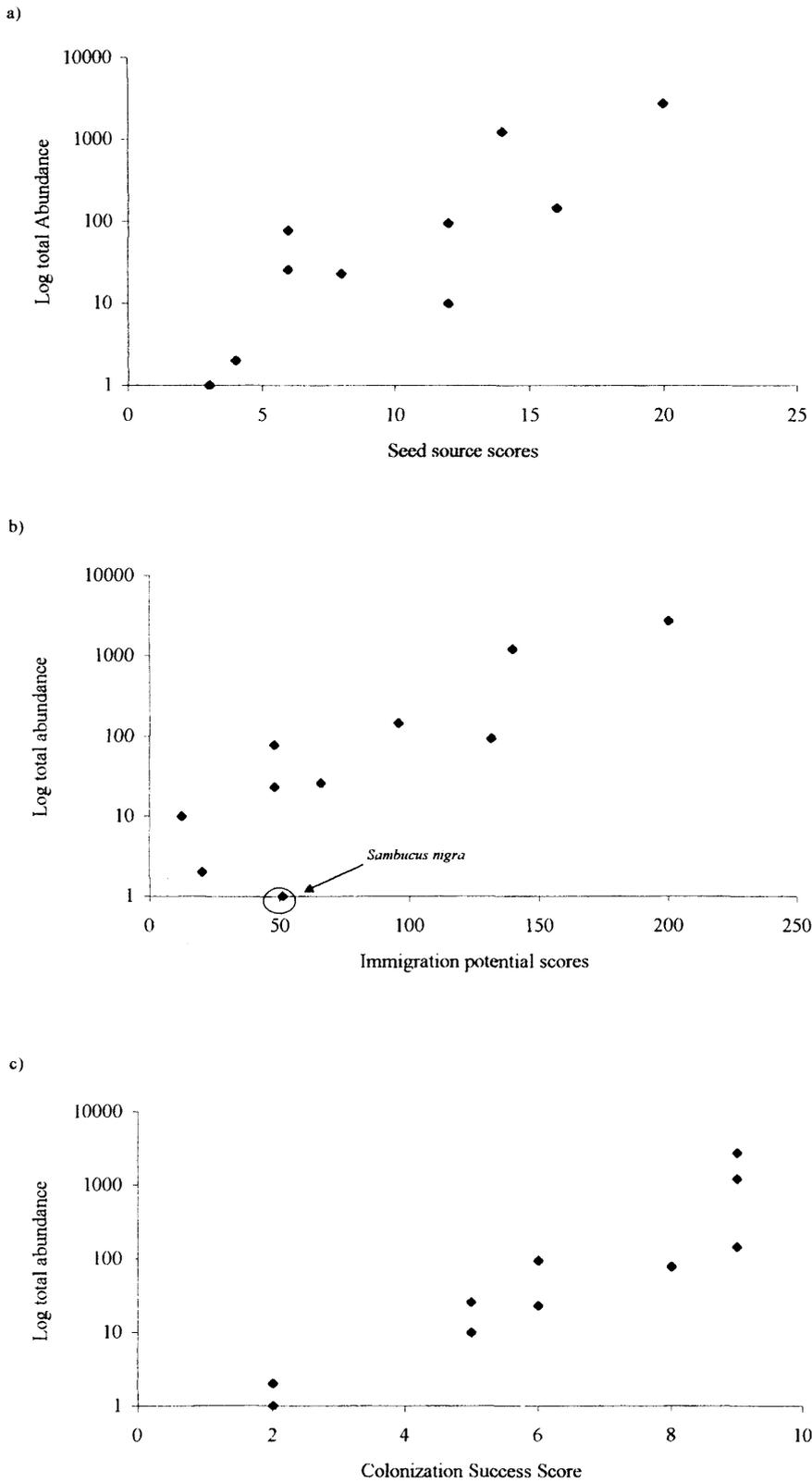
A highly significant correlation ($n = 10$, $r_s = 0.80$, $p < 0.01$) was found between seed source availability and the total abundance of individuals in the colonizing phase. Significant correlations were detected between the total abundance and immigration potential ($n = 10$, $r_s =$

0.767, $p < 0.02$) and colonization success ($n = 10$, $r_s = 0.888$, $p < 0.01$).

The initial plotting of log total abundance and the seed source scores showed a series of outliers, but a linear trend could be detected (Figure 5.12a). Calculation of the immigration potential scores incorporated the availability of bird dispersers, diluted the effect of the seed source abundance and brought outliers into the linear trend. This demonstrates the validity of including of bird disperser availability in the assessment of woody plant species immigration potential. However, the plotting of the immigration potential of *Sambucus nigra* with log total abundance, did create an outlier (Figure 5.12b), this was because of fewer individuals present than expected, or that immigration potential was overestimated. If the inclusion of potential bird dispersers is valid, then this index could direct further research as to why *Sambucus nigra* is less successful in colonizing the EHH, given the availability of seed sources and dispersal vectors. For example germination requirements, abiotic and biotic parameters could be investigated further.

Figure 5.12c displays the highly significant correlation between the log total abundance and colonization success scores. Those woody plant species given high immigration potential and colonization success scores were seen to be most abundant. These analyses suggest the woody plant species immigration and colonization are strongly associated with seed source abundance and bird disperser availability.

Figure 5.12 Correlations with the log total abundance of woody plant species in three Experimental Hawthorn Hedgerows with seed source, potential immigration and colonizing success score values



5.7 Modelling the spatial characteristics of additional woody plant species in three EHH.

The mean number and spatial distributions of individuals woody plant species are displayed in Appendices 5.7 and 8. The patterns of abundance and distributions of each woody plant species were found to be complex (see Section 5.4). In this section, three measures of the spatial pattern of each species, size-class category and EHH are used to simplify and help to decipher underlying processes. Each of these three measures can be used as a basis for modelling spatial distributions:

- spatial variability (calculated from the dispersion index (Greig-Smith 1983));
- spatial correlation between individuals of a species at different stage of development (i.e. size-class correlation within a locality);
- spatial contiguity of the plant species (measured by nearest neighbour analysis techniques).

5.7.1 Spatial variability

The spatial variability in the distribution of woody plant species refers to the extent to which the abundance of individuals varies along the length of a hedgerow. Dispersion is a concept that is closely related to spatial pattern and refers specifically to the arrangements of points on a plane (Dale 1999). A commonly used technique to investigate dispersion of individuals, using counts in quadrats, is the Dispersion Index (Dale 1999, Waite 2000). This index is provided by the variance-mean ratio:

$$I = \frac{S^2}{\bar{X}}$$

Based on the Null Hypothesis, this index assumes that individuals occur independently of each other, so that all regions of the same size have the same probability of containing a given number of individuals (Dale 1999). This dispersion is referred to as a Poisson (random) distribution and the dispersion index, I , will approach unity. Values of I below 1.0 indicate a species that has a more regular distribution (with a standard deviation lower than the mean). Values above 1.0 indicate that the species has a more varied distribution (with a standard deviation greater than the

mean) and has been referred to as a contagious distribution (clumped or aggregated). The significance of departure from the Poisson distribution can be assessed using the Chi squared test if the sample size exceeds 30 (Elliott 1971):

$$\text{Normal variable } d = \sqrt{2\chi^2 - \sqrt{2(n-1)} - 1}$$

If $d \leq 1.96$ the null hypothesis is accepted; $d < -1.96$ suggests a regular distribution and $d > 1.96$ implies a clumped distribution. Although the index of dispersion is an extremely useful way of testing patterns, it is affected by the total number of individuals in the complete sample (Waite 2000). The results of the Chi-squared test in the dispersion data set found that where $I > 1$, all the distributions were significantly contagious ($d > 1.96$). The values of d were proportionally larger, reflecting the large number of samples. As a result, the likelihood of finding non-significant contagious dispersion values was reduced ($d < 1.96$)(Vic Smith pers. com. 1999).

The negative binomial distribution is frequently used to model clumped pattern (Waite 2000). As part of this investigation, negative binomial analyses were performed for data where the sample variances were greater than the mean to test the significance of the contagious dispersions. However, the results could not be tested for significance because of the small number of cases. A negative binomial model was constructed on an Excel spreadsheet and the majority of the contagious dispersions resembled a negative binomial model, the exceptions being the distributions of *Rosa canina* and *Rubus* agg. These species had means lower than the variance; values of $I > 1$ and significance of d indicated contagious distributions. This anomaly is possible due to the contiguity of individuals; few individuals occupying many quadrats along the length of the EHH (wide dispersion).

Care is needed in interpretation of the results from this section; in practice, a mean-variance ratio may reflect a wider-variety of spatial pattern than depicted by the index rationale. Dale (1999) warns that this method should not be used in isolation, and that other aspects of spatial pattern

should be analysed.

Values of I and d for additional woody plant species found in the EHH (by aspect), are shown in Table 5.17 (Appendix 5.9). The values show a considerable range, from 1.0 (*Quercus robur*, *Fraxinus excelsior*, *Ligustrum vulgare*, and more rarely, *Cornus sanguinea*) to over 10 (for *Cornus sanguinea* in Hedge 1 and *Ligustrum vulgare* in Hedge 8). No values less than 1.0 were obtained. The woody plant species are thus classified as having either a Poisson (random) or ‘contagious’ distribution, as identified by this index. No significant differences were found between the other hedgerow aspects (Wilcoxon test for matched pairs) or between each hedgerow (Kruskal-Wallis test) There was a tendency for higher values in the coppiced hedgerow (Hedge 1): *Cornus sanguinea*, *Prunus spinosa*, *Rubus* agg. and *Rosa canina* all attain their highest indices here, suggesting that the coppiced management may influence the spatial variability of these species. Coppice management may encourage vegetative propagation (because of the cut stem bases) and is therefore more likely to create clumped distribution patterns.

Five species were found to have dispersion values equal to 1 (*Cornus sanguinea*, *Euonymus europaeus*, *Ligustrum vulgare*, *Fraxinus excelsior* and *Quercus robur*). These results indicate that some differences in spatial patterns occurred between the three EHH. Individuals of *Ligustrum vulgare*, for example, had dispersion values equal to 1 (random dispersion) in the coppiced and laid hedgerows, but were found to have values greater than 1, (contagious dispersion), in the unmanaged hedgerow. *Cornus sanguinea* and *Euonymus europaeus* displayed a contagious dispersion in the coppiced and laid hedgerows, yet were found to have a random dispersion in the unmanaged hedgerow. The tree species *Quercus robur* and *Fraxinus excelsior* were found randomly dispersed in each experimental hedgerow.

Table 5.17 Dispersion index: Variance/Mean for the distribution of total number of individualsa) each species in Hedge 1 (Coppiced) (per m³)

Hedge 1 (Coppiced)	West				East			
	s ²	x	I	d	s ²	x	I	d
Tree and shrub spp.								
<i>Cornus sanguinea</i>	7.10	0.37	19.19	53.03	3.28	0.25	13.12	64.66
<i>Prunus spinosa</i>	3.06	0.52	5.89	38.13	0.85	0.23	3.70	26.96
<i>Euonymus europaeus</i>	0.86	0.19	4.53	31.51	0.28	0.13	2.15	16.87
<i>Quercus robur</i>	0.03	0.03	1.00	6.50	0.01	0.01	1.00	6.50
<i>Fraxinus excelsior</i>	0.02	0.02	1.00	6.50	-	-	-	-
<i>Ligustrum vulgare</i>	0.01	0.01	1.00	6.50	-	-	-	-
<i>Sambucus nigra</i>	-	-	-	-	-	-	-	-
<i>Viburnum lantana</i>	-	-	-	-	*	-	-	-
Climbing spp.								
<i>Rubus</i> agg. spp.	10.86	5.11	2.13	16.66	27.20	7.82	3.48	25.69
<i>Rosa canina</i>	3.06	0.52	5.89	38.13	0.85	0.23	3.70	26.96
<i>Lonicera periclymenum</i>	*	-	-	-	*	-	-	-

* = only one individual located

b) for each species in Hedge 4 (Laid) (per m³).

Hedge 4 (Laid)	West				East			
	s ²	x	I	d	s ²	x	I	d
Tree and shrub spp.								
<i>Cornus sanguinea</i>	0.09	0.08	1.13	7.12	0.07	0.06	1.17	7.51
<i>Prunus spinosa</i>	0.53	0.22	2.41	17.02	0.58	0.19	3.05	20.95
<i>Euonymus europaeus</i>	0.80	0.21	3.81	25.07	0.13	0.09	1.44	9.97
<i>Quercus robur</i>	0.01	0.01	1.00	5.90	0.02	0.02	1.00	5.90
<i>Fraxinus excelsior</i>	0.03	0.03	1.00	5.90	0.02	0.02	1.00	5.90
<i>Ligustrum vulgare</i>	0.02	0.02	1.00	5.90	0.01	0.01	1.00	5.90
<i>Sambucus nigra</i>	*	-	-	-	-	-	-	-
<i>Viburnum lantana</i>	-	-	-	-	*	-	-	-
Climbing spp.								
<i>Rubus</i> agg. spp.	15.32	6.78	2.26	16.04	9.89	5.99	1.65	11.64
<i>Rosa canina</i>	0.53	0.22	2.41	17.03	0.58	0.19	3.05	20.96
<i>Lonicera periclymenum</i>	0.04	0.02	2.00	14.25	0.02	0.01	2.00	14.25

* = only one individual located

c) for each species in Hedge 8 (Unmanaged) (per m³).

Hedge 8 (Unmanaged)	West				East			
	s ²	x	I	d	s ²	x	I	d
Tree and shrub spp.								
<i>Cornus sanguinea</i>	0.02	0.02	1.00	4.63	0.01	0.01	1.00	4.63
<i>Prunus spinosa</i>	0.87	0.38	2.29	12.81	0.36	0.24	1.50	8.21
<i>Euonymus europaeus</i>	0.03	0.03	1.00	4.63	0.01	0.01	1.00	4.63
<i>Quercus robur</i>	0.02	0.02	1.00	4.63	0.02	0.02	1.00	4.63
<i>Fraxinus excelsior</i>	0.01	0.01	1.00	4.63	0.02	0.02	1.00	4.63
<i>Ligustrum vulgare</i>	2.91	0.28	10.39	40.07	1.34	0.13	10.31	39.86
<i>Sambucus nigra</i>	-	-	-	-	-	-	-	-
<i>Viburnum lantana</i>	-	-	-	-	-	-	-	-
Climbing species								
<i>Rubus</i> agg. spp.	9.21	5.67	1.62	9.00	7.36	5.35	1.38	7.38
<i>Rosa canina</i>	0.87	0.38	2.29	12.81	0.36	0.24	1.50	8.21
<i>Lonicera periclymenum</i>	0.16	0.09	1.78	9.94	0.35	0.16	2.19	12.26

Bold values = results of Chi-squared test (*d*), s² = variance, x = mean, I = Index of dispersion.

5.7.2 Size-class correlation

Spearman rank correlation was used to assess the spatial association between woody plant size-classes and distance along the EHH. Treating each woody plant species in each hedgerow transect separately, the data for size-classes

- 1 and 2;
- 1 and 3;
- 2 and 3;

in quadrat order (equating with distance) were correlated. A high correlation indicates that individuals of each size-class occur in similar positions along the length of the experimental hedgerows. If a correlation was found in the distributions of the three developmental stages, it would provide indication of vegetative propagation and/or adult reproduction within the hedgerow or colonization patterns that were repeated over time. If woody plant species were colonizing as separate cohorts and single individuals, there would be little correlation between size-classes. Correlation values for each species in each experimental hedgerow, by aspect, are displayed in Table 5.18. Due to the large data set, significant correlation values were taken as the maximum value given for 30 degrees of freedom (critical value $0.478 = p < 0.01$, $0.305 = p < 0.05$ (Fowler and Cohen 1992)). A critical threshold of 0.31 was used to test the significance of the size-class correlation and additionally compensates for the likelihood of Type II error. Mean size-class correlates are taken to act as an index of association between individuals in the three size-classes.

Highly significant correlations between individuals of *Cornus sanguinea* in the three Size-classes and distance were found in the coppiced hedgerow (Hedge 1), ($r_s =$ between 0.81-0.91, $p < 0.01$). A clear graduation between the three EHH is apparent for individuals of *Prunus spinosa*, with the highest mean correlation coefficient values each side of the coppiced hedgerow (Hedge 1) ($r_s = 0.39$, $p < 0.05$), intermediate in the laid hedgerow (Hedge 4) ($r_s = 0.29$, n.s.), and no correlation in the unmanaged hedgerow (Hedge 8) ($r_s = 0.06$ n.s.). These results show that *Prunus spinosa* had individuals of different sizes that were highly correlated with distance along

Table 5.18 Positive rank correlation coefficients between individuals in the three size-classes

Association: Size-classes	Rank correlation coefficients															
	West							East								
	1 & 2	Sig.	1&3	Sig.	2&3	Sig.	Mean	Sig	1 & 2	Sig.	1&3	Sig.	2&3	Sig.	Mean	Sig.
Hedge 1																
<i>Cornus sanguinea</i>	<i>0.90</i>	***	<i>0.91</i>	***	<i>0.90</i>	***	<i>0.90</i>	***	<i>0.82</i>	***	<i>0.89</i>	***	<i>0.81</i>	***	<i>0.84</i>	***
<i>Prunus spinosa</i>	<i>0.42</i>	***	0.28	n.s.	<i>0.46</i>	*	<i>0.39</i>	*	<i>0.33</i>	*	0.28	n.s.	<i>0.51</i>	***	<i>0.37</i>	*
<i>Rosa canina</i>	<i>0.36</i>	*	0.08	n.s.	<i>0.33</i>	*	0.26	n.s.	<i>0.51</i>	***	<i>0.31</i>	*	<i>0.43</i>	*	<i>0.42</i>	*
<i>Rubus</i> agg.	0.08	n.s.	0.02	n.s.	0.23	n.s.	0.11	n.s.	<i>0.37</i>	*	0.29	n.s.	<i>0.46</i>	*	<i>0.37</i>	*
<i>Euonymus europaeus</i>	0.16	n.s.	-	-	-	-	0.05	n.s.	0.20	n.s.	0.02	n.s.	0.22	n.s.	0.15	n.s.
Hedge 4																
<i>Euonymus europaeus</i>	<i>0.44</i>	*	0.19	n.s.	0.23	n.s.	0.29	n.s.	-	-	-	-	-	-	-	-
<i>Prunus spinosa</i>	0.19	n.s.	0.22	n.s.	<i>0.47</i>	*	0.29	n.s.	0.21	n.s.	-	-	<i>0.53</i>	***	0.25	n.s.
<i>Rubus</i> agg.	0.29	n.s.	0.12	n.s.	<i>0.31</i>	*	0.29	n.s.	0.13	n.s.	-	-	0.29	n.s.	0.14	n.s.
<i>Rosa canina</i>	0.15	n.s.	0.07	n.s.	0.10	n.s.	0.11	n.s.	0.05	n.s.	-	-	0.07	n.s.	0.04	n.s.
Hedge 8																
<i>Ligustrum vulgare</i>	<i>0.56</i>	***	0.22	n.s.	<i>0.88</i>	***	<i>0.55</i>	***	<i>0.51</i>	***	<i>0.57</i>	***	<i>0.89</i>	***	<i>0.66</i>	***
<i>Lonicera periclymenum</i>	-	-	<i>0.41</i>	*	-	-	0.14	n.s.	-	-	-	-	<i>0.57</i>	***	0.19	n.s.
<i>Prunus spinosa</i>	-	-	0.19	n.s.	-	-	0.06	n.s.	-	-	-	-	-	-	-	-
<i>Rosa canina</i>	0.02	n.s.	0.09	n.s.	0.20	n.s.	0.10	n.s.	0.23	n.s.	0.12	n.s.	-	-	0.12	n.s.
<i>Rubus</i> agg.	0.05	n.s.	0.20	n.s.	<i>0.32</i>	*	0.19	n.s.	-	-	-	-	0.24	n.s.	0.08	n.s.

Significant values in italic, mean correlation values in bold. * = p<0.05, *** = p<0.01.

the coppiced hedgerow: displaying a spatial association between size-classes in this EHH, yet no such association was found in the other two EHH.

Individuals of *Euonymus europaeus* were most highly correlated on the western side of the laid hedgerow (Hedge 4) (between size-classes 1 and 2 ($r_s = 0.44$, $p < 0.05$). Significant correlations were found in the unmanaged hedgerow for *Ligustrum vulgare* ($r_s =$ between 0.51-0.89, $p < 0.01$) and *Lonicera periclymenum* (Western side between size-classes 1&2: $r_s = 0.41$, $p < 0.05$, Eastern side between size classes 2&3: $r_s = 0.57$, $p < 0.01$). *Ligustrum vulgare* and *Lonicera periclymenum* may have a greater tolerance to the shaded conditions; obtaining a higher spatial association between the three size-classes by either reproducing through vegetative propagation or arising from seed production from parent plants *in situ*. The pattern of colonization success could have also resulted from repeated seed deposition by dispersal vectors favouring the taller hedgerow structure.

Significant correlations with distance in the eastern side of the coppiced experimental hedgerow (Hedge 1) were found for individuals of *Rosa canina* within the all three size-classes of the climbing species (mean $r_s = 0.42$, $p < 0.05$). Coefficients for size-classes 1 and 2, and 2 and 3 on the western side of this hedgerow were also significant (1&2: $r_s = 0.36$, $p < 0.05$, 2&3: $r_s = 0.33$, $p < 0.05$). The other significant coefficients found for climbing species was for *Rubus* spp. between size-classes 2 and 3 on the western sides of Hedges 4 ($r_s = 0.31$, $p < 0.05$) and 8 ($r_s = 0.32$, $p < 0.05$).

Significant correlations between any of the size-class for *Fraxinus excelsior* and *Quercus robur* were not found in any of the hedgerows. This suggests that, for these two tree species, no spatial association occurred between individuals in the three size-classes, and that colonizing, surviving and establishing individuals are found in different locations.

5.7.3 Index of Contiguity

Contiguity refers to the extent to which individuals occupy adjacent quadrats within the experimental hedgerows. Highly contiguous distributions suggest either that a species is highly clustered (and thus individuals occur in close proximity) or that the species is ubiquitous (and thus occurs in all, or almost all, quadrats). A Nearest Neighbour Analysis (NNA) was chosen to assess the occupancy of quadrats along the lengths of experimental hedgerows surveyed. The analysis was taken from Turner (1989) and (Forman 1995):

$$q^{ij} = \frac{n_{ij}}{n_i}$$

where n_{ij} = number of grid cells of type i adjacent to type j

n_i = number of occupied cells.

The results indicate whether a population is distributed contiguously along the length of the experimental hedgerows. Values <1 reveal that individuals are contiguous, values >1 indicate decreasing contiguity and values of 2 indicate no contiguity. The NNA was performed on the distribution of the combined size-classes for each species in each experimental hedgerow (Table 5.19).

Table 5.19 Results of the nearest neighbour analysis

Woody plant species	Hedge 1		Hedge 4		Hedge 8	
	West	East	West	East	West	East
<i>Cornus sanguinea</i>	0.63	0.89	1.57	1.91	2	2
<i>Euonymus europaeus</i>	1.43	1.6	1.36	1.5	2	2
<i>Fraxinus excelsior</i>	1.8	-	2	2	2	2
<i>Ligustrum vulgare</i>	2	-	2	1	1	0.8
<i>Lonicera periclymenum</i>	2	2	2	2	1.63	1.17
<i>Quercus robur</i>	2	2	2	2	1	1
<i>Prunus spinosa</i>	1.04	1.33	1.37	1.42	1.27	1.36
<i>Rosa canina</i>	0.09	0.18	0.1	0.5	0.13	0.42
<i>Rubus agg.</i>	0.09	0.06	0.05	0.05	0.02	0.02

Bold = contiguous distributions

There were no significant differences in the NNA values between the two sides of each experimental hedgerow (Wilcoxon test for match pairs) or between hedgerow aspects across the

three EHH (Kruskall-Wallis test).

High contiguity was detected for:

- *Cornus sanguinea*: on each side of Hedge 1;
- *Ligustrum vulgare*: on the eastern side of Hedge 8;
- *Rosa canina* and *Rubus* agg.: in all hedgerow transects.

For *Rosa canina*, contiguity was strongest in the western side of Hedge 1, whereas contiguity of *Rubus* agg. was higher in the unmanaged hedgerow (Hedge 8). Non-contiguous distributions (index ≥ 1) were found for the following woody plant species:

- *Euonymus europaeus*;
- *Fraxinus excelsior*;
- *Lonicera periclymenum*;
- *Prunus spinosa*;
- *Quercus robur* in Hedge 1 and 4;
- *Ligustrum vulgare* on the western sides of Hedge 1 and 4;
- and *Cornus sanguinea* in both Hedge 4 and 8.

These results indicate that for the species *Cornus sanguinea* (on each side of Hedge 1), *Ligustrum vulgare* (on the eastern side of Hedge 8), *Rosa canina* and *Rubus* agg. (in all hedgerow transects), the distribution is such that individuals were found in close proximity.

5.7.4 Development of a spatial distribution model

Whilst each type of the three analyses described above reveals important information about the distribution of species in the EHH, individually they give limited insight. A greater understanding may be achieved by combining these methods of describing spatial distributions. As an aid to explanation and management, it is clearly helpful to apply these results as a basis for modelling the spatial patterns to examine the processes that influence woody plant species colonization in hedgerows. Such a model would be useful to interpret and predict patterns of

colonization and inform management and conservation practices.

The index of dispersion (I) and the mean size-class correlates, for example, can be coupled to provide four categorisations of colonization patterns shown by different woody plant species (Table 5.20). This combination allows the description of woody plant species occurring as single individuals, when mean correlation coefficients (Index of size-class association) are non-significant (<0.31) or multiple stems when mean index of size-class association are significant (>0.31). The Dispersion Index values give a spatial measure of isolation or contagiousity.

A further incorporation of the index of contiguity into this model gives a multifactorial perspective of the spatial patterns (Table 5.21). This additional distribution measure allows the degree of contiguity to be incorporated into the description of distribution patterns for each woody plant species found in the three EHH. These descriptions can be used to interpret observed patterns, to formulate hypotheses and to examine causal mechanisms and spatial processes.

5.7.5 Results of the model

The results of applying the model described above are displayed in Figure 5.13. The two tree species, *Fraxinus excelsior* and *Quercus robur* are classified as spatially spread, isolated individuals in each of the three experimental hedgerows. *Ligustrum vulgare* were also classified as spatially isolated individuals in Hedges 1 and 4. *Lonicera periclymenum* were found as single individuals in Hedge 1, and groups of individuals in the same size-class in Hedge 4, suggesting that this species arrives and colonizes as single individuals, but singular deposits are made in close proximity. In Hedge 8, however, in the unmanaged hedgerow, both of these species are found with multiple cohorts, in close proximity. These results indicate that either repeated colonization events or vegetative propagation was occurring and those individuals were more successful in this taller unmanaged hedgerow.

Table 5.20 Procedure for identifying colonization patterns of woody plant species within the Experimental Hawthorn Hedgerows: Variance/mean ratios and correlation coefficients between size classes.

		Dispersion Index	
		1	> 1
Correlation coefficients	Non significant	(A) Random: single individuals intermittently dispersed	(B) Single individuals, contagiously dispersed
	Significant	(C) Random: multiple stems intermittently dispersed	(D) Multiple stems contagiously dispersed

Table 5.21 Development of model for assessing woody plant species colonization patterns within the Experimental Hawthorn Hedgerows: from Table 5.20 and Index of contiguity

		Index of contiguity	
		1 or >1	<1
Dispersion & Size Class correlation	A	I Spatially spread isolated individuals	
	B	II Singular cohorts not in close proximity	V Single individuals with contiguity
	C	III Spatially spread multiple cohorts or vegetative propagation	
	D	IV Multiple cohorts or veg. propagation in close proximity	VI Multiple cohorts or veg. propagation with contiguity

Figure 5.13 Analysis of the spatial distribution of woody plant species found in three EHH (1)

Significant size-class coefficient threshold $r_s = 0.31$

		Hedge 1		Hedge 4		Hedge 8	
		West	East	West	East	West	East
<i>Fraxinus excelsior</i>	Index of Size-class Association	-	-	-	-	-	-
	Index of Dispersion	1	-	1	1	1	1
	Index of Contiguity	1.8	-	2	2	2	2
	Pattern						
<i>Quercus robur</i>	Index of Size-class Association	-	-	-	-	-	-
	Index of Dispersion	1	1	1	1	1	1
	Index of Contiguity	2	2	2	2	1	1
	Pattern						
<i>Ligustrum vulgare</i>	Index of Size-class Association	-	-	-	-	0.55	0.66
	Index of Dispersion	1	-	1	1	10.39	10.31
	Index of Contiguity	2	-	2	1	1	0.8
	Pattern						
<i>Lonicera periclymenum</i>	Index of Size-class Association	-	-	-	-	0.14	0.19
	Index of Dispersion	*	*	2	2	1.78	2.19
	Index of Contiguity	2	2	2	2	1.63	1.17
	Pattern						
<i>Cornus sanguinea</i>	Index of Size-class Association	0.90	0.84	-	-	-	-
	Index of Dispersion	19.19	13.12	1.13	1.17	1	1
	Index of Contiguity	0.63	0.89	1.57	1.91	2	2
	Pattern						
<i>Euonymus europaeus</i>	Index of Size-class Association	0.05	0.15	0.29	-	-	-
	Index of Dispersion	4.53	2.15	3.81	1.44	1	1
	Index of Contiguity	1.43	1.6	1.36	1.5	2	2
	Pattern						
<i>Prunus spinosa</i>	Index of Size-class Association	0.39	0.37	0.29	0.25	0.06	-
	Index of Dispersion	5.89	3.7	2.41	3.05	2.29	1.5
	Index of Contiguity	1.04	1.33	1.37	1.42	1.27	1.36
	Pattern						
<i>Rosa canina</i>	Index of Size-class Association	0.26	0.42	0.11	0.04	0.10	0.12
	Index of Dispersion	5.89	3.7	2.41	3.05	2.29	1.5
	Index of Contiguity	0.09	0.18	0.1	0.5	0.13	0.42
	Pattern						
<i>Rubus</i> spp.	Index of Size-class Association	0.11	0.37	0.29	0.14	0.19	0.08
	Index of Dispersion	2.16	3.48	2.26	1.65	1.62	1.38
	Index of Contiguity	0.09	0.06	0.05	0.05	0.02	0.02
	Pattern						

Size-class coefficient critical value >0.31 in bold

- = size class correlation taken as non significant

* = one individual of *Lonicera periclymenum* - dispersion taken as 1

Key

- I Spatially isolated individuals
- II Contagiously dispersed single individuals, not contiguous
- III Single individuals with contiguity
- IV Contagiously dispersed, multiple cohorts or veg propagation
- V Contagiously dispersed, multiple cohorts or veg propagation with contiguity

Three colonization patterns were detected for *Cornus sanguinea*. The model detects the progressive colonization of multiple size-classes in Hedge 1. In Hedge 4, individuals within singular size-classes were found in close proximity, whereas, in Hedge 8 only isolated individuals were detected. Single individuals of *Euonymus europaeus* were also spatially isolated in Hedge 8. *Euonymus europaeus* was found to be colonizing as contagiously (clumped) dispersed single individuals in Hedges 1 and 4.

Prunus spinosa was assessed as colonizing the coppiced EHH as multiple cohorts, indicating repeated patterns of immigration or duplication by vegetative propagation. A different spatial pattern was found in the laid and unmanaged hedgerows (Hedges 4 and 8), as single individuals contagiously dispersed. This model indicates a contiguous distribution for the climbing species, *Rosa canina* and *Rubus* agg. Single individuals in close proximity were indicated along Hedges 8 and 4, and the western side of Hedge 1. Both species were found in multiple cohort sizes on the eastern side of Hedge 1.

5.7.6 Testing critical correlation coefficient values

The uncertain aspect of this model is the critical threshold of the correlation coefficients for the spatial association between size-classes (set at 0.31). To test the robustness of this spatial interpretation model, critical correlation coefficients were altered to 0.25, 0.35 and 0.48. Reducing the critical correlation coefficient value to $r_s = 0.25$ changes four out of the total 52 distribution descriptions, (26 correlation results) (Figure 5.14, changes shaded grey). Three changes in pattern occurred in Hedge 4, for *Euonymus europeaus*, *Prunus spinosa* and *Rubus* spp. The fourth change in pattern was found in Hedge 1 for *Rosa canina*. Increasing the critical value to 0.35 had no affect on the initial model result. Four changes occurred when the critical coefficient value was increased to $r_s = 0.48$, (two at 0.37, one 0.39 and one at 0.42) (Figure 5.15). This increase would strengthen the confidence limit (d.f.=30, $r_s = 0.478$, $P < 0.01$).

Figure 5.14 Analysis of the spatial distribution of woody plant species found in three EHH (2)

Significant size class coefficient threshold $r_s = 0.25$

		Hedge 1		Hedge 4		Hedge 8	
		West	East	West	East	West	East
<i>Fraxinus excelsior</i>	Index of Size-class Association	-	-	-	-	-	-
	Index of Dispersion	1	-	1	1	1	1
	Contiguity	1.8	-	2	2	2	2
	Pattern						
<i>Quercus robur</i>	Index of Size-class Correlation	-	-	-	-	-	-
	Index of Size-class Association	1	1	1	1	1	1
	Contiguity	2	2	2	2	1	1
	Pattern						
<i>Ligustrum vulgare</i>	Index of Size-class Correlation	-	-	-	-	0.55	0.66
	Index of Size-class Association	1	-	1	1	10.39	10.31
	Contiguity	2	-	2	1	1	0.8
	Pattern						
<i>Lonicera periclymenum</i>	Index of Size-class Association	-	-	-	-	0.14	0.19
	Index of Dispersion	*	*	2	2	1.78	2.19
	Contiguity	2	2	2	2	1.63	1.17
	Pattern						
<i>Cornus sanguinea</i>	Index of Size-class Association	0.90	0.84	-	-	-	-
	Index of Dispersion	19.19	13.12	1.13	1.17	1	1
	Contiguity	0.63	0.89	1.57	1.91	2	2
	Pattern						
<i>Euonymus europaeus</i>	Index of Size-class Association	0.05	0.15	0.29	-	-	-
	Index of Dispersion	4.53	2.15	3.81	1.44	1	1
	Contiguity	1.43	1.6	1.36	1.5	2	2
	Pattern						
<i>Prunus spinosa</i>	Index of Size-class Association	0.39	0.37	0.29	0.25	0.06	-
	Index of Dispersion	5.89	3.7	2.41	3.05	2.29	1.5
	Contiguity	1.04	1.33	1.37	1.42	1.27	1.36
	Pattern						
<i>Rosa canina</i>	Index of Size-class Association	0.26	0.42	0.11	0.04	0.10	0.12
	Index of Dispersion	5.89	3.7	2.41	3.05	2.29	1.5
	Contiguity	0.09	0.18	0.1	0.5	0.13	0.42
	Pattern						
<i>Rubus</i> spp.	Index of Size-class Association	0.11	0.37	0.29	0.14	0.19	0.08
	Index of Dispersion	2.16	3.48	2.26	1.65	1.62	1.38
	Contiguity	0.09	0.06	0.05	0.05	0.02	0.02
	Pattern						

Size-class correlation coefficient values ≥ 0.25 in bold

shaded grey = changed critical value

- = size class correlation taken as non significant

* = one individual of *Lonicera periclymenum* - dispersion taken as 1

Key

- I Spatially isolated individuals
- II Contagiously dispersed single individuals, not contiguous
- III Single individuals with contiguity
- IV Contagiously dispersed, multiple cohorts or veg propagation
- V Contagiously dispersed, multiple cohorts or veg propagation with contiguity

Figure 5.15 Analysis of the spatial distribution of woody plant species found in three EHH (3)

Significant size class coefficient threshold $r_s = 0.48$

		Hedge 1		Hedge 4		Hedge 8	
		West	East	West	East	West	East
<i>Fraxinus excelsior</i>	Index of Size-class Association	-	-	-	-	-	-
	Index of Dispersion	1	-	1	1	1	1
	Contiguity	1.8	-	2	2	2	2
	Pattern						
<i>Quercus robur</i>	Index of Size-class Association	-	-	-	-	-	-
	Index of Dispersion	1	1	1	1	1	1
	Contiguity	2	2	2	2	1	1
	Pattern						
<i>Ligustrum vulgare</i>	Index of Size-class Association	-	-	-	-	0.55	0.66
	Index of Dispersion	1	-	1	1	10.39	10.31
	Contiguity	2	-	2	1	1	0.8
	Pattern						
<i>Lonicera perichyemenum</i>	Index of Size-class Association	-	-	-	-	0.14	0.19
	Index of Dispersion	*	*	2	2	1.78	2.19
	Contiguity	2	2	2	2	1.63	1.17
	Pattern						
<i>Cornus sanguinea</i>	Index of Size-class Association	0.90	0.84	-	-	-	-
	Index of Dispersion	19.19	13.12	1.13	1.17	1	1
	Contiguity	0.63	0.89	1.57	1.91	2	2
	Pattern						
<i>Euonymus europaeus</i>	Index of Size-class Association	0.05	0.15	0.29	-	-	-
	Index of Dispersion	4.53	2.15	3.81	1.44	1	1
	Contiguity	1.43	1.6	1.36	1.5	2	2
	Pattern						
<i>Prunus spinosa</i>	Index of Size-class Association	0.39	0.37	0.29	0.25	0.06	-
	Index of Dispersion	5.89	3.7	2.41	3.05	2.29	1.5
	Contiguity	1.04	1.33	1.37	1.42	1.27	1.36
	Pattern						
<i>Rosa canina</i>	Index of Size-class Association	0.26	0.42	0.11	0.04	0.10	0.12
	Index of Dispersion	5.89	3.7	2.41	3.05	2.29	1.5
	Contiguity	0.09	0.18	0.1	0.5	0.13	0.42
	Pattern						
<i>Rubus</i> spp.	Index of Size-class Association	0.11	0.37	0.29	0.14	0.19	0.08
	Index of Dispersion	2.16	3.48	2.26	1.65	1.62	1.38
	Contiguity	0.09	0.06	0.05	0.05	0.02	0.02
	Pattern						

Size-class correlation coefficient values ≥ 0.48 in bold
 shaded grey = changed critical value
 - = size class correlation taken as non significant
 * = one individual of *Lonicera perichyemenum* - dispersion taken as 1

Key

- I Spatially isolated individuals
- II Contagiously dispersed single individuals, not contiguous
- III Single individuals with contiguity
- IV Contagiously dispersed, multiple cohorts or veg propagation
- V Contagiously dispersed, multiple cohorts or veg propagation with contiguity

In this study, degrees of freedom ranged between 127 and 246. The testing of the critical value shows that a range of 0.30-0.36 was stable. Patterns of woody plant species most likely to reproduce vegetatively were affected by the strengthening of the test for the index of size class correlation: *Prunus spinosa*, *Rosa canina* and *Rubus* spp. on the eastern side of Hedge 1 and *Prunus spinosa* on the western Hedge 1. Observations in the field do suggest multiple stem growth within the coppiced hedgerow. Differentiation between the level of significance in the size-class correlation results may be a matter of returning to the original data to make further comparisons to find an acceptable choice.

The use of combined spatial analyses has provided a preliminary experimental model as a basis for examining woody plant species distributions and colonization patterns. The results have shown, however, that it may have considerable value in attempting to interpret pattern and process. Results suggest that additional woody species colonizing the three EHH may be influenced by:

1. reproductive ability of individual species;
2. hedgerow management regimes;
3. a hedgerow aspect;

factors not detected when the spatial analyses were used in isolation.

5.8 Comparison of colonization, survivorship and establishment success

5.8.1 Temporal changes 1970-1997: species colonization, survivorship, and establishment.

In this section, comparisons are made between species abundance in each of the three Experimental Hawthorn Hedgerows, and data sets for 1970-1973 made available by researchers at Monks Wood Experimental Station (Appendix 5.10). The aim of these comparisons was to examine similarities and differences in the numbers of individuals and species found colonizing the EHH, and to investigate if patterns of survivorship and establishment could be detected. Although these data were derived from different methods, direct comparisons could be made by

using data for total and mean number of individuals present in each size-class and by hedgerow aspect.

Only one individual of *Cornus sanguinea* was identified in the eastern side of Hedge 1, between 1970 and 1972 (Figure 5.16). This present study revealed a high density of individuals of this species nearest Judith's hedge on both sides of Hedge 1 (See Appendix 5.8). The increasing population of this species can be seen in each of the three size-classes. Individuals were not found surviving in Hedge 8 in any of the previous or present surveys. *Cornus sanguinea* has not successfully established, either in the laid (Hedge 4) or the unmanaged (Hedge 8) experimental hedgerows.

Euonymus europaeus was first recorded as colonizing individuals on each side of Hedge 4 in 1973 (Figure 5.17). Three individuals representing the second size-class were located in Hedge 1 during the 1973 survey. Since then individuals have become established in Hedge 1 and 4. *Euonymus europaeus* was not reported in Hedge 8 in previous studies but limited colonization was observed in Hedge 8 in this current study.

Figure 5.18 presents the temporal variation in the total number of individuals of *Fraxinus excelsior* in each of the three experimental hedgerows. The data from previous researchers reveal that this species was an early colonist of the young hedgerows. In 1970, individuals of *Fraxinus excelsior* were present in each of the three size-classes in Hedge 1 and 4, but fewer individuals were found colonizing Hedge 8. Data collected in 1997 reported a smaller number of colonists in each of the experimental hedgerows surveyed. The high numbers of colonists in the earlier studies may reflect the lack of competition within the young developing hedgerows in the 1970s. On the western aspects, there is little variation in the number of colonists under the three current hedgerow management regimes. On the eastern aspects, however, colonization

Figure 5.16 Temporal change in the mean number of *Cornus sanguinea*

NB: Standard error bars for 1997 data only

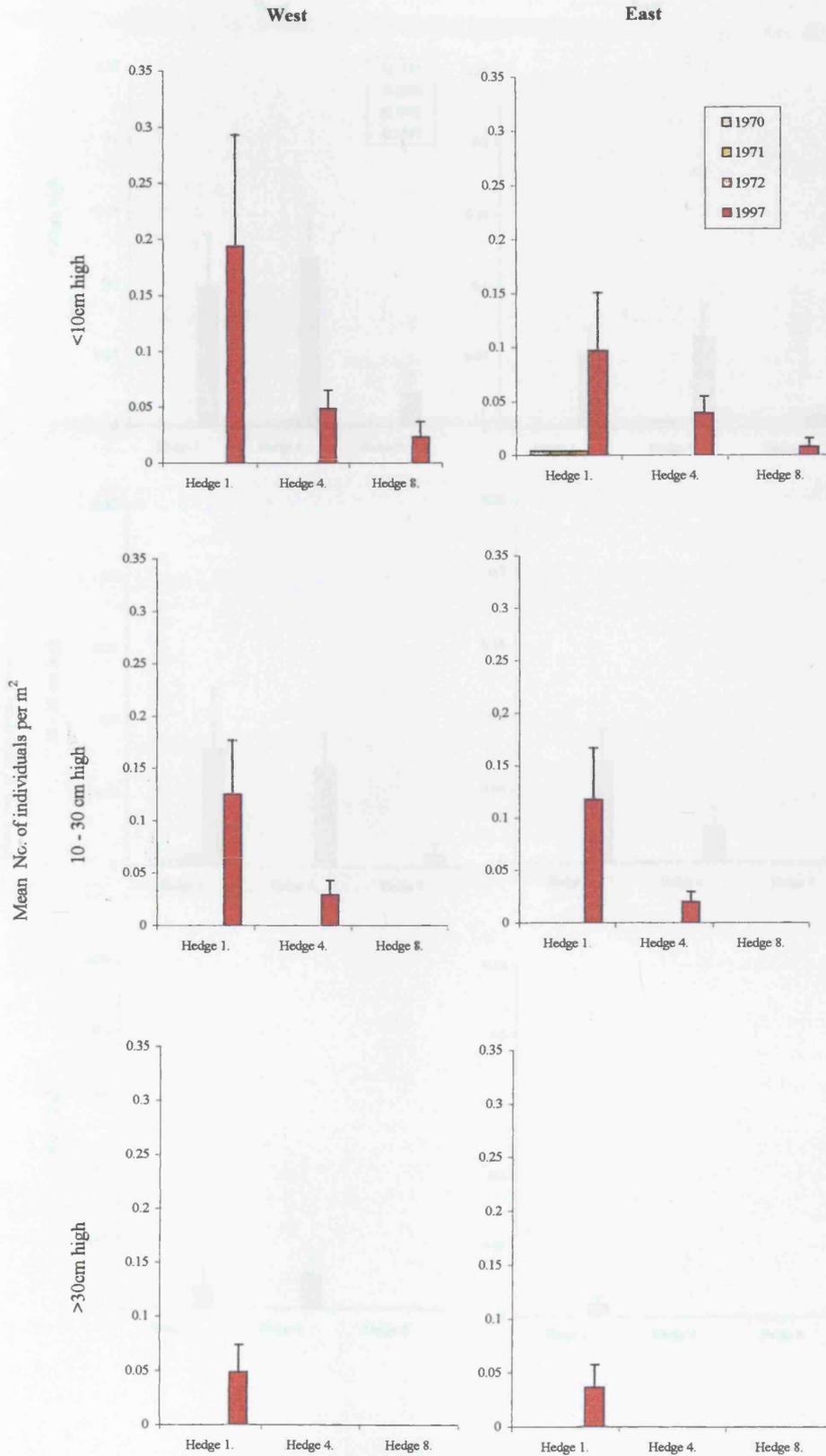


Figure 5.17 Temporal change in the mean number of *Euonymus europaeus*

NB: Standard error bars for 1997 data only

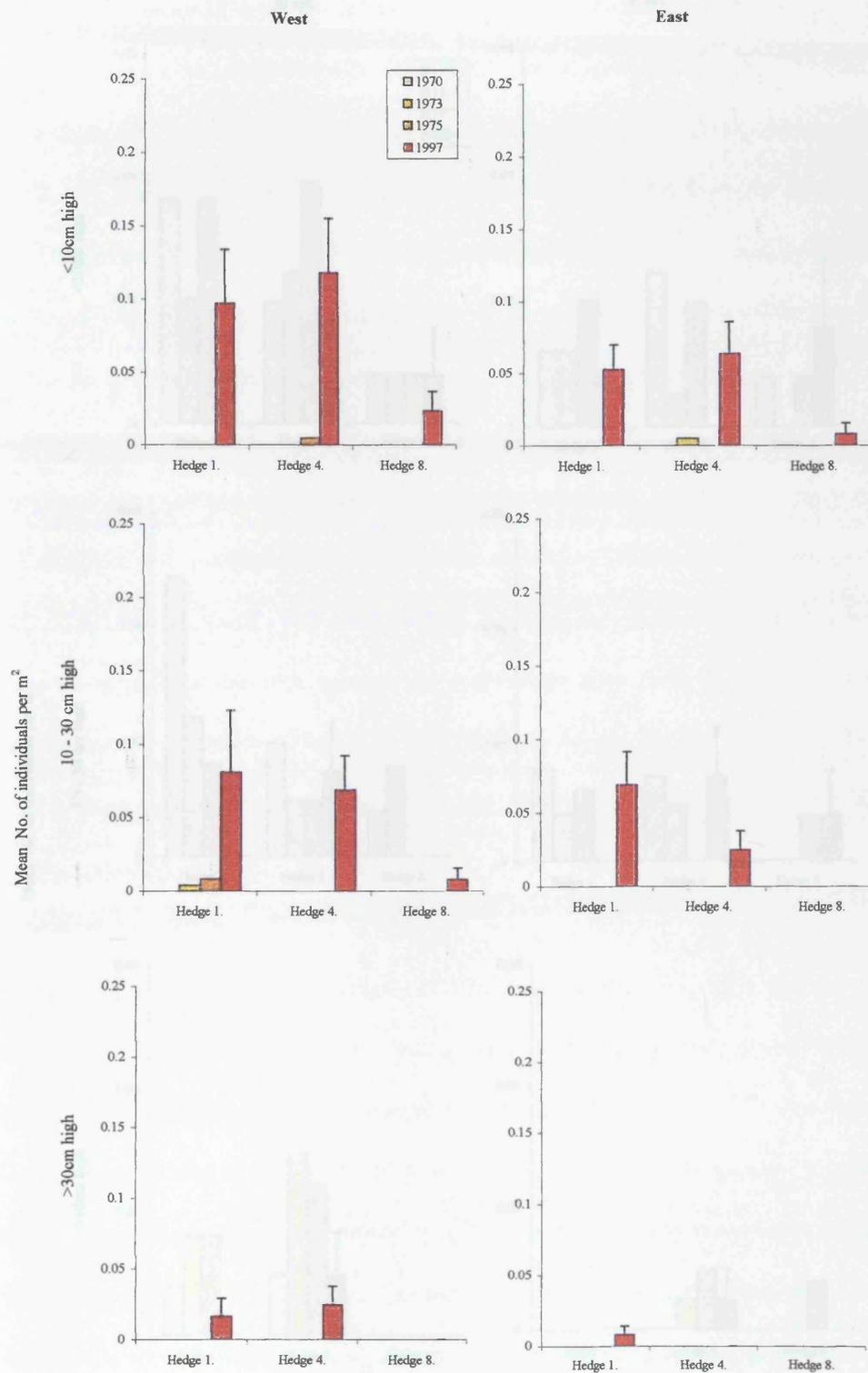
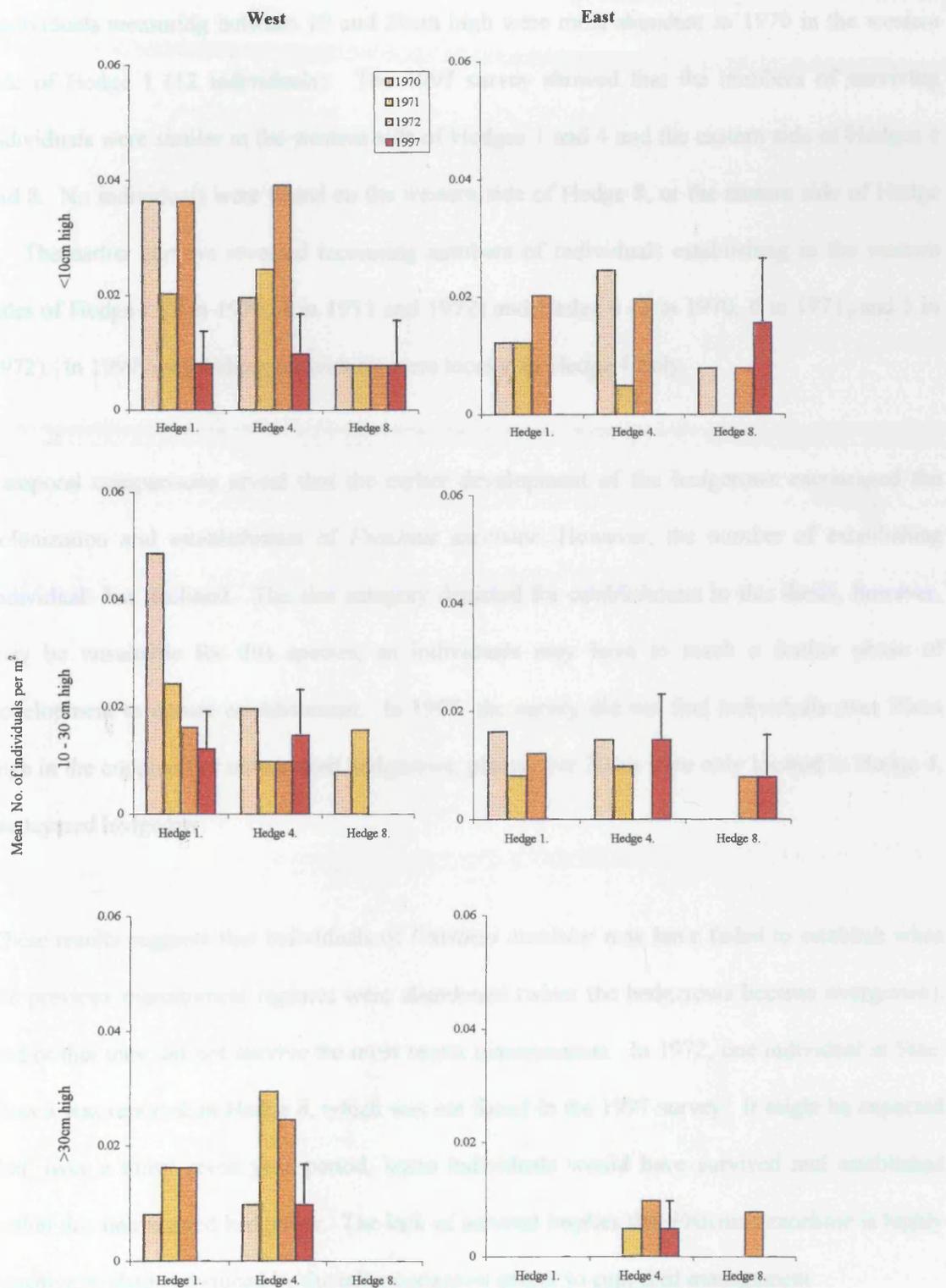


Figure 5.18 Temporal change in the mean number of *Fraxinus excelsior*

NB: Standard error bars for 1997 data only



appears more variable.

Individuals measuring between 10 and 30cm high were most abundant in 1970 in the western side of Hedge 1 (12 individuals). The 1997 survey showed that the numbers of surviving individuals were similar in the western side of Hedges 1 and 4 and the eastern side of Hedges 4 and 8. No individuals were found on the western side of Hedge 8, or the eastern side of Hedge 1. The earlier surveys revealed increasing numbers of individuals establishing in the western sides of Hedge 1 (2 in 1970, 4 in 1971 and 1972) and Hedge 4 (2 in 1970, 6 in 1971, and 5 in 1972). In 1997, establishing individuals were located in Hedge 4 only.

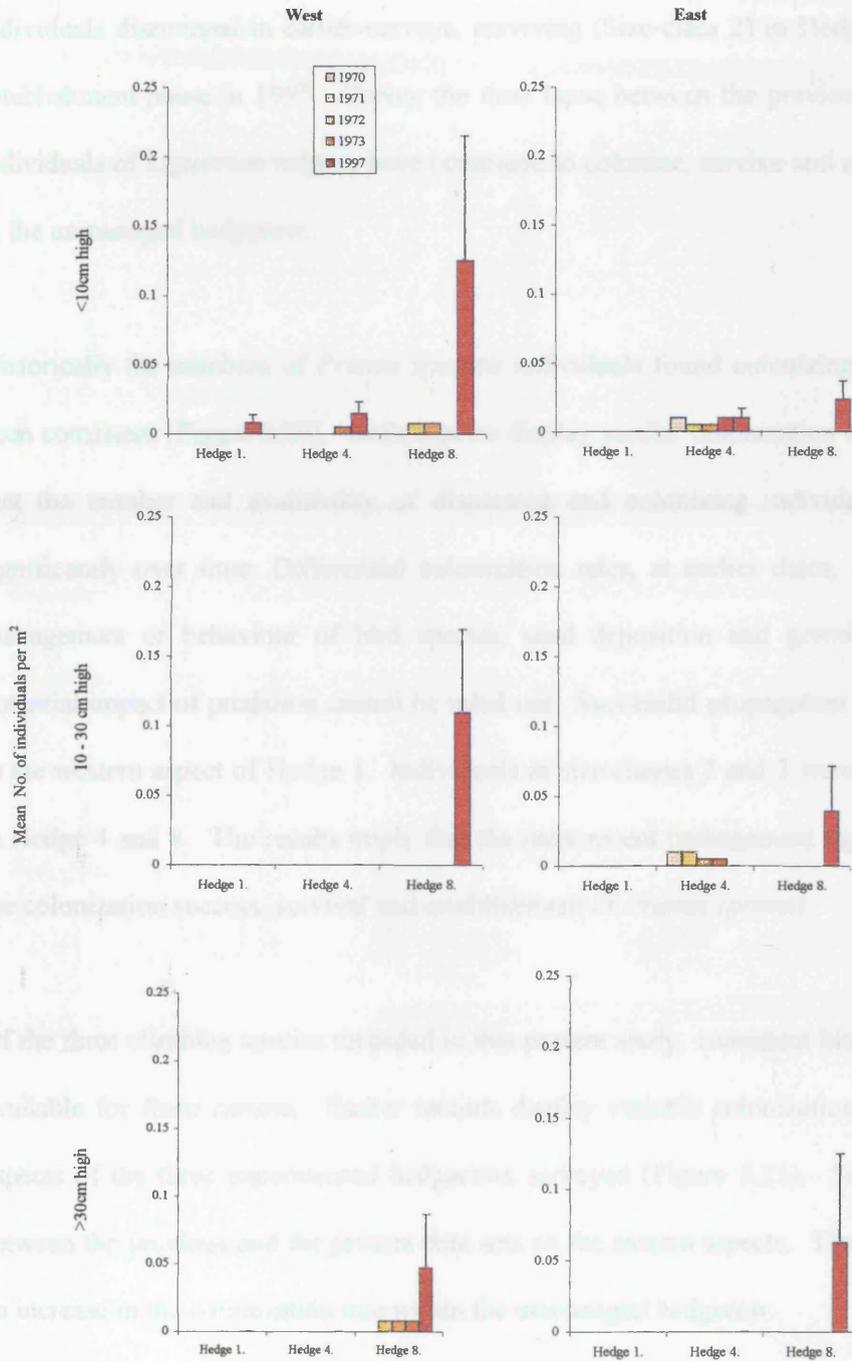
Temporal comparisons reveal that the earlier development of the hedgerows encouraged the colonization and establishment of *Fraxinus excelsior*. However, the number of establishing individuals has declined. The size category depicted for establishment in this thesis, however, may be unsuitable for this species, as individuals may have to reach a further phase of development to ensure establishment. In 1997, the survey did not find individuals over 30cm high in the coppiced or unmanaged hedgerows; plants over 30cm were only located in Hedge 4, the layered hedgerow.

These results suggests that individuals of *Fraxinus excelsior* may have failed to establish when the previous management regimes were abandoned (when the hedgerows became overgrown), and/or that they did not survive the most recent managements. In 1972, one individual in Size-class 3 was reported in Hedge 8, which was not found in the 1997 survey. It might be expected that, over a thirty-seven year period, some individuals would have survived and established within this unmanaged hedgerow. The lack of survival implies that *Fraxinus excelsior* is highly sensitive to shade produced by the taller hedgerow and/or to coppiced management

The colonization of *Ligustrum vulgare* was first detected in 1970, with two individuals located

Figure 5.19 Temporal change in the mean number of *Ligustrum vulgare*

NB: Standard error bars for 1997 data only



on the eastern side of Hedge 4. One individual was first found in the western side of Hedge 8 in 1971 (Figure 5.19). The first individuals colonizing Hedge 1 were found in 1997. None of the individuals discovered in earlier surveys, surviving (Size-class 2) in Hedge 4, had reached the establishment phase in 1997. During the time lapse between the previous and present survey, individuals of *Ligustrum vulgare* have continued to colonize, survive and establish within Hedge 8, the unmanaged hedgerow.

Historically the numbers of *Prunus spinosa* individuals found colonizing Hedge 1 and 4 have been consistent (Figure 5.20). Both aspects display similar colonization events. This indicates that the number and availability of dispersing and colonizing individuals has not changed significantly over time. Differential colonization rates, at earlier dates, could be due to past management or behaviour of bird species, seed deposition and germination success. The potential impact of predation cannot be ruled out. Successful propagation is particularly evident in the western aspect of Hedge 1. Individuals in size-classes 2 and 3 were found less successful in Hedge 4 and 8. The results imply that the most recent management regimes have influenced the colonization success, survival and establishment of *Prunus spinosa*.

Of the three climbing species recorded in this present study, consistent historical data were only available for *Rosa canina*. Earlier records display variable colonization between the western aspects of the three experimental hedgerows surveyed (Figure 5.21). Similarities were found between the previous and the present data sets on the eastern aspects. The comparisons indicate an increase in the colonization rate within the unmanaged hedgerow.

The survivorship of *Rosa canina* is seen to have increased significantly in the coppiced and layered hedgerows by 1997, particularly on the western aspects. Individuals measuring 10-30cm in height were least abundant in the unmanaged hedgerow. These results suggest that the most recent hedgerow management has enhanced the survivorship of *Rosa canina*. Shading within

Figure 5.20 Temporal change in the mean number of *Prunus spinosa*

NB: Standard error bars for 1997 data only

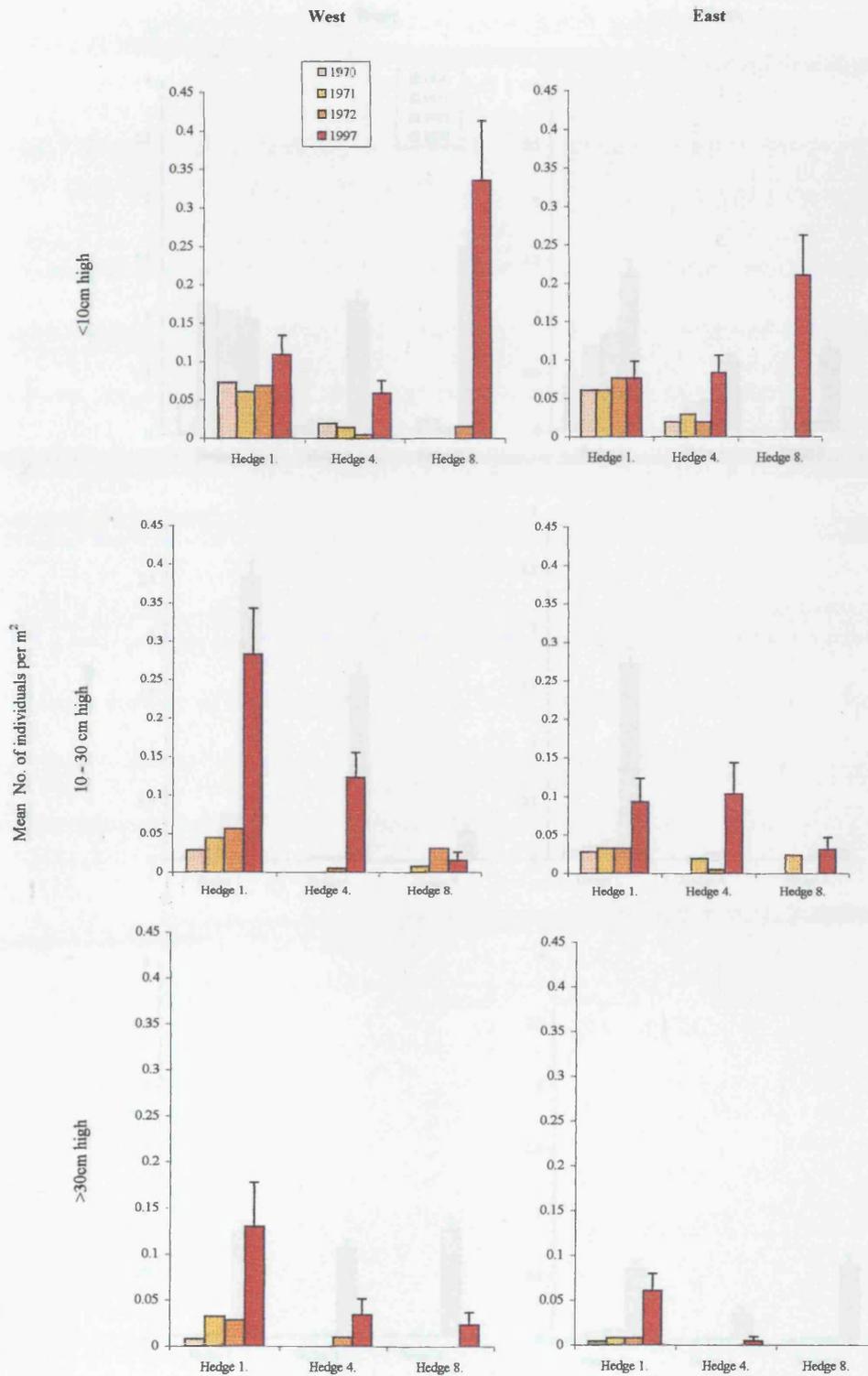
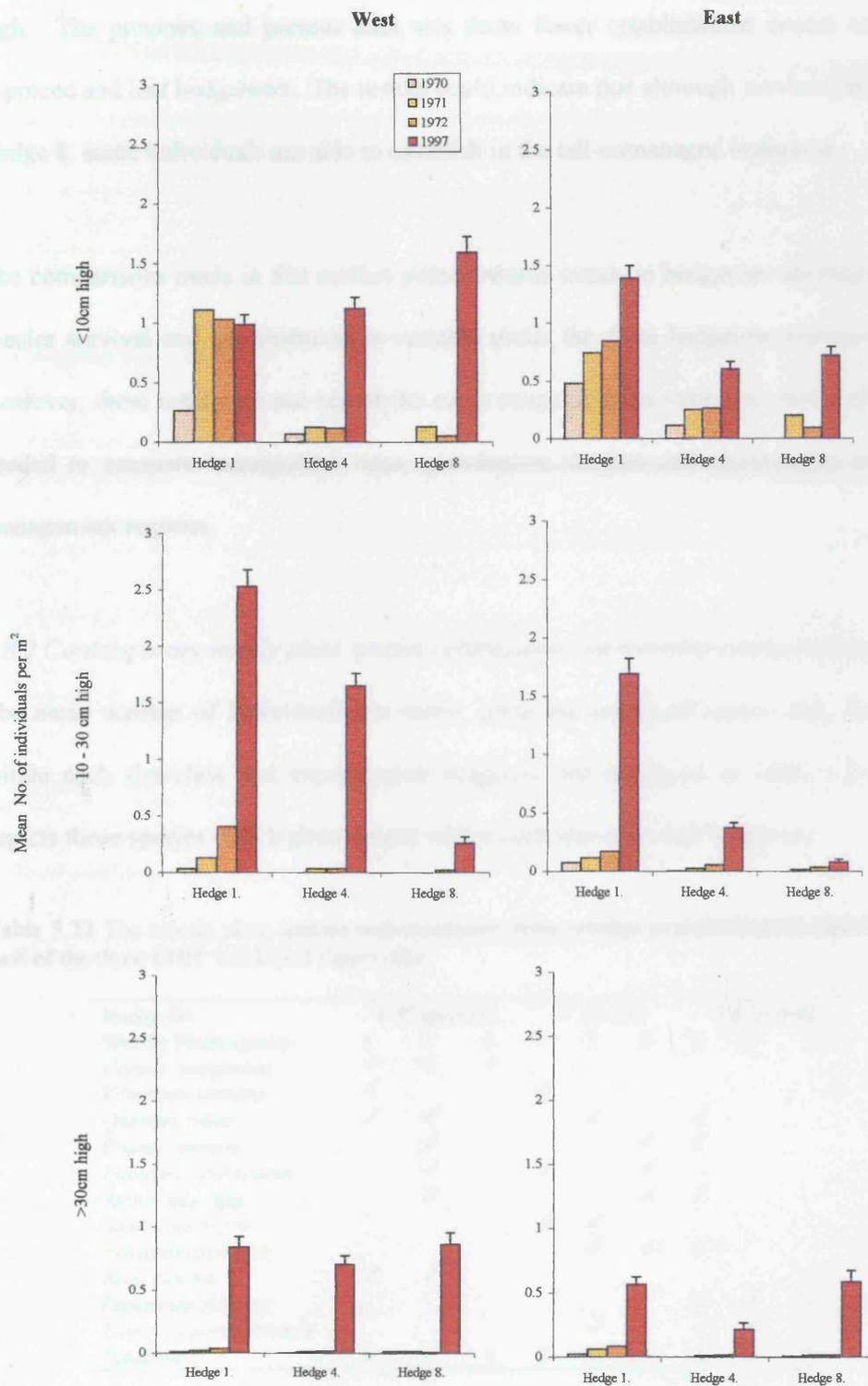


Figure 5.21 Temporal change in the mean number of *Rosa canina*

NB: Standard error bars for 1997 data only



the unmanaged hedgerow may reduce further development. The variability in survivorship between the three management regimes was not reflected by individuals measuring over 30m high. The previous and present data sets show fewer establishment events occurred in the coppiced and laid hedgerows. The results could indicate that although survivorship is reduced in Hedge 8, some individuals are able to establish in the tall-unmanaged hedgerow.

The comparisons made in this section point towards trends in hedgerow development. Woody species survival and establishment is variable under the three hedgerow management regimes. However, these results do not reveal the exact cause of these variations and further studies are needed to compare immigration rates, germination success and survivorship under differing management regimes.

5.8.2 Contemporary woody plant species colonization, survivorship and establishment.

The mean number of individuals per metre, using the combined aspect data, for each species within each size-class and experimental hedgerow are displayed in Table 5.22. Table 5.23 depicts those species with highest means within each size-class and hedgerow.

Table 5.23 The woody plant species with maximum mean number of individuals in each size-class within each of the three EHH: combined aspect data

Hedge No	1 (Coppiced)			4 (Laid)			8 (Control)		
	1	2	3	1	2	3	1	2	3
Woody Plant species									
<i>Cornus sanguinea</i>	✓	✓	✓						
<i>Viburnum lantana</i>	✓			✓					
<i>Quercus robur</i>	✓	✓			✓		✓		
<i>Prunus spinosa</i>		✓				✓	✓		
<i>Euonymus europaeus</i>		✓		✓		✓			
<i>Rubus</i> agg. spp.		✓				✓	✓		
<i>Sambucus nigra</i>				✓	✓				
<i>Fraxinus excelsior</i>					✓	✓	✓		
<i>Rosa canina</i>	✓	✓							✓
<i>Ligustrum vulgare</i>							✓	✓	✓
<i>Lonicera periclymenum</i>					✓		✓	✓	✓
Total No.	4	6	1	3	4	4	6	2	3

Table 5.24 summarises the number of woody plant species colonizing, surviving and establishing in each experimental hedgerow. The unmanaged hedgerow was found to have the

highest number of species in the colonization phase (6 species). The highest number of species surviving was found in the coppiced hedgerow (6 species), whilst the most number of establishing species was found in the layered hedgerow (4 species).

Table 5.22 Mean number of individuals per metre length of hedgerow for each species in each of the three EHH: combined aspect data

	Size-class	Hedge 1 (Coppiced)	Hedge 4 (Laid)	Hedge 8 (Control)
<i>Cornus sanguinea</i>	1	0.29	0.09	0.03
	2	0.24	0.05	0
	3	0.09	0	0
<i>Euonymus europaeus</i>	1	0.15	0.18	0.03
	2	0.15	0.09	0.008
	3	0.02	0.03	0
<i>Fraxinus excelsior</i>	1	0.01	0.01	0.02
	2	0.01	0.03	0.01
	3	0	0.02	0
<i>Ligustrum vulgare</i>	1	0.01	0.03	0.15
	2	0	0	0.15
	3	0	0	0.11
<i>Lonicera periclymenum</i>	1	0	0.02	0.16
	2	0	0.02	0.02
	3	0.01	0	0.07
<i>Prunus spinosa</i>	1	0.19	0.15	0.55
	2	0.38	0.23	0.05
	3	0.19	0.23	0.02
<i>Quercus robur</i>	1	0.02	0.01	0.03
	2	0.02	0.02	0
	3	0	0	0
<i>Rosa canina</i>	1	2.38	1.73	2.31
	2	4.22	2.02	0.34
	3	1.40	0.92	1.45
<i>Rubus</i> agg. spp.	1	4.00	5.03	5.95
	2	5.77	4.60	3.68
	3	3.19	3.24	1.39
<i>Sambucus nigra</i>	1	0	0.01	0
	2	0	0.01	0
	3	0	0	0
<i>Viburnum lantana</i>	1	0.01	0.01	0
	2	0	0	0
	3	0	0	0

Table 5.24 Number of woody plant species colonizing, surviving, and establishing in the three EHH

Hedge No.	1 (Coppiced)	4 (Laid)	8 (Control)
Size-class 1	4	3	6
Size-class 2	6	4	2
Size-class 3	1	4	3

5.8.3 Percentage survivorship of individual woody plant species: comparisons of hedgerow management.

The mean numbers of individuals per metre of the woody plant species found in the three size-classes were used to calculate the percentage of survivorship and establishment. For this analysis, it is presumed that each successful colonizer (Size-class 1) develops into the subsequent survivorship (Size-class 2) and establishment phases (Size-class 3) as set out in Chapter 2. Therefore, those individuals in the latter two size-classes represent previous generations that have succeeded to reach later developmental stages. Results are presented in Table 5.25.

Table 5.25 Percentage values for survival and establishment success.

	Size Class	Hedge 1 (Coppiced)		Hedge 4 (Laid)		Hedge 8 (Unmanaged)	
		West	East	West	East	West	East
<i>Cornus sanguinea</i>	1-2	64.95	120.62	61.23	51.28	0	0
	2-3	38.89	30.77	0	0	0	0
<i>Euonymus europaeus</i>	1-2	83.51	130.19	25.42	31.25	0	0
	2-3	19.75	11.59	0	0	0	0
<i>Fraxinus excelsior</i>	1-2	148.15	0	150.00	0	0	50
	2-3	0	0	66.67	33.33	0	0
<i>Ligustrum vulgare</i>	1-2	0	0	0	0	87.2	169.57
	2-3	0	0	0	0	43.12	161.54
<i>Lonicera periclymenum</i>	1-2	0	0	66.67	0	0	26.75
	2-3	0	0	0	0	0	204.35
<i>Prunus spinosa</i>	1-2	259.63	120.78	206.78	123.81	4.76	14.69
	2-3	45.94	65.59	28.69	4.81	143.75	0
<i>Quercus robur</i>	1-2	166.67	100.00	0	0	0	0
	2-3	0	0	0	0	0	0
<i>Rosa canina</i>	1-2	256.07	121.53	146.93	62.23	16.19	10.85
	2-3	33.12	33.35	42.67	58.02	332.95	751.28
<i>Rubus</i> agg. spp.	1-2	180.37	126.20	104.95	79.91	54.80	70.22
	2-3	57.14	54.00	87.76	51.36	35.99	39.52

The percentage values for survivorship and establishment for each species were examined using a Kruskal Wallis test. Values for each EHH and each hedgerow aspect were compared. Significant differences were not found. Using Wilcoxon Test for matched pairs, percentage values for all the species on each side of each EHH were tested for significance. A significant difference was found for the survivorship of individuals in Hedge 4 ($n = 7$, $T = 1$, $p < 0.05$). All other comparisons between hedgerow aspect proved non-significant.

Variability between hedgerow management and aspect was found when the percentage survivorship and establishment values for individual species were explored. *Cornus sanguinea* and *Euonymus europaeus* are shown to be developing through the survivorship phase in the coppiced and layered hedgerow. Between 30-40% of individuals of *Cornus sanguinea* and 11-20% of *Euonymus europaeus* were establishing in Hedge 1. These two species were not successfully establishing in the layered hedgerow and were not reaching the survivorship phase in the unmanaged hedgerow.

Around 150% of individuals of *Fraxinus excelsior* were found to be into the survivorship size-class in the western sides of Hedges 1 and 4. This suggests that more than one generation of individuals were found in this developmental phase. Fifty percent of individuals were found surviving on the eastern side of Hedge 8, representing a possible 50% mortality rate of colonizing individuals. Sixty seven percent of individuals were reaching the establishing phase on the western side of the layered hedgerow and around 33% of individuals were establishing on the eastern side. *Ligustrum vulgare* was found reaching the survival and establishment phases of development on the eastern side of the unmanaged hedgerow only.

Lonicera periclymenum was found to have the highest percentage reaching the second size-class in the layered hedgerow, but no establishing individuals were found. *Quercus robur* was found to be surviving well in the coppiced hedgerow, but establishment of this species was not located.

More individuals of *Prunus spinosa* attaining Size-class 2 were found on the western side of Hedges 1 and 4. Twenty-seven percent individuals of *Lonicera periclymenum*, 15% of *Prunus spinosa* and 11 % *Rosa canina* that continued to survive into Size-class 2 were low within the unmanaged hedgerow, in comparison to the percentage of individuals reaching the establishment phase; 204%, 143%, 300-700% respectively.

The percentage of individuals of *Rubus* agg. continuing into size-classes 2 and 3 was noted to be relatively consistent across each hedgerow aspect and management regime, although a higher value was obtained on the western side of Hedge 1. These results indicate that this climbing species is well established within each of these experimental hedgerows, regardless of management, and that a sustainable presence of future generations is extremely likely.

5. 9 Summary of results

In the 1970s researchers at ITE, Monks Wood witnessed the first arrivals of additional woody plant species in the newly planted EHH. This study has provided additional information on the patterns and processes of woody plant species colonization, survivorship and establishment.

Pollard *et al.* (1974) proposed that the initial flourish of woody plant species colonization would decline as the experimental hedgerows develop and out-compete new arrivals. In this study, colonizing individuals have been identified in each of the hedgerows surveyed. Autecological accounts of woody plant species for the available seed sources surrounding the Hawthorn Hedge Field, revealed that only two extant species (*Rubus* agg. and *Sambucus nigra*), are able to retain seeds in a long-term seed bank. It is concluded therefore, that new colonists of the remaining ten woody plant species in the EHH are representative of annual immigration.

In this chapter, the relative abundance of seed sources in the boundaries surrounding the Hawthorn Hedge Field, and availability of bird dispersers were shown to be significantly correlated to colonization success and abundance of individuals found within three experimental hedgerows. The question of how distance from seed source influences immigration success, and to what extent bird dispersers extend distances of woody plant species' seed deposition in hedgerows, isolated in agricultural landscapes, need further study.

An examination of the spatial pattern of tree and shrub species diversity produced by individuals

in the colonizing phase displayed distinct differences at the Monks Wood and Judith's Hedge ends of each of the three experimental hedgerows. Climbing species were examined separately and displayed less spatial variation along the lengths of hedgerow. The observed spatial variation in woody tree and shrub species could be due to higher rates of immigration from Judith's Hedge, caused by more frequent bird visitation and seed deposition. However, another cause of spatial pattern could be because seed and seedling predation may be greater at the Monks Wood end. Further studies are needed to elucidate the actual cause of these spatial variations. Observations of bird behaviour patterns could be compared with patterns of plant distributions and the behaviour and distributions of potential predators would be revealing.

The assessment of woody plant species dispersal took account of seed dispersal from birds and did not assess the potential contribution of mammals. A wide-variety of mammals have been recorded in and around the study site. These include: Wood Mice, Bank and Field Voles, Common, Water and Pigmy Shrews, Stoats, Weasels, Grey Squirrels, Harvest Mice, Brown Rats, House Mice, Rabbits, Hares, Heghogs, Foxes, Badgers (passing through), Muntjack, Chinese Water, Roe and Fallow Deer (Sparks pers.com.). All of these species have a potential to feed on seeds or seedlings and may also contribute to the dispersal of seeds within the EHH field. The assessment of potential dispersal and immigration of woody plant species through these potential dispersal vectors is problematic, as the behaviour and feeding preferences of these species are less well known. With further research and observational studies, there is potential to include these species into the immigration model described in this thesis.

If colonization events conformed to traditional successional processes, then wind-dispersed woody plant species would be expected to be the first arrivals in the EHH. Between 1969-1971, Pollard (1973) noted that seedlings of *Fraxinus excelsior* were frequently found colonizing the experimental hedgerows, with the occasional presence of *Acer campestre*. This period would depict the time when the newly planted hedgerows were developing and providing opportunity

for the colonization of early successional species. In this study, far fewer colonizing individuals of *Fraxinus excelsior* were found, seven in total, and *Acer campestre* was absent. Other wind-dispersed species, *Salix* spp., and *Clematis vitalba*, found within the surrounding boundaries, were not located in the experimental hedgerows. Only three established individuals of *Fraxinus excelsior* were located in the layered hedgerow (Hedge 4). Between 1975-1990 the experimental hedgerows had grown into tall-unmanaged hedgerows. The failure of these wind-dispersed species to survive and establish may reflect intolerance to the competition experienced within the hedgerows as the planted experimental hedgerows became established and/or become overgrown. Results also imply that traditional hedgerow laying techniques are beneficial, allowing young trees to develop whilst the rest of the hedgerow is cut and laid down.

McDonnell and Stiles (1983) suggested that immigration of woody plant species would reflect the composition of surrounding seed sources. Peart (1989) proposed that where a higher seed production occurred, a denser seed rain would be produced, leading to greater seed input to colonizable sites. This study shows that, although the majority of the species within the surrounding seed sources were found colonizing the experimental hedgerows, species with a limited seed source and/or few or no available bird dispersers had little immigration potential. For example, the low scores derived from seed source abundance and immigration potential of *Viburnum lantana* were reflected in the low colonization success. In past surveys, it was noted that *Prunus spinosa* was the most abundant of the (mid-successional) shrub species colonizing the EHH: this held to be true in this current study. During the assessment of seed sources surrounding the Experimental Hawthorn Hedge Field, *Prunus spinosa* was found to be the dominant shrub in all four boundaries.

Although the above examples support the views of McDonnell and Stiles, and Peart, the additional contribution of seed dispersal vectors increasing the likelihood of immigration success, and the complexity of spatial and temporal processes that influence colonization, survivorship and

establishment success, is introduced in this thesis.

Prunus spinosa was assessed as having a moderate immigration potential, given the availability of potential bird dispersers and seed source availability. It was not possible to measure germination rates within the three hedgerows surveyed, but individuals in the smallest size-class were most abundant, frequent and at higher densities within the unmanaged hedgerow (Hedge 8). In contrast, survivorship and establishment was found to be greater in the coppiced hedgerow (Hedge 1).

Rubus spp. were the most abundant climbing woody plant species within the seed source boundaries. The immigration potential of these species was assessed to be high and surveys of the experimental hedgerows have shown that seed dispersal, colonization and establishment has been most successful. Life history strategies of these species: dispersal, seed bank persistency, and the ability to propagate vegetatively have enabled these climbing plants to be prolific within the Experimental Hawthorn Hedgerows. The shrub species *Sambucus nigra* also has the ability to retain seeds in a long term seed bank, but does not propagate vegetatively. This species was calculated to have Seed Source Score of 3, and had the highest number of potential bird dispersers scoring an Immigration Potential Score of 51. The assessment predicted a moderate immigration potential for *Sambucus nigra*, yet colonization success was limited. A variety of hypotheses could be investigated to ascertain the causative processes involved. As the seed source was limited, the large number of dispersal vectors may be largely irrelevant, because only a limited number of seeds would be available. Available seeds may have high predation rates and/or *Sambucus nigra* may have a specific germination requirement, such as disturbed ground, not met within the EHH. This example provides validity to the methods of seed source and immigration assessment, as it raises further questions concerning the processes occurring during immigration and colonization.

Pickett (1982) observed three phases of population trends in the colonization of an 'old' field. These phases were not equivalent to the traditional 'stages' of succession. All species that were present in the first 20 years of change were present throughout the time span. Thus, species did not simply come and go, but dominance of species altered through time. Pickett found that for those instances where the ecophysiology, life history characteristics, and population properties are known, they correlated with the population pattern and individual distributions of populations over time. He suggested that differential adaptation and species response were the casual mechanisms of population patterns.

Hooper's Rule (see Chapter 1) suggests that colonization of additional woody plant species is a rare event, stating that approximately one additional species per 30 yards/metres of hedgerow colonizes every hundred years. This study has shown that a maximum of nine tree and shrub species were found colonizing a hedgerow in thirty year old hedgerows, seven species were found in the survivorship phase (4 species nearest Judith's Hedge in the coppiced hedgerow). Within the three experimental hedgerows, four woody tree and shrub species were found within the establishment phase (4 species located nearest Judith's Hedge in the coppiced hedgerow). Over the thirty-year period six woody plant species have maintained a presence within the hedgerow. Some species have increased in abundance, whereas others have declined. During the initial surveys, species such as *Sorbus torminalis*, *Acer campestre* and *Rhamnus catharticus* were found (Pollard 1973). These species were not detected in this study, and individuals have failed to survive and establish. After a flourish of colonizing individuals of *Fraxinus excelsior*, few have reached the establishment phase. Individuals of *Sambucus nigra* and *Virburnum lantana* were found colonizing the EHH for the first time.

A comparison between woody plant species signifies the elements of successful immigration and colonization. A persistent seed bank and the ability to propagate vegetatively are life history strategies that would aid the colonization process (as shown in Chapter 4), but the abundance,

locality and dispersal of seeds are indeed a crucial factor in the initial phases of the immigration process.

Researchers of bird populations on farmland have suggested that tall unmanaged hedgerows are of greater conservation benefit. If taller hedgerows were favoured by many bird species, they would act as foci for recruitment. Guevara *et al* (1986) found that a higher percentage of seeds deposited by birds were found under trees; this may be the case in taller hedgerows. Seeds would be deposited whilst birds were occupying the tall hedgerow habitat. In this study, the woody plant species *Ligustrum vulgare*, *Lonicera periclymenum*, and *Prunus spinosa* were found to be more abundant in the taller, unmanaged EHH. However, these results are not indications of immigration and deposition, but reflect colonization success. There is a need to compare seed deposition by birds by monitoring behaviour in the three EHH and to identify which seeds are being deposited in which hedgerow. In contrast, the results from this study also indicate that keeping hedgerows tall may be detrimental for young individuals: not in the germination and emergent phase of development, but in the survivorship phase. In Hedge 8, the unmanaged hedgerow, the survival and establishment of three shrub species, *Euonymus europaeus*, *Cornus sanguinea* and *Prunus spinosa* were less successful; although colonizing individuals were most abundant in this hedgerow. However, for two other species *Ligustrum vulgare* and *Lonicera periclymenum* establishment was greater. These species may have specific tolerance to the conditions found within tall-unmanaged hedgerows.

To examine the processes that influence the pattern of colonization and development of woody plant species, an analytical model was derived from spatial pattern descriptors. Results indicated that initial colonization occurred with single individuals. This process was particularly evident in the distribution of the tree species *Fraxinus excelsior* and *Quercus robur*, the shrub species *Ligustrum vulgare*, *Cornus sanguinea* and *Ligustrum vulgare*, and the climbing species *Lonicera periclymenum*.

Contagious distributions and correlations between each size-class and distance along the lengths of hedgerows surveyed indicated multiple sized individuals found in close proximity. Significant correlations suggested propagation from vegetative reproduction, repeated colonization events or seed production within the EHH. Contagious distributions with no correlations between size-classes may also indicate repeated patterns of colonization.

The models presented in this thesis are in development. There is a need to test the assumptions made. For example:

a) the seed source assessment index could be tested by sampling larger distances away from the seed source, and the application of genetic matching with seed source and colonizing individuals.

b) the model that estimates the immigration potential of woody plant species could be refined by the following studies at Monks Wood :

- **the monitoring of bird abundance and behaviour in the EHH and surrounding boundaries;** to identify if regular seed dispersal and deposition reflect repeated immigration patterns found in this study;
- **the monitoring of mammal abundance and behaviour;** to identify addition contributions to seed dispersal and impact of predation.

c) The model that describes the spatial distribution of woody plant species found colonizing the EHH could be strengthened by:

- **the monitoring of fruit productivity within the hedgerows;** to identify the likelihood of seed production within the hedgerows attributing to spatial pattern (autocorrelation);
- **the development of a spatial diffusion model;** to quantify spatial patterns of immigration and colonization from Monks Wood and Judith's Hedge.

An ultimate endpoint of these observations is to incorporate seed source abundance, immigration potential, predation, colonization, survivorship and establishment into predictive local or

landscape scale models. Such a models can utilise distance from seed source, dispersal vector availability (bird, mammals, insects and humans), and woody plant species response to hedgerow management to predict sustainability of woody plant species diversity. To some extent, this thesis has indicated that some of these processes can be modelled in such a way. However, the processes of immigration, colonization, survival and establishment may not be so predictable at larger landscape scales. Further studies would need to be carried out in hedgerows under other management regimes (eg. regular mechanical flailing, irregular trimming, and different stages of layered and coppiced hedgerow development) and on different soil types. The degree to which development of newly arrived individuals is successful may also vary in geographic regions in the United Kingdom and further abroad.

The overall conclusion from this study is that seed source abundance, proximity and availability of dispersers need to be assessed at the landscape scale. Increasing woody species diversity in hedgerows remote from potential seed sources is more likely to be governed by chance events. If a remote hedgerow is managed in a detrimental way, in other words, intensively managed with poor habitat quality for birds (or mammals), then the chance of immigration colonization, survivorship and establishment will diminish further. If hedgerows were left unmanaged and provided a suitable habitat and produced fruits, then dispersal vectors may regularly visit; increasing the probability of immigration from nearby seed sources. Results presented in this thesis suggested that for some woody plant species, colonizing individuals may fail to establish. Therefore, tall derelict hedgerows could act as propagule sinks.

Chapter 6 Thesis evaluation

6.1 Evaluation of Methods

6.1.1 Choice of study site locations

The research presented in Chapter 3 examined the distribution of herbaceous and woody plant species along ten transects crossing woodland and Enclosure hedgerow transition zones. The choice of sites for this study was complicated by practical limitations in both the planning stages and fieldwork. On the outset, the distributions of plant species in hedgerows next to small semi-natural ancient woodland plots, or next to larger, commercially managed, woodlands with a remnant ancient woodland flora, could have been examined. Smaller woodlands, however, can “experience” higher proportions of “edge effect” (Chapter 2), and often have few or no Enclosure hedgerows adjoining them. Alternatively, woodland interior and edge plant communities in larger woodlands are considered to be more discernible. Larger woodlands would also have a greater circumference, which would increase the possibility of having hedgerows adjoining them. Although larger woodlands are more likely to have the woody species composition and physical structure altered through commercial management, it was decided that these woodlands would be examined for this thesis. This choice produced a valid and contemporary scenario that reflects much woodland within the British Isles, that has been altered in physical structure and composition by varying degrees of commercial management and disturbance over time.

Preliminary surveys were carried out prior to the study, by using maps and by examining suitable sites in the field. When choosing species-poor hedgerows adjoining remnant ancient woodlands, in many cases where boundaries were detected by documentary evidence, they were later found to be absent in the field (hedgerow removal) or were fence-lines rather than hedgerows. Choice of study sites was affected by land access, suitability of woodlands and number of adjoining hedgerows.

Results in Chapter 3 revealed a disparity in the spatial scales in which herbaceous and woody plant species occurred. In Chapter 4, the scale of sampling was reduced, to reflect the results of herbaceous plant species in the previous chapter and to obtain data from a finer spatial scale. The study site for this chapter was chosen from the ten woodland/hedgerow transects used in the previous study. The woodland transect sampled was considered to have had comparatively less impact from commercial management, with very few exotic woody plant species present and natural regeneration was seen to be occurring. To examine the spatial scale at which immigration and colonization events were occurring, the change in sampling methods and study site choice accommodated a larger spatial scale. The Experimental Hawthorn Hedgerows, at the Institute of Terrestrial Ecology Research Station at Monks Wood, provided an opportunity to observe woody plant species colonization in hedgerows of known origin. These hedgerows were also in close proximity to large areas of relict semi-natural ancient woodland communities, which have had minimal commercial management. However, this field was not suitable for examining the distribution of herbaceous plant species because of the past-history. It was uncertain if relict woodland herbaceous plant communities had survived grassland management, and/or whether the herbaceous plant species composition of the site had been altered in previous grassland field experiments by the Institute of Terrestrial Ecology.

6.1.2 Sampling and experimental design

The complexities of examining edge effects around woodlands create practical difficulties for researchers, who often measure two or three variables to correlate with changes in vegetation composition and structure (Murcia 1995). Environmental variables could be interdependent and in continual flux. For a true assessment, a specialist study should attempt to monitor atmospheric behaviour, edaphic factors and plant species responses over long periods of time. The influence of the surrounding landscape structure on the atmospheric properties and movements also requires further investigation, as it may be relevant in the dynamics of wind-dispersal of plant pollen and seeds. This type of analysis was beyond the scope of this thesis.

Results within this thesis suggest that variation in hedgerow microclimate under different management regimes may ultimately influence plant species colonization and establishment success. As the presence of hedgerows of the appropriate age and location was limited in the study locations of Chapter 3, the management and structure of the hedgerows surveyed were considered to be of secondary importance (Chapter 3). Hedgerow structure was compared in the study of the three Experimental Hawthorn Hedgerows at Monks wood (Chapter 5). Results have shown that further research is needed into hedgerow micro-environments under different hedgerow management regimes and to correlate abiotic variables with woody plant species colonization success.

Interactions between woodlands, hedgerows, and the surrounding landscape are largely uncontrollable and relatively unknown. The movements of dispersers, conditions for seed germination, competition, and predation are all external processes with the potential to determine the presence of additional plant species immigrating, colonization and establishing in hedgerows. This thesis does not address each of these external processes, but infers process by the interpretation of spatial pattern. Results have indicated that these processes could be researched in more detail.

6.1.3 Data replication

Data replication is a major problem with studies set in situ within the environment: the approach taken in this thesis. Murcia (1995) warns of the use of pseudo-replications when sampling across woodland edges. In practice, true replication in the field is very difficult to achieve because of the inherent variability in woodland management practice, planting regimes and landscape history, within or between larger commercially managed woodlands and in adjoining hedgerows.

Sample replication also posed strategic problems in Chapter 4. Bigwood and Inouye (1988) recommended that the accuracy of seed bank estimates could be improved by taking a large

number of small samples, or by sub-sampling larger areas. It was decided to take sub-samples and samples of the seed bank along one woodland transect and along each side of an adjoining hedgerow. To replicate this procedure would create large volumes of samples that necessitate handling in the laboratory and the use of extensive greenhouse facilities. Time constraints and shortage of greenhouse space limited this study to sampling one location.

The major error made in many contemporary analyses is confusing control of events (treatments) with control of the observational process. Circumstances in which 'replication' denotes the ability to repeat a treatment should be distinguished from those in which it means taking repeated observations (Eberhardt and Thomas 1991). There could be a debate as to whether the Experimental Hawthorn Hedgerows at Monks Wood complied with standard experimental conditions. The management of the experimental hedgerows could be regarded as a repeatable process, but the colonization events are not. Hedgerow management has a direct effect on the physical structure of hedgerows. It was understood that the management of these experimental hedgerows has been inconsistent in the past. It is not possible to account for previous regimes, which may have influenced past colonization of woody species, colonization in the experimental hedgerows. The success or failure of past management was expected to manifest itself in the largest size class. Any effect of more recent management events may be evident in all three size classes.

In each of the investigations presented, it was presumed those random or variable events such as:

- a) wind strength and orientation (which may influence the direction and the distance of wind dispersed seeds);
- b) chance biotic interactions (where a bird or mammal may accidentally disperse an adhered or ingested seed);
- c) woody plant species productivity (influenced by phenology, predation and climatic events)

were not possible to replicate. It is understood that the studies within this thesis are representative of conditions and unpredictable events that are possibly unique to the areas studied and the time scales in which each study was performed. It is unlikely that the data presented in this thesis reflected similar situations present in the wider landscape, but these types of studies can indicate the patterns of plant species distribution that may help the understanding of landscape scale processes.

6.1.4 Analysis

Transect sampling is a particularly appropriate method to examine the spatial distribution plant species along environmental gradients (Shimwell 1971, Grieg-Smith 1979), within communities (Grieg-Smith 1952, Greig-Smith 1983) and seed banks (Roberts 1981). The choice of this type of sampling, however, presented problems in the analysis of the results, as many statistical methods require random sampling techniques. Another problematic consequence of this type of sampling method to detect spatial pattern was that much of the data were non-normally distributed, further restricting analysis to non-parametric testing. Data transformation was attempted: no real improvement was gained, or the transformation threatened to dissociate the spatial aspects of the research by removing extreme values.

Throughout the period of post-graduate research, various methods of spatial analysis were researched and tried. It became apparent that very few ecologists have embarked on research quantifying the spatial aspects of plant distribution, beyond the traditional descriptive measures of gradient analysis. Methods of spatial analysis such as spatial diffusion models, used in epidemiology have been used by ecologists to analyse alien plants invasions (Hastings 1996), while in the field of geography, the use spatial statistics, such as autocorrelation, is rapidly expanding with the aid of Geographical Information Systems. It was not until the final stages of writing this thesis that a text (Dale 1999) was published that examined the spatial attributes of plant populations in ecology. Even at the end of this text, Dale (1999) states that the field of spatial pattern analysis in plant ecology is really only just beginning. In order to study spatial

pattern and answer questions about the relationships between pattern and processes that either rise to it or are affected by it, Dale (1999) states that there is a need to be able to detect pattern reliably and to quantify its characteristics. Analyses presented in this thesis are robust methods, and are able to detect patterns reliably; nevertheless, they are mostly descriptive in character. This thesis attempted to obtain the best measures of pattern by combining different methods and used quantitative data where possible in order to identify key spatial characteristics in plant species distribution in hedgerows. It is recognised that the model presented in Chapter 5 interpreting spatial distribution characteristics of woody plant species, is embryonic and can be developed further.

6.1.5 Autecological comparisons

Autecological comparisons made within this research were mainly derived from the work of Grime *et al.* (1988) and Hodgson *et al.* (1995). Although incomplete, this data set is the result of experimental research carried out within the United Kingdom and was thought the most valid, contemporary information at the onset of the thesis. Where possible, further sources of autecological information were gathered. One source not utilised in this thesis was that of the Ellenburg system (i.e. Ellenburg *et al.* 1991). This system was derived to examine the autecological response to climate and edaphic factors in central Europe (Hermy *et al.* 1999). During the later stage of this research increasing number of authors have been using this system to compare plant communities both in Europe and the U.K. (Bossuyt *et al.* 1999, Hermy *et al.* 1999, McCollin *et al.* 2000a, McCollin *et al.* 2000b). It may be pertinent to re-examine the data in this thesis using the Ellenburg values before publication. Further research could also examine if the possibility that edaphic and microclimate gradients exist across the woodland and hedgerow transition zones and whether Ellenburg values of plant communities of the woodland, transition and hedgerow correlate with these gradients.

6.1.6 Interpretation

Considerable care was taken during the interpretation of results in this thesis. In Chapter 3, data for all ten transects were combined to detect trends in the patterns of plant distributions. Analysis of herbaceous plant species diversity did not find a significant difference between transects surveyed, justifying the amalgamation of data.

Bigwood and Inouye (1988) found that seed distributions within the seed bank are generally clustered, although patterns encountered may be due to chance or autocorrelation (Warr *et al.* 1993). In Chapter 4, clusters of seeds within the seed bank were detected for some species, and spatial autocorrelation was considered a significant factor. However, it is debatable whether these patterns are due to chance. Seed deposits could occur in clusters, for instance, deposited by a dispersal vector, albeit biotic (bird or animal droppings) or abiotic (localised wind traps). It is possible, however, that clusters and spatial relationships can occur that are related to the position and productivity of the parent plants within the above ground vegetation, either present at the time of survey or when former parent plants were in place. This poses problems in the interpretation of seed distribution when spatial patterns are examined. The limitations in interpreting processes from patterns of distribution are recognised.

Major assumptions were made in the assessment of seed source abundance in Chapter 5. No account was made for seed sources, other than those in the immediate vicinity of the EHH Field. Some woody plant species are dispersed by both birds and mammals. Birds, in particular, can traverse large areas and cross many landscape elements. There is a possibility that additional individuals plants located in the three EHH have been dispersed from parent plants from further afield. Genetic correspondence and observations of bird and mammal movements may determine this.

6.2 Evaluation of results

Kent and Ballard (1988) promote the use of plant studies that link community ecology and individualistic plant ecology. They state that problems arise when ecologists are unable to relate the understanding attained from individualistic studies with the larger dynamics occurring within communities or vice versa. A deductive approach that interprets descriptive data can guide the formulation of detailed hypotheses at the individual plant level; the results of such hypotheses can then provide valuable insights at the community scale (Kent and Ballard 1988). This thesis examines the dynamics of plant distributions at both the individual and community level. By understanding the mechanisms and processes that contribute towards the spatial distribution of individual plant species this thesis attempts to interpret the consequences of these processes on the plant communities in species-poor hedgerows.

6.2.1 *Distribution of herbaceous plant species of ancient woodland*

Previously, empirical studies have supplied evidence of plant species colonizing hedgerows in close proximity to woodlands of ancient origin (Peterken and Game 1981, Corbitt *et al.* 1999). However, the capability (or spatial scale) of plant species that disperse out from woodland communities is known to vary. The term ‘ancient woodland indicator’ is commonly given to plants restricted to woodlands of ancient origin, pre-dating 1600AD (*sensu* Rackham 1986). Many reasons for the restriction in the distribution of some woodland species have been proposed. Species that do disperse into recent woodlands are found to be tolerant to soil nitrification, suggesting that ancient woodland indicator species are intolerant of nutrient-rich soils (Grime 1979).

Regional variation in the strength of species affinity to ancient woodlands, particularly in the north of the British Isles, could indicate climatic factors and in some cases extreme variation in tolerances to altitude and geology (Rackham 1986). However, some species are anomalous and variations in demography could not be accounted for by soil variation alone. Peterken and Game (1984) concluded that the restrictions on the distribution of woodland plant ‘indicator’

species were more likely to be due to restricted seed production and limited dispersal powers. Indeed, some deciduous forest herbs lack any special seed dispersal mechanism; with seeds simply fall off the parent plant, so that distance of dispersal is often no more than the height of the parent plant's stem (Bierzychudek 1982). Species with heavy anemochorous (wind dispersed) seeds, myrmecochores (ant dispersed) and barochores (falling with gravity) do not favour efficient long distance dispersal (Dzwonko and Loster 1992).

In Chapter 3, ten hedgerows adjoining woodlands with remnant ancient woodland communities were surveyed. Three distinct plant communities were identified across the woodland and hedgerow transition: 1) Species located in the woodland only: *Woodland Group*, 2) species found in both the woodland and hedgerow: *Transition Group* and 3) species in the hedgerow only: *Agricultural / Landscape Group*. Within the first community grouping, species were spatially restricted to the woodland quadrats and showed no signs of colonization success beyond the woodland boundary.

Comparative analysis of autoecological characteristics had shown that the three community types could not be separated by a single life history strategy. Instead, each of the community groups were composed of species that represented a wide variety of strategies: typical of the complexities found in plant community ecology. However, consistent patterns could be discerned. Soil pH, perennial life-history, 'competitive/stress-tolerant/ruderal' (CSR) strategies, transient seed banks, and a capacity for vegetative propagation were all possible determinants of the woodland group. Hermy *et al.* (1999) noted the preponderance of hemicryptophytes, geophytes and ant-dispersed plants found in ancient woodland communities. In this study, the same number of plant species with hemicryptophytes and ant-dispersal strategies were found in the woodland and transition groups, and geophytes were more abundant in the transition community.

In forest soils, the number of viable seeds in the seed bank is low (Kellman 1974, Kramer and Johnson 1987, Warr *et al.* 1993) compared to other habitats (Thompson and Grime 1979, Roberts 1981). The autecological comparisons made in Chapter 4 supported the results in Chapter 3, in that “woodland” herbaceous plant species tend not to be retained within a seed bank for long periods. The seed dispersal of these herbaceous plant species also tended to be spatially limited.

Given the limited regeneration from the seed bank, many woodland plant species would be dependent upon their reproductive capability under conditions of stress (vegetative propagation) for the expansion of populations. The species typically associated with woodlands have limited spatial and temporal dispersal strategies and tend to consist of species that allocate more resources to promote plant longevity (perennials). Woodland herbs can reproduce both by seed and vegetative means (Bierzychudek 1982). Rhizomes, stolons and bulbs produce new individuals near to or attached to the parent plant. This strategy reduces risk to offspring (Grime 1987) and gives a competitive advantage when space is a restricting resource (Lovell and Lovell 1985). This method of multiplication contributes to the mass expansion of individuals. For clonal dioecious (single sex) species, vegetative propagation may be the only method of colonizing new habitats when there is a sexual imbalance amongst the population (van der Pijl 1982). Vegetative reproduction is possibly a response to stress, competition for space and reduced vitality. Strategies of shaded habitats included stress-tolerators, stress-tolerant/competitors, and the intermediate competitive/stress-tolerant/ruderal group. The capacity to produce dry matter under shaded conditions is a result of morphological adaptation and phenology (Henry and Aarssen 1997). Wintergreen and spring flowering (vernal) are the main phenological strategies of woodland herbaceous species, which attain optimum productivity before the tree canopy closes (Bierzychudek 1982).

The effectiveness of vegetative propagation for colonizing new sites is dependent on the ability of a species to spread away from or detach from the parent plant (van der Valk 1992). Results

in Chapters 3 and 4 were consistent with the view that few woodland plants species were able to colonize adjoining hedgerows through vegetative propagation. The spatial scale of this form of dispersal from woodland could be larger than in those herbaceous plant species reliant on continual seed release in the immediate vicinity of a parent plant, as described above. However, in terms of the landscape scale, vegetative spread is inherently local and in the immediate region of the woodland edge. Because of the transient nature of woodland seed banks, the survival of such species must be dependent on viable populations above the ground. If competitive species aggressively use resources (especially space), then selection processes would favour woodland species with vegetative reproduction strategies.

6.2.2 *Herbaceous plant species of agricultural landscapes*

Regional population dynamics are related to life cycles that determine dispersal ability and species longevity (Eriksson 1996). Species with increased mobility are those with 'r' selection strategies. It could be interpreted that 'disturbed landscape species' can operate as a metapopulation within agricultural landscapes. These species are able to colonize spatial and temporal sites (Bergelson *et al.* 1993), and have good core populations in the wider landscape. Dispersal of agricultural (external or landscape) herbaceous plant species may operate in both the spatial and temporal scale. Wind-dispersal is related to spatial dispersal strategies. Life history strategies, such as seed bank persistency and competitive ability, allow populations to persist in a temporal scale. In this thesis, species classified as belonging to the agricultural/landscape group were dominated by competitive annuals or biennials producing seeds with persistent seed banks. These results supported those of other researchers. Hodgson and Grime (1990) and Thompson *et al.* (1998) found that annuals and biennials tended to have persistent seed bank characteristics, whereas long-lived perennials that were associated with more stable environments, particularly within woodlands, were less likely to remain dormant within the soil.

Seed banks of arable soils are mainly composed of annual seeds (Brenchley and Warington

1930, Kropac 1966, Roberts 1981) and can be dominated by one or two species with high densities (Kropac 1966). The frequency of cultivation and the use of modern selective herbicides influences the density and viability of arable seed banks (Roberts 1962). In regularly disturbed habitats, short-lived annuals and biennials tend to have persistent seed bank characteristics. There is often a disparity between the species composition of the seed bank and the corresponding above ground vegetation (Thompson and Grime 1979).

Vegetation within a woodland edge comprises both shade-tolerant woodland plant species and light-demanding plant species from the external landscape (Ranney *et al.* 1981, Matlack 1994a, Fox *et al.* 1997). Evidence from other researchers have shown that arable weeds and other undesirable invasive and highly competitive species are capable of dispersing into woodlands (Kellman 1974, Grubb 1977, Beatty 1991, Warr *et al.* 1994, Csontes *et al.* 1996, Davies and Waite 1998). The 'external' herbaceous plant species have potential to exclude woodland type species by aggressively competing for resources. Csontes *et al.* (1996) found that 42% of species in a plantation seed bank were from external sources; 67% of these were wind-dispersed. Small woodlands, particularly disturbed ones, and, perhaps more significantly elongated woodlands, were found to contain more wind-dispersed (anemochorous) species from the surrounding matrix (Dzwonko and Loster 1989). These wind-dispersed species are not necessarily those that will enhance the quality of species diversity within woodlands, as they mainly consist of agricultural species and competitive colonizers of secondary succession (Janzen 1983). Results from Chapters 3 and 4 demonstrated that wind-dispersed 'external landscape species' were not only dispersing into the woodland edge and but also into adjoining hedgerows, and in each of these habitats they were entering a persistent seed bank. Few of these species, however, were found successfully colonizing the woodland or hedgerow. The woodland edge and hedgerow may act as a "sink" for such species, as seeds, carried by wind, are trapped within existing vegetation.

The implications of “external” species dispersing into woodlands were recognised by Brown and Oosterhuis (1981). If competitive “disturbed landscape species” are able to persist in the soil within woodlands, then subsequent disturbance, such as woodland management, may encourage the establishment of these non-woodland species at the expense of less competitive, less stress-tolerant species. The implication of “disturbed landscape species” being retained in hedgerow seed bank (sink) is that any major disturbance, such as ploughing a hedge-bank, will encourage germination of disturbed species, thus providing propagules (a seed source) that may disperse into nearby woodland edges, and out-compete less aggressive woodland and hedgerow species within the hedge itself.

6.2.3 Herbaceous plant species of hedgerow and woodland edge

Venable and Brown (1993) proposed four models for dispersal strategies: 1) risk reduction, 2) escaping negative effects of crowding, 3) high concentrations of parents and siblings through vegetative expansion, and 4) directed dispersal (see Chapter 2). Chapter 3 revealed that the transition community shared characteristics with the woodland group and those species from the surrounding landscape. Transition and landscape species were more likely to be retained within the seed bank, escaping the negative effects of crowding. However, some transition species also had a capability to propagate vegetatively (strategy 3), whilst others could be dispersed by animal vectors (strategy 4), and consisted of species that were stress-tolerant/competitors, competitors and ruderal strategists and fruit-producers. Plant colonists of recent woodland are more likely to be those that have ruderal and competitive characteristics, and are dispersed by birds (Bossuyt *et al.* 1999).

In this thesis, similarities were found in the composition of the transition plant community to those typically found in secondary woodland. Hovering and flying anemochores (wind dispersed), endozoochores and epizoochores (seeds externally transported) are the best colonizers of secondary woodland (Dzwonko and Loster 1992, Dzwonko 1993, Matlack 1994b). The results of Chapter 4 found that 71% of the of herbaceous plant species in the

transition community in both vegetation and the seed bank were considered to be dispersed by animal or human agencies; similar to those commonly associated with secondary woodland communities.

This thesis did not provide direct evidence of dispersal vectors moving plant species between woodland and adjoining hedgerows. However, the fact that some herbaceous species are located in both the hedgerow and woodland indicated a degree of commonality in colonization success, habitat requirements, and inferred the lack of barriers to dispersal. This commonality also infers that plant species are dispersing between the two habitat types. As the majority of the species were found to be dispersed by animal (or human) vectors, it is suggested that habitat utilisation and movement occur between these two landscape elements. Further studies are needed to substantiate whether woodland edges or hedgerows act as seed sources for such plant species, and in which directions disperser vector movements occur.

6.2.4 Woody plant species

The spatial distribution of shrub species was found to occur at a larger landscape scale than investigations in Chapter 3 and 4 could detect. Chapter 5 focused on the potential contribution of bird dispersal in increasing species richness in species-poor hedgerows. As Fenner (1987) stated, many mid-successional stages of temperate forest seres are often characterised by berry-bearing shrubs, with seeds that are mainly dispersed by birds, whereas seeds of late-successional species tend to have an array of dispersal characteristics. In spite of the dominance of shrub species in mid-successional stages, and their importance in hedgerow ecology, surprisingly little is known about the reproductive ecology of these species (Fenner 1987).

The composition of surrounding vegetation (local species pool, (Zobel 1992)) and availability of seeds and fruits influences the composition of species immigrating into a developing community (Borgegård 1990). The findings in Chapter 5 showed that the composition of seed sources and disperser availability are possible factors when considering the immigration success

of woody shrub species. Within this study, the relative abundance of seed sources in close proximity to the Experimental Hawthorn Hedgerows was found to correlate with additional woody plant colonization success. Dispersal vector availability was also a contributory factor to the immigration processes. However, within the wider landscape, distance of seed/food sources, and behaviour of bird dispersers may determine the scale of dispersal.

Fenner (1987) stated that seeds of berried-plants are likely to disperse very unevenly. He proposed that seeds could be deposited in concentrated groups and often with a mixture of seeds from other berried plant species. Howe (1989) argued that, although some seeds may accumulate under song posts and breeding sites, the majority of seeds dispersed by birds would be deposited singularly, as relatively unprotected seeds and seedlings that would result in isolated individuals. Chapter 5 revealed that the majority of woody plant species found within the EHH were isolated individuals, supporting Howe's view.

Howe (1989) also appreciated that seeds consumed and deposited by larger mammals would be of mixed composition and clumped-dispersed. He proposed that plant species dispersed by large mammals would invest heavily in allelochemicals, lignification and mechanical protection against predation. These strategies would protect against a variety of agents of density-dependent seed and seedling mortality during colonization and establishment. In the absence of large animals depositing seeds within the EHH, it was found that there were other potential causes for the creation of clumping patterns in plant distribution. Clumped patterns can be derived from clonal vegetative growth in situ, or by repeated deposition by a dispersal vector. Density-dependent factors, such as predation, could potentially limit the spatial expansion of these species as well. Adaptive protection against predation, suggested by Howe (1989) for mammal dispersed plant species, may also apply to species reproducing vegetatively.

In unpublished data, Forman and Baudry (1984) found clusters of individuals of forest herbs, nearly at random, down the length of wide hedgerows from woods near Millstone, New Jersey.

They concluded that, rather than forest herbs moving progressively down the hedgerow as a corridor, somehow a species disperses to a point in the hedgerow and spreads in that immediate area (Forman and Baudry 1984). In Chapter 5 of this thesis it was found that clumped or contagious distributions of woody plant species were not always associated with vegetative propagation. Therefore, patterns in spatial distribution could have been derived from multiple or repeated deposition. Further studies would be needed to identify the processes operating and to examine whether the spatial patterns are created by either immigration or predation, and whether species found propagating in situ have defence mechanisms against predation.

7.1 Hedgerows: plant community development

7.1.1 Successionary processes

This thesis has demonstrated that, although hedgerows originate from the manipulation of existing vegetation or are planted, it cannot be assumed that they are immune from ecological processes. Hooper's Rule (see Chapter 2) was based on an assumption that colonization of woody plant species in hedgerows would occur linearly over time. This assumption to date has not been tested and the actual mechanisms and processes that contribute to increasing plant diversity in hedgerows are poorly understood.

It is widely accepted that most types of vegetation are subject to temporal change, both in species composition and relative importance of constituent life forms (Grime 1979). Ecologists have been searching for causative explanations as to why certain plant species are associated with particular community types. Community development through successionary processes is one such possible explanation. Clements (1916) defined succession as a sequential development of plant communities, particularly for the early colonization phase. In such development, it is accepted that when individuals die, other individuals or species replace them and that changes in dominance occur over time (Miles 1987). Researchers have examined colonization sequences in old field successions and in woodlands of varying age (e.g. Pickett 1982, Christensen and Peet 1984) and others have sought to discover deterministic factors to explain alternative pathways in succession (e.g. Halpern 1988, Peart 1989, Barik *et al.* 1996, Burke and Grime 1996, Cullen *et al.* 1998).

Gleason (1917) suggested that developing communities are changing in structure and composition, and that the distribution of individual species is dependent on their environmental requirements. This development in the theory of succession steered empirical studies into

investigating the micro-scale processes, which determine habitat requirements, competitive ability, coexistence, soil and climatic tolerances of plant species (Connell and Slatyer 1977, Noble and Slatyer 1980).

Temporal comparisons of woody plant species colonizing the Experimental Hawthorn Hedgerows have shown that the abundance of individuals and species composition changed not only over time, but as the hedgerows changed in physical structure. Change in hedgerow structure can be either long term, with development into tall linear features or in shorter cycles, relating to traditional coppicing / layering or annual trimming. In the early developmental stages of the EHH, the pioneer species *Fraxinus excelsior* was found to be the most abundant of the woody plant species to colonize. With the exception of those that had established in the laid hedgerow, the majority of colonizing individuals had failed to survive and establish within the coppiced and unmanaged hedgerows. This was probably due to intolerance to the changes in hedgerow structure and the impact of hedgerow management.

Gleason (1917) also proposed that succession was dependent upon the dispersal ability of plant species and the process of immigration. He proposed that seed sources, from which immigrants are drawn, may vary in space and time. Two widely distant, but essentially similar, environments could result in different plant associations. The contribution of immigration processes and the dispersal ability of plants have received less attention, in comparison to other aspects of research into plant community development. This thesis has demonstrated that seed source and seed disperser availability were important processes when examining plant community development in species-poor hedgerows.

As mentioned in Chapter 2, Grubb 1987 stated that the major difference between primary and secondary succession is that many colonizers in secondary succession are dispersed in time rather than through space (Grubb 1987). In this and other research (see Chapter 6) it has been shown that seeds of herbaceous and woody plant species with an affinity to ancient woodland

have a tendency to be transient within the seed bank and have a limited dispersal ability (Chapters 2, 3, 4 and 5). Secondary succession plant communities tend to be composed of species tolerant of conditions found in woodlands, and to have a persistent seed bank and long distance dispersal strategies. This thesis found these characteristics for species located in transitional herbaceous plant community; found in both woodland and hedgerow (Chapter 3 and 4). The climbing woody plant species *Rosa canina* and *Rubus* agg. were found to have successfully colonized and become established in each of the three EHH (Chapter 5). The success of these species was attributed to the abundant seed source, bird disperser availability, seed bank persistency and the ability to propagate vegetatively.

Seeds of later successional woody tree and shrub species tended to be bird dispersed and have transient seed banks (Chapter 2 and 6). In theory, when unpredictable 'safe sites' for germination become available for colonists within a hedgerow, recently dispersed seeds would need to be present for successful colonization. This implies that seeds of later successional species need to be available from continuous immigration. In turn, because of the mutualistic relationship between plant and seed disperser, the seed dispersers would need to be continuously visiting and dispersing seeds into hedgerows. Therefore, the woody plant species composition and their abundance within a developing hedgerow plant community would be dependent upon seed source availability and abundance, and the availability of potential birds dispersers. This was found to be the case in Chapter 5.

In the conceptual model introduced in Chapter 2, a secondary mode of immigration was highlighted. Secondary immigration can arise from persistent seed banks and/or vegetative propagation of relict populations as depicted in secondary succession. In isolated species-poor communities, primary immigration would be restricted to those species with long distance modes of dispersal, with or without dispersal vectors. The composition of the seed bank in species-poor isolated plant communities and the level of disturbance within that community

may determine the contribution of secondary immigration and ultimately the species composition of secondary successional communities.

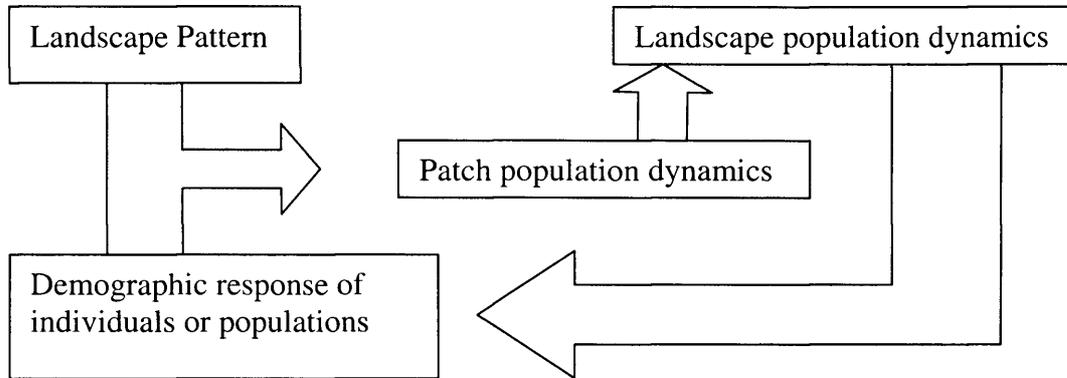
7.1.2 Spatial and temporal dynamics in plant community development

In recent decades, researchers have tended to argue against predictable chains of events that lead to the development of a vegetation climax, favouring dynamic processes that are complex and context dependent. The quest for unifying generalised theories has been abandoned and has now been replaced with the focus on the main mechanisms of succession, modelling, and predicting succession and the understanding of the processes that determine the structure and species composition of vegetation (Miles 1987, McCook 1994)

Metapopulation dynamics focuses on the extinction risks of a global population by evaluating the local population dynamics linked in space and time by inter-patch migration events (Hanski and Gilpin 1991, Hanski *et al.* 1995). Smaller and spatially related habitat patches may be capable of sustaining viable populations through metapopulation dynamics and the presence of many small and fragmented habitat patches could contribute to the biodiversity of the landscape as a whole (Hanski 1997; 1999). However, some taxa with limited dispersal or migratory ability may react more slowly to changes in the global population and may thus be under greater risk of stochastic extinction processes. Immigration, colonization and establishment into neighbouring patches may be determined by landscape pattern and the demographic response of individuals or populations, and in turn the dynamics of populations may be determined by processes occurring within the landscape (Figure 7.1).

Processes that occur in inter-patch regions may play an integral part in landscape population dynamics (Merriam 1988, Hanski 1997) and it is in this context that hedgerows may play an important role in the dynamics of plant populations within agricultural landscapes.

Figure 7.1 Systems driving populations in a landscape mosaic: Landscape pattern and individual demographic behaviour combine to shape population dynamics in patches (after Urban and Shugart 1986).



There is a need to divide and simplify interactions and processes that occur at both landscape and local scales, as the present level of understanding is limited at the present by conceptual development. The source-sink model offers an additional concept to help understand spatial processes and is perhaps more accessible to those interested in the formation of plant communities. However, Kadmon and Tielbörger (1999) pointed out that there were virtually no experiments that test for the existence of sources and sinks in natural plant populations.

To date, the basic criterion for identifying source-sink or metapopulations is that dispersal should occur between local populations. In metapopulations, colonization and extinction events of a larger population occurs at local levels. If populations are becoming locally extinct on a regular basis, it may reflect an inability of individuals to reproduce and maintain viable populations (sink population). It can be difficult to identify sink populations in remnant vegetation and because of the dynamics of remnant populations over time (Eriksson 1996). Seed dormancy is a factor that could decrease the likelihood of detecting strong evidence of source-sink dynamics (Kadmon and Tielbörger 1999). This thesis was able to infer that continuous immigration was occurring in the experimental hedgerows at Monks Wood as mainly bird-dispersed and transient woody plant species were colonizing the EHH. Temporal immigration was inferred from the presence of individuals in three different size classes.

Directed dispersal from high-quality patches, as defined by some independent criteria, to low quality patches could also indicate source-sink populations (Eriksson 1996). The thesis did not provide direct evidence of immigration occurring via directed dispersal. Results indicated that directed dispersal could occur but further research in the movement of dispersal vectors is required for confirmation.

Sink habitats are also defined when immigration from external seed sources exceeds mortality (Kadmon and Tielbörger 1999). Comparisons between the abundance of the woody plant species found in each of the three size classes indicated that, for some species, the experimental hedgerows were acting as seed sinks, and for other more established species, the experimental hedgerows had become seed sources.

Chapter 5 also revealed that colonization, survivorship, establishment and extinction processes, were context dependent, with hedgerow development and structure influencing sink function. Thus, 'sink function' could be seen as a dynamic process, changing over time: equating with successional processes. Studies such as those presented in this thesis can contribute to the understanding of the interactions between spatial and temporal dynamics of plant species, and how complex processes determine the spatial configuration of plant populations in the landscape.

Results from this thesis strongly suggest that hedgerow habitats may act as sinks for many plant species or sources for others. Diffendorfer (1998) proposed that the term 'sink' reflects complex processes and that a response of species to a habitat or 'sink' conditions is variable, and dependent upon life history characteristics and habitat requirements. Cyclical changes in species composition of a sink could result from the rise or retention of dormant propagules under varying environmental conditions (e.g. climate, disturbance or management). Watkinson and Sutherland (1995) also warn that population change could also be the result of pseudosink

dynamics: when a population in a poor habitat is supported by immigration allowing a few individuals to survive.

Eriksson (1996) presented a hypothetical relationship between dispersal capability and persistence over time in the context of metapopulation theory. This supports the proposed conceptual model in Chapter 2, where primary and secondary immigration processes contribute to the dynamics of plant populations in the landscape. In Eriksson's model, space and time control the capacity of plant communities to respond to regional dynamics. Plant 'metapopulations' can be retained in the landscape in the form of remnant populations. Therefore seed or propagule dormancy separates the controlling factors that determine the spatial and temporal dynamics in animal and plant populations, although dormancy does occur for some organisms in the animal world but generally not with animals that have been used to illustrate metapopulation dynamics to date. A habitat may act as a seed sink for a period of time and then revert to or change into a seed source as conditions or circumstances change or vice versa. For animals, once extinct within a local population, recolonization is the only way populations can re-emerge.

Metapopulation theory and the source-sink model are in the developmental stage, and aim to incorporate species immigration, colonization and sustainability of populations within contemporary landscapes. There is a grey area within the development of both theories, and perhaps in time, each will be considered part of the same dynamic process. As yet, metapopulation theory has focused upon the movement of mobile organisms, such as mammals and insects, and has been widely accepted in population biology and beyond, as a method to monitor the sustainability or maintenance of populations in the wider landscape. This field of research has yet to fully incorporate the landscape dynamics of vegetation development.

Further development in the theory is needed to understand the mechanics and the spatial dynamics of vegetation development in the wider landscape **over time**. A model of vegetation

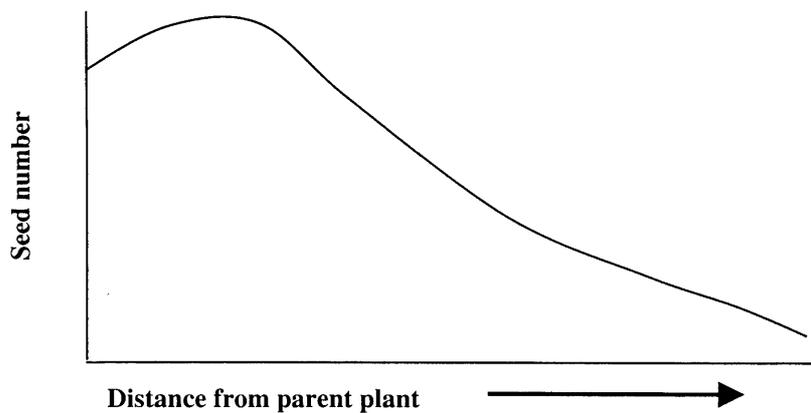
development not only needs to incorporate seed-source availability, seed dispersal and life history characteristics of individual species, but also the impact of temporal changes in habitat structure and composition, and species abundance.

7.1.3 Modelling immigration processes

Plant immigration can be limited by the lack of seed source (McClanahan 1986, Tilman 1997), distance of seed source (Dzwonko and Loster 1987, 1988, Allen 1997), promoted by propagules adapted for long distance dispersal (Noble and Slatyer 1980, McClanahan 1986), and availability of dispersers. Once a fruit is taken from a parent plant, the behaviour of a dispersal vector will determine where and when the seeds within the fruit will be deposited. There have been few empirical studies on the movement of seeds by dispersal vectors. However it may be assumed that many mammals and invertebrates that disperse seeds are influenced by habitat quality and habitual behaviour. Behaviour patterns in birds have been shown to determine the habitat in which the seeds are dispersed. Existing vegetation within developing sites can act as a recruitment focus, promoting the establishment of bird-dispersed woody plant species (McDonnell and Stiles 1983, Guevara *et al.* 1986). This successional process is called nucleation (Yarranton and Morrison 1974), and incorporates directed dispersal theory. It is possible that hedgerows could act as recruitment loci for shrub species, particularly when hedgerows provide fruits that encourage the visitation by bird or other dispersal vectors.

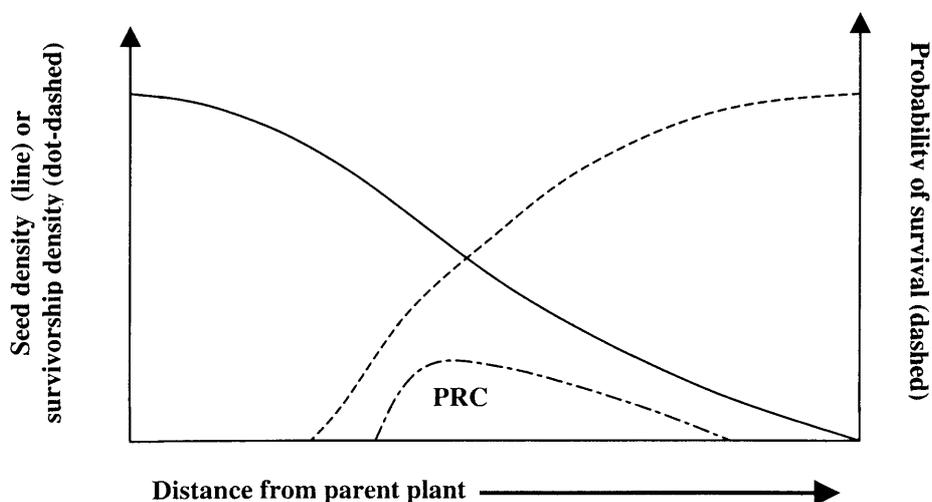
Birds can extend the natural seed-fall area by increasing the diameter of a seed shadow produced by gravity (Janzen 1970, Hoppes 1988). Seeds falling beneath parent plants create a concentrated food source for foragers (Figure 7.2). The further a fruit or seed is dispersed away from the parent plant reduces the risk of predation and increases the chance of successful germination (Webb and Wilson 1985, Barik *et al.* 1996, Barot, *et al.* 1999). Therefore, plants that attract dispersal vectors should be favourably selected for, against those with limited dispersal.

Figure 7.2 The pattern of seed rain from a parent plant (after Harper 1977).



As described in Chapter 2, many hedgerow tree and shrub species produce seeds and berries that are attractive to dispersal vectors: some birds species are particularly important, utilising this additional food source. Species of birds less sensitive to habitat fragmentation are more mobile and deposit and disperse seeds within the wider agricultural landscape. If directed dispersal were taken to represent *immigration fitness*, then shrubs and trees are very likely to be successfully dispersed. Janzen (1970) proposed that population recruitment occurs in a region where the benefit of dispersal and the probability of survival (or forces of extinction) are at equilibrium (Figure 7.3).

Figure 7.3 Janzen's (1970) distance hypothesis model of tree recruitment. Seed density is the solid line, the probability of survival is the dashed line. Consequently, the population recruitment curve (PRC) is at some distance away from the parent tree (Hutchings 1986).



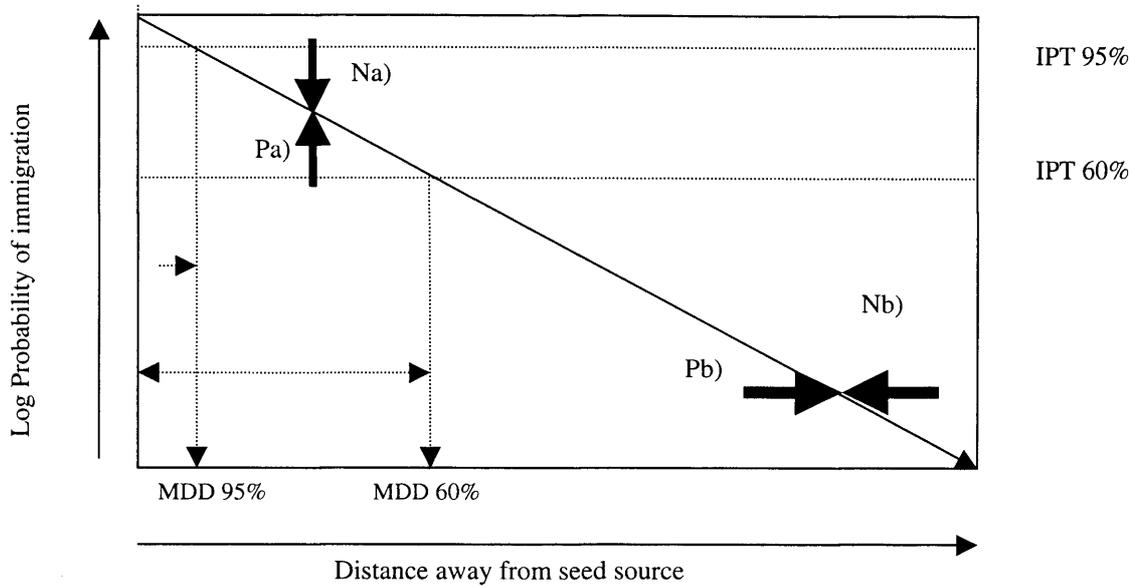
In the context of this thesis, the relative abundance of woodland seed sources and availability of bird dispersers were found to promote immigration potential of woody plant species in species-poor hedgerows. Plant immigration, described in Chapter 2, is assumed to be dependent upon seed source composition, dispersal mode, availability of dispersal vectors, and distance to new habitat. The topic of immigration is important for ecologists today as, increasingly, researchers are directing their efforts towards gaining a holistic view of landscape function, habitat restoration and creation. The distributions of herbaceous plant species in Chapters 3 and 4 were found to be operating at much smaller scales.

Figure 7.4 and Table 7.1 present a new model that could be used to determine or test the relationships between seed source availability, the probability of immigration and seed dispersal distance. This model shows the possible determinants that influence the probability of immigration (immigration threshold) and the maximum distance a dispersule may attain (converted to a logarithmic scale). **Negative factors (N)** represent influences that may cause loss of potential immigrants, for example: low numbers of reproducing adults, high pre-dispersal predation, and diseased fruits and/or seeds. **Positive factors (P)** may increase immigrants to the system. These factors may include the abundance and productivity of parent plants. These influences on immigration potential can be quantitatively measured in the field by calculating seed source abundance, predator activity, and fruit/seed production within the seed source **(a)**. The values of these factors can be used to calculate the **Immigration Probability Threshold**.

The maximum dispersal distance can be calculated by evaluating factors that allow emigration beyond the seed source **(b)**. In the absence of dispersal vectors the dispersal distance would be determined by:

- a) height of plant;
- b) weight of seed;
- c) wind strength and direction.

Figure 7.4 Probability of immigration and dispersal distance model



N = negative pressures, P = positive pressures, a) = factors influencing immigration, b) = factors influencing dispersal distance, IPT = Immigration probability threshold, MDD = maximum dispersal distance.

Table 7.1 Probability of immigration threshold and maximum distance model

	Negative	Positive	Quantitative measure	
Immigration (a)	Few seed producers	Abundance of adult plants	Seed source abundance	(IPT) Immigration Probability Threshold
	Pre dispersal predation / disease	Production of seeds / fruits	Fruit productivity Pre-dispersal predation Seed viability	
Distance (b)	Heavy seed / fruits fall under parent plants	Lighter seeds / fruits wind blown	Weight of seeds and distance of seed shadow	(MDD) Maximum Dispersal Distance
	Fallen seeds / fruits remain under parent plant	Fruits / seeds eaten and dispersed	Availability of dispersers Food preference of dispersers: - observations of visitation - behaviour on parent plants	
	Barrier for disperser movement	Landscape pattern and disperser perception (scale)	Landscape pattern: - nearest habitat, food source, shelter - corridor function (structure) Disperser vagility: - movement patterns - behaviour	

The distance a propagule is dispersed could also be influenced by:

- a) fruit attractiveness, whether eaten and dispersed by dispersal vectors;
- b) barriers to dispersal vectors (Critical Threshold of seed source habitat);
- c) landscape pattern and disperser perception (scale).

Quantitative measures to calculate the **Maximum Dispersal Distance** values could be made by assessing the:

- a) availability of dispersers;
- b) attractiveness of seed and fruits to potential dispersers (seed condition, seed preferences);
- d) distances to nearest habitat, food source, or shelter;
- e) corridor function, condition and structure;
- f) disperser movement and behaviour patterns.

The contributions that each of the above factors make to the overall maximum dispersal distance could be modelled and each contributing factor could be theoretically manipulated and weighted to develop hypotheses for empirical testing.

7.1.4 Colonization and establishment

Seed dispersal distances do not necessarily correlate with patterns of plant colonization and establishment, as several factors determine the fate of a deposited seed (MacDonald and Smith 1990, Forman 1995). Colonization was defined in Chapter 2 as the germination of seeds or propagation of vegetative shoots, surviving and grow under competitive and predatory pressures. Pickett (1982) proposed that differential tolerance, competition, replacement and relationships with dispersers and predators, were major influences in successional community development. Whether a population increases or decreases in abundance during succession depends therefore not only on the ability of its seedlings to grow in the presence of adult plants, but also on the ability to hold sites by suppressing establishment of seedlings under their own

canopies (Peart 1989). Temporal comparisons of woody plant species composition in Chapter 5 had shown the expansion and decline of individuals of *Fraxinus excelsior*. This species was suggested to be intolerant to changing conditions over time within the EHHs.

For plant species to coexist within stable but complex plant communities, inherent strategies to compete for resources, tolerate inter and intra-specific competition, external and internal biotic and abiotic pressures could determine success or failure. It is possible that these inherent characteristics of individual species may create the deterministic patterns of successional community development. Therefore the interplay of ecological processes and environmental variation at both local and landscape scales can strongly influence the pattern of plant community development and species assembly (Drake *et al.* 1993). At the local scale, pattern is produced by the interaction of biotic and abiotic processes, which influence fluctuating populations over space and time (den Boer 1981, Fahrig and Merriam 1985). Community assembly consists of a sequence of states and transitions in species composition and can be the result of random events, interspecific interactions, or environmental change (Drake *et al.* 1993).

This thesis provides an example of how local processes can influence the community assembly of woody plant species in species-poor hedgerows. In Chapter 5 differing woody plant species responded to three hedgerow structures. *Lonicera periclymenum*, and *Ligustrum vulgare* were more successful under the shaded conditions of an unmanaged hedgerow, whereas, for example *Cornus sanguinea* had displayed a greater colonization and survivorship in the EEH that had been coppiced. Not only do these results highlight the differing response of colonizing woody plant species to the physical structure of hedgerows and possible sensitivity to environmental conditions, they also add a temporal dimension to the survivorship and establishment of community assembly. It is proposed that the assembly of woody plant species communities in these species-poor hedgerows has changed over time and that the physical intervention of management will redirect the community assembly.

Life history characteristics are important factors in the overall analysis of plant species composition (Froberg and Eriksson 1997). Autecological studies investigate individual species attributes, such as distribution, survival and reproductive ability (Crawley 1986). Seed bank persistency, competitive ability and physiological resistance to predation are determinants, and in turn are dependent on the ecological niche, tolerance and habitat requirements of individual species. The success of colonization may also be determined by safe site availability; that is, the biotic and abiotic condition within the habitat a plant is deposited. These are determined by disturbance, microclimate and magnitude of predation (see Chapter 2).

Once colonization has occurred, establishment is viewed in this thesis as a further stage in the successional processes. Establishment was defined in Chapter 2 as when an individual has reached a stage of growth where competitive and predatory pressures do not limit continued development into sexual reproductive maturity. Thus, individuals have some permanent presence within a plant community. As to whether a permanent, sustainable presence reflects reproductive adults, producing offspring (via vegetative propagation, or seed), or as a population retained in a persistent seed bank is a concept still to be developed.

7.2 Hedgerows: potential contribution to landscape networks and corridor function

7.2.1 Corridor function and quality

The principle of corridor function was developed from island biogeography theory and more recently the metapopulation model (Dawson 1994). Metapopulation theory dictates that the ratio between the probability of habitat patches being colonized by dispersing individuals and patch extinction rates will be highly influenced by the permeability of the various structural components of the landscape (Fry 1994). Permeability, in this context, relates to the extent and rate of dispersing species moving across the landscape. Corridors are seen to reduce isolation and enhance movement across fragmented landscapes. The practicalities of studying organisms at the landscape scale and the difficulties of measuring the dynamics of patch-corridor interactions have meant that few studies have achieved statistically definitive answers (Dawson

1994). Consequently, the function of linear features in the landscape has become a major debate.

For species in general, ease of movement, reduced risk of mortality and increased survival are the main factors determining dispersal success. Habitat connectivity and quality may be the two primary variables controlling the conduit function in corridors (Henein and Merriam 1990). Forman (1995) suggested that additionally, both internal and external features of linear habitats contribute to corridor function.

It has been shown that fencerows and lines of vegetation connected to woodlands or areas of semi-natural habitat may act as foci for bird, insect and mammal mobility within agricultural landscapes (Wegner and Merriam 1979, Arnold 1983, Bennett 1990, Saunders and Rebeira 1991, Charrier *at al.* 1997, Verboom and Huitema 1997).

With the aid of modern computer technology and the digitalisation of landscape features such as habitat-patch size, length of hedgerow networks and degree of landscape connectivity, data can be manipulated to create virtual landscapes in which hypothetical species behaviour can be modelled. Gustafson and Gardiner (1996) performed such a study, creating a virtual organism dispersing from woodland edges into neighbouring habitat patches. The patches were modelled with defined probabilities of immigration-emigration rates and frequency of visitation success by successful dispersers. The organism was instructed to imitate random-walk behaviour patterns. Corridors and barriers were perceived by the modelled organism by specific movement rules at given varying spatial scales. Gustafson and Gardiner reported that 89% of the variability of movement success was accounted for by differences in size and isolation of forest patches, with closer and larger patches achieving greater exchange rates of dispersing organisms. Visualisations also showed that corridors did not enhance overall dispersal success, as they acted as cul-de-sacs that delayed or prevented species arriving at habitat destination within an assigned number of movements. It may be that this model demonstrates how

corridors can act as sinks for dispersing organisms but there is a possibility of secondary dispersal movement to more favourable habitats. Secondly, dispersers may not be controlled by random decision-making and have particular habitat preferences that lead to directed dispersal. For example, developing vegetation along a fencerow encourages further usage by birds, thus promoting further plant colonization through bird dispersal (Fritz and Merriam 1996). Therefore the physical structure within linear vegetated features may promote or constrain dispersal of plants from woodland edges (Fritz and Merriam 1996). There is a possibility that such animal movement may influence the distribution of plant species with adaptive long distance dispersal mechanisms (such as adhesion or ingestion), but there is a lack of empirical evidence to support this.

Evidence of plant immigration via animal or bird dispersal vectors may indicate the process of directed dispersal, and indirectly corridor function. Plant species without specific modes of dispersal, or the unavailability of dispersal vectors would be reliant on random dispersal events or vegetative spread. This thesis has demonstrated that few 'woodland' herbaceous plant species disperse into and colonize hedgerows in close proximity to woodland and that the spatial scales of immigration, effectiveness of colonization and success of establishment may be dependent upon life history characteristics and habitat requirements of a plant species. The question still arises as to whether immigration and colonization into hedgerows can be interpreted as plant movement and corridor function. Rosenberg *et al.* (1997) distinguished:

- I) *Corridors* as linear features that provide movement between habitat patches, but not necessarily for reproduction. Thus not all life history requirements of a species may be met within a corridor.
- II) *Habitat* as a patch that provides resources needed for survivorship, reproduction and movement.

As shown in this thesis, for some plant species, hedgerows may provide suitable conditions for survivorship, reproduction and establishment: proof of habitat function in hedgerows. However, for hedgerows to function as corridors for plant movement, plants, in theory, would

progressively colonise along the length of hedgerow into an adjoining new woodland or hedgerow. For many plant species, this would be achieved by small-scale seed dispersal or vegetative spread and would require the hedgerow to function as a habitat, promoting this linear 'movement' through survivorship and reproduction. Alternatively a seed dispersal vector that is using a hedgerow as a movement corridor could disperse plants. It is proposed that hedgerows are more likely to act as potential habitats and seed sources for plants and that the corridor function scenario is more applicable for plant dispersal vectors.

The availability of animal or human dispersal vectors, and their behavioural and movement patterns, may determine the spatial pattern and scale of seed deposition of plant species. Wiens *et al.* (1985) considered movement within landscape as fundamental, affecting the spatial configuration of ecosystem processes. Within a habitat patch, vectors that find a boundary impermeable would have their movements deflected back into the habitat patch by the boundary. When the matrix surrounding a habitat patch is hostile to vector movement, the systems within the habitat patch become self-contained, leading to the localisation of activities. If an organism is able to disperse from or between woodland patches, it experiences abrupt shifts in both spatial patterns of vegetation structure and microclimate (Stamps *et al.* 1987). The degree to which organisms are affected by these shifts is known as a Critical Threshold (Turner and Gardener 1991). Habitat specialists (plant or animal), with limited dispersal capabilities, are presumably more sensitive to these ecological changes than more vagile species.

In fragmented woodlands, the critical threshold for the habitat specialist would be influenced by the extent of the edge effect, which in turn is governed by the degree of fragmentation, habitat area and shape. Constrained inputs and outputs of a habitat patch are effectively creating what Wiens *et al.* (1985) described as a closed system, a proposed function of habitat fragmentation and isolation. Therefore, one assumes that animal or plants less affected by fragmentation, found in woodlands and not influenced by physical boundaries, will disperse out into the wider landscape regardless of external conditions. Vagile species may perceive the larger landscape

as an area that is functionally connected experiencing little or no limitations on their mobility between habitat patches. With and Crist (1995) developed a computerised percolation model which simulated animal responses to differential landscape patterns and degrees of fragmentation. Their results suggest that those animals with a higher dispersal capability were less sensitive to critical thresholds and could tolerate higher degrees of habitat fragmentation, while those species with poor powers of dispersal had higher critical thresholds and tended to aggregate within the isolated habitat. Empirical evidence was shown to support the hypothetical model with small woodland mammals in Brazilian forests (Stevens and Husband 1998). It is feasible that the principle of critical threshold could be applied to plant species dispersal. Quinn *et al.* (1994) had previously demonstrated the association between plant dispersal and the degree of aggregation within habitat patches.

Animals or plants sensitive to the effects of fragmentation may '*perceive*' hedgerows adjoining the woodland edge as a '*softer*' transition, or boundary and may utilise a hedgerow for movement, food sources or habitat *per se*, and reduce critical threshold levels of a fragmented habitat. Thus, hedgerows adjoining woodland habitats could influence the movement of animals and plants (via dispersal vectors). If a landscape is hostile, with few hedgerows adjoining and traversing the landscape, even the most common species, attributed to secondary woodlands, will not be transported at high frequencies or densities. Therefore, plant dispersal and dispersal vector movement may be dependent upon hedgerow availability and proximity.

Although this thesis does not find definitive answers to the corridor dilemma, the type of information gained about the spatial patterns of plant colonization, particularly of those dispersed by animals and birds, could be useful when compiling computer simulations. As more information on animal and bird behaviour, movement and plant dispersal patterns becomes available, future refinements of such techniques could provide valuable insights into the functional dynamics of corridors in fragmented landscapes.

7.2.2 *The role of Wildlife Corridors in European and UK strategies for conservation*

Ecological research into landscapes has demonstrated that nature must be seen as a dynamic system reacting to complex environmental and land-use conditions (Jongman 1995). Since the early 1970s, international governments have been developing conservation strategies and striving to improve the relationships between people and the environment. Agreements have been made at international conventions to halt degradation, to conserve the most vulnerable natural or near-natural habitats or ecosystems and protect unique or rare flora and fauna of a given region (Anon. 1998a).

The United Nations Conference on Environment and Development (The Earth Summit) brought 179 heads of governments together in Rio de Janeiro, in June 1992. Attention focused on critical global issues of sustainable development and protection of natural resources (Anon. 1998a). In 1993, the Maastricht conference 'Conserving Europe's Natural Heritage' sent out a serious message about the fragmentation of habitats in Europe (Jongman 1998). The *European Habitats Directive* (92/43/EEC) provided a legislative framework to ensure measures are taken to maintain and restore natural habitats and species of wild fauna and flora of community interest. The underlying aim of this directive was to create an Ecological Network of protected areas throughout Europe by the year 2004: Natura 2000 (Anon. 1998a). The European Conservation Institutes Research Network (CONNECT) provide a framework for an ecological approach to landscape planning and conservation in agricultural landscapes (Butovsky *et al.* 1998).

A major initiative, the Pan-European-Ecological-Network, has adopted such an approach to nature conservation in Europe, it plans to construct conservation strategies that cross national, regional and municipal boundaries, influencing political and economic policies. The Network not only intends to protect the large important sites but will include the principle of corridor networks to aid species dispersal, immigration and migration in the wider landscape (Walters and Bouwma 1998). The 'Ecological Network' includes core habitat areas, wildlife corridors

and buffer zones that are based upon the metapopulation model and island biogeography theories (Jongman 1995). A network could also facilitate the shifting of habitat patches across the landscape in mosaic patterns of disturbance and recovery by providing colonization sources and refugia (Forman and Baudry 1984).

An obvious way to facilitate the flow of species, individuals, genes and energy between habitat patches is to widen existing corridors of appropriate habitat and eliminate barriers between preserves and other natural areas (Noss and Harris 1986). The network is viewed as a large-scale 'environmental life support system' preserving quality of life, ecological balance, natural cycles and ecosystem productivity (Walters and Bouwma 1998). The main functions of the networks are (Miklós 1998):

- to break isolation of ecosystems created by densely urbanized and industrial areas
- to make ecological conditions more favourable in intensively used areas surrounding protected sites.

Hedgerows are an integral part of a larger landscape network. The total area of hedgerow habitat must equate to one of the major habitat types and network features within the UK. Noss and Harris (1986) recommended that network types should be identified and examined for their potential to contribute to preservation of the regional biota and maximise connectivity through the landscape. They foresaw that the differing scales of species' immigration was dependent on the dispersal capacity of species and their response to habitat type and structure, and warned that some corridor types could act as barriers rather than facilitate movement.

Hedgerows have recently been accepted as having historical and cultural importance through the implementation of the Hedgerows Regulations 1997 (Anon 1997a). Hedgerows also contribute to characteristic landscape structure and aesthetics in different regions of the United Kingdom. Although the profile of hedgerows has risen in recent years in the U.K., it is still uncertain whether or not hedgerows or other anthropogenic strips of vegetation are beneficial as wildlife

corridors (Harris and Scheck 1991). However, the contribution of linear features, such as ancient hedgerows, to biodiversity and landscape conservation, was recognised in the United Kingdom's Biodiversity Action Plan (BAP) in 1994 (Anon 1998c). The objective of this plan is to state a vision for biodiversity and its place in society. The plan is to focus on protection, scientific understanding, sustainable land use, and an equitable sharing of benefits, costs and involvement of private and public organisations and local communities (Anon 1998d).

BAP aims to take stock of indigenous species and semi-natural habitats in the UK and to plan for the recovery of endangered, threatened and vulnerable groups through sustainable development within the wider countryside. Species-rich ancient hedgerows are included in the BAP process as they are considered potential reservoirs of biodiversity where many plants are absent or rare in the surrounding landscape. Habitat Action Plans (HAPs) are being prepared, which will include a summary of the habitat status, important issues affecting ancient hedgerows, and targets and requirements to meet those targets (Anon. 2000a).

The Department of Environment Transport and the Regions (DETR) are funding a long-term national survey, recording a wide range of landscape attributes in 1km square samples across the United Kingdom (The British Countryside Survey (BCS)). The BCS aims to provide a repeatable national database using a framework which can accommodate land classification, examine interactions between various relevant parameters and to provide a predictive tool to assess impact of spatial and temporal change (Bunce 1981). To evaluate ecological factors that affect landscape biodiversity, a related project aims to quantify changes in land-use, landscape pattern and fragmentation of semi-natural habitats from the BCS data sets from 1984 onwards (Barr, *et al.* 1996). Measures and indices of landscape components, such as patch size, shape, perimeter, connectivity or connectedness, are calculated by a computerised model. However, these indices are geometric measures and do not include more directly related parameters such as food, breeding resources and habitat requirements (Fry and Sarlov-Herlin 1995). The aim of these projects is to supply the DETR with statistical information on changes in the important

indicators of environmental sustainability. With measures of change, policy-making can focus on key areas that are most detrimental, or make positive contributions to landscape biodiversity.

7.3 Hedgerow diversity and legislation

The Hedgerows Regulations 1997 (Anon. 1997a) acknowledged the threat of hedgerow removal to the cultural and ecological value of the British landscape and provided legislative procedures to slow down the removal rates. However, as they stand, the Regulations afford protection only for those hedgerows of most ecological and historical importance (around 20% of hedgerows) (Anon 1998b). At present, the protection does not include species-poor hedgerows, and the landscape character of regions significantly altered through Enclosure Acts in the 18th and 19th Centuries. The regulations also create a mindset that species-poor hedgerows are seen as a disposable commodity within landscapes, irrespective of their potential contribution to biodiversity at present and in the future.

Shortly after the release of the regulations (27th May 1997), the Environment Minister, Michael Meacher, responded to criticisms of these legislative procedures by initiating a review process. A review group, made up of Government departments, statutory agencies, local authorities, utility companies and farming and conservation groups, was set up to evaluate the regulations and acknowledged concerns raised and charged to make recommendations as how the regulations could be changed to strengthen hedgerow protection (Anon 1998b).

The plant species composition of hedgerows can reflect local traditions and regional distributions of woody plant species (Anon 2000b). One concern was how the value of a hedgerow was also likely to be dependent upon the local situation and landscape context and how a set of nationally prescribed criteria for defining 'important' hedgerows may not match local expectations (Anon. 1998b). It was proposed that local authorities could have greater freedom to include local perceptions within the valuation process. However, local decision-making would reduce consistency and predictability of the outcome, which is important for

landscape planning and business strategy making, and such an approach would require a change to the primary legislation.

A key element of the Hedgerows Regulations 1997 was to define the importance of a hedgerow. There were concerns that the criteria laid down were too complex and did not recognise the landscape or aesthetic value of hedgerows. The review group has proposed developing fewer and simpler criteria to represent the:

- landscape / amenity;
- historical / archaeological;
- and ecological importance of hedgerows.

The review recommended free-standing criteria, so that if a hedgerow met a particular criterion, it would be protected under the regulations, rather than meeting several criteria.

The Review Group is currently considering the results of the ADAS investigation (Anon. 2000c). The main conclusion one can gain from the ADAS report is that there are complexities within the evaluation processes and, more importantly, that it is almost impossible to simplify criteria to cover national decision-making for landscape and nature conservation. Ecological researchers are seeking to provide landscape planners and government advisors with answers to planning dilemmas. However, because of the marginal conservation status of hedgerows there is little empirical evidence or ecological data to aid the evaluation process. If the present government adopts the landscape and connectivity criteria as a main tool in evaluating hedgerows, rather than stressing the historical elements and ecological diversity, then increased protection could be given to more hedgerows attached to semi-natural habitats. However, if the landscape criteria are combined with other criteria then the review process will have failed to simplify the evaluation process. Additionally, if the criteria for historical and/or ecological importance are retained, limited extra protection will be achieved.

The loss and damage of linear features, including hedgerows, has been acknowledged as a vital component, affecting the future sustainability of the British landscape. Hedgerows are now accepted as having historical and cultural importance, providing varying characteristic landscape features in different regions of the United Kingdom. Hedgerows and other field boundaries are also recognised as potential reservoirs of biodiversity, where many plants are absent or rare in the surrounding landscape (Anon. 1998e). However, there is little understanding of the ecological consequences of hedgerow loss to landscape processes. With political recognition, this area of research may attract the much needed funding. Ecologists are increasingly addressing the need to understand the contribution hedgerows make to the functioning systems of landscapes and how best to manage and increase their ecological value.

This thesis has demonstrated that even the most species-poor hedgerows have the potential to contribute to biodiversity in agricultural landscapes. The regulations review process still does not recognise this fact, and there is a real possibility that after the review, species-poor hedgerows will have no protection.

7.4 Hedgerow management and conservation: implications for landscape ecology

7.4.1 Financial restrictions influencing hedgerow management.

In the past two decades, farming and land use policies have begun to change direction. A national financial recession and over-production in the 1980s enforced a re-evaluation of food production strategies in Europe. A set-a-side scheme was introduced to give farmers financial compensation for leaving land fallow for short periods of time; reducing production of arable crops. The privatization of the Milk Marketing Board and supermarket sales forced reductions in the price of milk. Bovine Spongiform Encephalopathy (B.S.E) in cattle herds and the threat of the human form of this disease has created a financial crisis for both dairy and beef farmers. Between 1997-2000, the high value of the British currency has also affected the export of British beef, pork, chicken and lamb and European imports have reduced market prices dramatically.

Traditionally, farmers keeping dairy, beef and sheep were solely dependent on mixed or pasture farming methods, which in turn promoted the maintenance and retention of hedgerow systems. The increased financial crisis in livestock farming has led to farmers selling to larger corporate landowners, or converting to arable production. The emphasis on arable farming has increased the threat of hedgerow removal and cash crises have forestalled the costs involved in keeping and managing hedgerows. As a result, more hedgerows are falling into disrepair.

In a time of financial instability, hedgerow management is not a priority for farmers. Larger arable farmers are increasingly planting single species crops, that have high cash returns and European subsidies, on a whole farm and hedgerows are regarded as unnecessary obstacles to efficient operations on their land. The widespread change from manual management of hedgerows to either extensive mechanical methods or the complete absence of management has affected the quality of England's hedgerow stock (Bannister and Watt 1994). Hedgerow dereliction is not a new phenomenon; Malden (1899) expressed concerns about the poor conditions of hedgerows in his time, but more recent evaluations of hedgerows in England and Wales found that increasingly hedgerows are falling into 'relict conditions' (Barr *et al.* 1994). Between 1984-1990, 4,600km per annum were estimate as falling into disrepair, whereas between 1990-1993, this figure had increased to 22,500km per annum. The effect of these recent agricultural changes on landscape function and biodiversity may not be evident for some time.

7.4.2 Hedgerow structure and management

Management, or the lack of it, largely determines hedgerow structure. The diversity of plant species within a hedgerow is, not unlike other semi-natural habitats, dependent upon its historical origins along with its past and present management. Shrubs or ground flora may be lost over time, owing to management practices, or fail to survive in marginally suitable habitats (Pollard *et al.* 1974). Adjacent land-use can substantially affect the composition of the herbaceous vegetation of hedgerows. Analysis showed that intensive land management

practices or lack of management were deleterious to the diversity of hedge-bottom flora (Cummins and French 1994, Bunce *et al.* 1994).

As a result of modern hedgerow management techniques (e.g. mechanical flailing), deteriorating and gappy hedgerows have little base structure or vegetative cover, and are consequentially less favourable both for habitat and corridor utility (Boone and Tinklin 1988, Baudry 1989, Tischendorf and Wissel 1997). Autecological research in this thesis revealed that many woodland and hedgerow species are not retained within a persistent seed bank. Regular disturbance, such as hedge bank and ditch maintenance, and chemical treatment, would therefore be beneficial for competitive agricultural herbaceous plant species with opportunistic and dormant life history characteristics, and detrimental to perennials, species with transient seed banks, and species surviving by vegetative propagation.

Flowers of *Crataegus monogyna* are produced on stems with two or three years of growth; annually cut shrubs will not flower and fruit freely (Pollard *et al.* 1974). It follows that annual cutting must have a deleterious effect on the fruit production (Sparks and Martin 1999). Reduced production of fruits and seeds, and lack of seed bank persistency of woody plant species ultimately results in a loss of regenerative capacity, leading to further deterioration of hedge structure. Once gappy, a hedge is neither stock-proof nor effective as a windbreak, and has little agricultural purpose: the farmer therefore has little reason to continue managing it or retaining it (Stephens 1994). Typically the hedgerow is then grubbed out or neglected completely.

Intensive hedgerow management not only reduces the regeneration capacity of woody plant species, but it also reduces food availability and habitat quality for wildlife as the variability in physical structure, flowering and fruit production is lost.

7.4.3 Hedgerow structure and bird populations

Hedgerow management, or the lack of it, affects the numbers of species and the population densities of birds in hedges (Moore *et al.* 1967). Lack (1992) regarded hedgerows as vital landscape components for bird conservation on farmland. He also considered that hedgerow management would have major effects on bird populations. Within an agricultural landscape, hedgerows may provide an alternative habitat for woodland birds where their preferred habitat is fragmented and/or territorial space is restricted (Williamson 1969, Krebs 1970, Hinsley *et al.* 1995a). Some bird species, such as the Nuthatch (*Sitta europaea*), have distinctive woodland habitat requirements and tend to remain closely tied to those habitats throughout most of the year (Matthysen and Schmidt 1987). Other bird species move out of woodland during the winter to feed in hedgerows, on agricultural land and in gardens (Fuller 1982). Hinsley *et al.* (1995b) provided indirect evidence that, for bird species, such as Long Tailed Tit (*Aegithalos caudatus*), Robin (*Erithacus rubecula*) and Bullfinch (*Pyrrhula pyrrhula*), the presence of hedgerows in the surrounding landscape increased the probability of breeding within woodlands. They also suggested that hedgerows provide additional cover for the birds to feed outside the woodland.

O'Connor and Shrubbs (1986) provided a comprehensive overview of bird populations on farmland. The utilisation of hedgerows by birds is associated with the various life processes and behaviour patterns, including: the choice of breeding sites, suitability of vegetation for nesting, risk of chick predation and food availability for foraging within agricultural landscapes (O'Connor 1984, Ims 1995). Hedgerows that are rich in shrub species tend to support more birds (Green *et al.* 1994), but whether birds favour these hedges because they are older *per se*, or because of the variety of food sources is, as yet, unknown. Older hedgerows are generally more diverse in plant species, provide a variety of fruits and seeds and a greater diversity of invertebrates for bird species to feed on (Pollard *et al.* 1974). Hooper (1970a) observed that tall Elm (*Ulmus* spp.) hedgerows had few birds compared to tall Hawthorn (*Crataegus monogyna*)

hedgerows. He considered that the differing structure for nesting within the hedgerows and availability of fruits were the explanatory factors.

Mason (1976) compared the breeding biology of birds within the Warbler family (Sylviidae). Whitethroats (*Sylvia communis*) were mainly found in hedgerows “with a greater vertical structure”. Sparks *et al.* (1996) found that many woodland bird species showed a preference for tall hedgerows, particularly the Wood Pigeon (*Columba palumbus*). The Robin (*Erithacus rubecula*), Blackbird (*Turdus merula*) and Wren (*Troglodytes troglodytes*) were also found to be more abundant in larger hedgerows, whereas the Yellowhammer (*Emberiza citrinella*) preferred shorter, managed hedgerows (Parish *et al.* 1992, Stoate and Szczur 1994). Many authors believe that tall unmanaged hedgerows are beneficial to bird populations. However, since each bird species has its own habitat preferences, it would be naïve to believe that a single structure or type of hedge would be ideal for all bird species (Sparks *et al.* 1996), as ecological niches separate them to varying degrees (Arnold 1983).

Hedgerows left unmanaged will develop into a line of large shrubs and trees. The lack of trees in an agricultural landscape will result in a low frequency of cavity nesting birds, such as the Little Owl (*Athene noctua*), Jackdaw (*Corvus monedula*) and the Stockdove (*Columba oenas*) (Sparks *et al.* 1996). Lack (1988) found the breeding success of some bird species was higher in hedgerows that consisted of mainly of shrubs, than in hedgerows that consisted of trees. He concluded that trees in hedgerows may not provide more suitable breeding sites for all bird species, but can provide additional foraging areas, protection from predators and are needed for song post and vantage points. However, the promotion of taller hedgerow structure for the benefit of bird species could be detrimental to other organisms; results presented in this thesis suggest that conditions created by taller-relict hedgerows will be detrimental to the regeneration and sustainability of the overall composition of shrub and tree species.

In this thesis the role of birds in dispersing fruits and seeds of tree and shrub species has been highlighted. Snow and Snow (1988) and Ridley (1930) both emphasised the lack of communication between the disciplines of botany and ornithology when investigating the distributions of woody plant species. Varying hedgerow management will not only provide suitable habitat for a selection of bird species, but it will promote hedgerow utilisation, landscape mobility of birds and in turn facilitate the immigration, colonization and establishment of additional woody plant species in species-poor hedgerows.

7.4.4 Hedgerow conservation

In recent years, increasing government funds have been allocated to agri-environment schemes. The Hedgerow Incentive Scheme, launched in 1992, was replaced by a broader Countryside Stewardship Scheme, and a programme for Environmentally Sensitive Areas by the Ministry of Agriculture, Fisheries and Food. These schemes encourage and provide financial assistance to farmers to adopt good practice and to reintroduce traditional management to hedgerows. There is evidence that hedgerow planting is increasing. Barr *et al.* (1994) estimated that hedge planting has increased from 1,220km per annum in the years 1984-1990 to 2,700km per annum between 1990-1993. Farmers are recommended to manage hedgerows in the following ways (Matthews 1987):

- hedgerow management should be varied to improve habitat diversity for wildlife;
- layering of hedgerows (in a 10-15year cycle) encourages dense and bushy growth from the bases of hedgerow, encourages good establishment of saplings and provides a habitat and cover for small mammals;
- promoting trees in hedgerows provides nesting habitat and song-posts for birds;
- decreasing in flail cutting frequencies results in increased diversity and abundance of hedge-bottom herbaceous species, and encourages birds;
- protecting newly planted hedgerows with fencing promotes good growth.

Farmers are also advised to continue to trim roadside hedgerows on an annual basis, but then to manage other internal farm hedgerows with less frequent trimming on rotation (Anon. 2000c).

It is also suggested that hedgerow verges should be expanded to provide the opportunity to allow hedgerows to grow wider, without encroaching on cultivated land (Anon. 1989). All types of hedgerow management should be carried out with local best practice and custom during the winter months between mid-November and early March, when the hedge is dormant. Under traditional styles of management, it is easier to identify promising saplings that will develop into hedgerow trees (Brooks 1975).

At the time of writing this thesis, issues such as genetically modified crops, biodiversity, and global warming are addressed regularly by the media and environmental awareness is growing in the general public. Landowners are voluntarily promoting 'environmentally friendly' holidays and consumer demand is leading to the return of organic mixed-arable production. The promotion of high productivity in agriculture through European subsidies is being increasingly questioned and calls are being made to reward farmers that take measures to safeguard and promote biodiversity on their land. Doubleday *et al.* (1994) advised that passive retention of hedgerows is not enough to prevent their deterioration; good research and recognition of the value of hedgerows for their agricultural, cultural and ecological functions is the positive way to convince farmers and land owners to implement positive hedgerow management.

7.5 Summary of the findings of this thesis

7.5.1 Findings for herbaceous plant species

- Dispersal of herbaceous plant species from woodland into adjoining species-poor Enclosure hedgerows was limited to those that reproduce vegetatively (Sections: 3.6, 4.10, 6.2.1).
- A variety of life history strategies was represented across the woodland-hedgerow transition herbaceous plant community, but analysis of spatial commonality suggested that for some species the transition zone was not a barrier to dispersal (Sections: 3.6, 6.2.3).
- Herbaceous plant species typical of the agricultural landscape were found to be dispersing into the woodland (evidence within the woodland seed bank), but not successfully colonizing the woodland sites (Sections 4.10, 6.2.2).

7.5.2 Findings for woody plant species

- Woody plant species were found to be dispersing at a larger spatial scale than herbaceous plant species (Sections: 3.6, 6.2.4).
- Many woody plant species were found to have limited temporal dispersal strategies (Sections: 5.6.2).
- Proposals were made for the implications of short-term persistency of seeds of woody plant species for the success of woody plant colonization in relation to seed sink function of hedgerows, the role of dispersal vectors and the impact of modern hedgerow management (Sections 7.1.1, 7.1.2, 7.4.3).
- The immigration potential of woody plant species in species-poor hedgerows correlated with seed source abundance and the availability of bird seed dispersal vectors (Sections: 5.6.7, 5.9).
- The colonization success of woody plant species in species-poor hedgerows correlated with seed source abundance and immigration potential (Sections: 5.6.7, 5.9).
- Responses of colonizing, surviving and establishing individuals within the three EHH suggested varying tolerance between woody plant species to conditions created by three management regimes (Sections: 5.8, 5.9).
- Using a multifactorial approach, the spatial distributions of woody plant species colonizing species-poor hedgerows were analysed (Section 5.7)

7.5.3 General findings

- Analysis of the spatial and temporal patterns of plant species immigration, colonization and establishment in species-poor hedgerows aids the understanding of ecological processes that occur at the local and landscape scale (Chapter 3).
- Plant immigration, colonization and establishment processes were demonstrated in species-poor hedgerows (Chapter 3, 4, and 5).

- Plant immigration and colonization from nearby woodland sources into species-poor hedgerows was found to be dependent upon spatial and temporal strategies of individual plant species, seed source abundance and the availability of seed dispersal vectors (Chapter 3, 4, and 5).
- Hedgerows may act as both a seed sink and potential seed source for agricultural herbaceous plant species (Chapter 4).
- Hedgerows can provide a *habitat* for plant species (Chapter 4, 5 and 7).
- Hedgerows may act as *corridors* for seed dispersal vectors (Chapter 3, 4, 5, and 7).
- For plant species, the corridor function of hedgerows may be dependent on the behaviour and movement of seed dispersal vectors (Chapter 7).
- In conclusion, a greater understanding of the functioning role of hedgerows in landscapes could be gained by:
 - i) researching the abiotic influences of hedgerow structure on the survivorship and establishment of plant species;
 - ii) researching the influence of hedgerow structure and fruit production on seed dispersal vector visitation and utilisation;
 - iii) the modelling of spatial and temporal immigration processes of plants and the movement seed dispersal vectors.

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Appendix 1 Introduction to thesis

1.1 Scientific and common names for plant species within this thesis: herbaceous plant species.

Scientific name	Common name	Authority
<i>Achillea millefolium</i>	Yarrow	L.
<i>Aegopodium podagraria</i>	Ground Elder	L.
<i>Ajuga reptans</i>	Bugle	L.
<i>Alliaria petiolata</i>	Hedge Garlic / Garlic Mustard	Bieb.
<i>Allium ursinum</i>	Wild Garlic / Ramsons	L.
<i>Angelica sylvestris</i>	Angelica	L.
<i>Anthriscus sylvestris</i>	Cow Parsley	L.
<i>Arctium lappa</i>	Burdock	L.
<i>Arum maculatum</i>	Lords and Ladies	L.
<i>Bryonia dioica</i>	White Bryony	Jacq.
<i>Calystegia sepium</i>	Hedge Bindweed	L. R.Br.
<i>Capsella bursa-pastoris</i>	Shepherd's Purse	L. Medicus
<i>Cardamine flexuosa</i>	Wavy Bittercress	With.
<i>Centaurea nigra</i>	Black Knapweed	L.
<i>Cerastium fontanum</i> subsp. <i>holostoides</i>	Common Mouse-ear	(Fr.) Salman, Ommering & de Voogd
<i>Chaerophyllum temulentum</i>	Rough Chervil	L.
<i>Chamaenerion angustifolium?</i>	Rosebay Willowherb	?
<i>Chenopodium polyspermum</i>	All-seed	L.
<i>Cicerbita macrophylla</i>	Common Blue-sow-thistle	Wild.
<i>Circaea lutetiana</i>	Enchanter's Nightshade	L.
<i>Cirsium arvense</i>	Creeping Thistle	Scop.
<i>Conopodium majus</i>	Pignut	(Gouan) Loret
<i>Convolvulus arvensis</i>	Field Bindweed	L.
<i>Dactylorhiza fuchsii</i>	Common-spotted Orchid	(Druce) Soo
<i>Epilobium</i> spp.	Willowherb	
<i>Filipendula ulmaria</i>	Meadowsweet	(L.) Maxim.
<i>Galium aparine</i>	Goosegrass / Cleavers	L.
<i>Galium mollugo</i>	Hedge Bedstraw	L.
<i>Geranium dissectum</i>	Cut-leaved Crane's-bill	L.
<i>Geranium molle</i>	Dove's-foot Crane's-bill	L.
<i>Geranium robertianum</i>	Herb Robert	L.
<i>Geum urbanum</i>	Wood Avens	L.
<i>Glechoma hederacea</i>	Ground-ivy	L.
<i>Gnaphalium uliginosum</i>	Cudweed	L.
<i>Hedera helix</i>	Ivy	L.
<i>Heracleum sphondylium</i>	Hogweed	L.
<i>Hyacinthoides non-scripta</i>	Bluebell	(L.) Chouard ex Rothm.
<i>Hypericum hirsutum</i>	Hairy St John's-wort	L.
<i>Hypericum perforatum</i>	Perforate St John's-wort	L.
<i>Lamiaeum galeobdolon</i>	Yellow Archangel	(L.) Ehrend and Polatschek
<i>Lamium album</i>	White Dead-nettle	L.
<i>Lapsana communis</i>	Nipplewort	L.
<i>Lonicera periclymenum</i>	Honeysuckle	L.
<i>Mercurialis perennis</i>	Dog's Mercury	L.
<i>Moehringia trinervia</i>	Three-veined sand-wort	(L.) Clairv.
<i>Myosotis arvensis</i>	Field forget-me-not	(L.) Hill
<i>Myosotis sylvatica</i>	Wood forget-me-not	Ehrh. ex Hoffm.
<i>Papaver rhoeas</i>	Common Poppy	L.
<i>Petasites hybridus</i>	Butterbur	(L.) P. Gaertner, B. Meyer and Scherb.
<i>Plantago lanceolata</i>	Ribwort	L.
<i>Plantago major</i>	Rat's-tails Plantain	L.
<i>Potentilla reptans</i>	Creeping Cinquefoil	L.
<i>Potentilla sterilis</i>	Barren Strawberry	(L.) Garcke.
<i>Primula vulgaris</i>	Primrose	Hudson
<i>Ranunculus repens</i>	Creeping Buttercup	L.
<i>Rumex obtusifolius</i>	Broad-leaf Dock	L.
<i>Rumex sanguineus</i>	Wood Dock	L.

Herbaceous plant species continued:

Scientific name	Common name	Authority
<i>Scrophularia auriculata</i>	Water Figwort	L.
<i>Scrophularia nodosa</i>	Common Figwort	L.
<i>Sisymbrium officinale</i>	Hedge Mustard	(L.) Scop.
<i>Solanum dulcamara</i>	Bittersweet	L.
<i>Sonchus asper</i>	Prickly Sow-thistle	(L.) Hill
<i>Stachys sylvatica</i>	Hedge Woundwort	L.
<i>Stellaria media</i>	Chickweed	(L.) Vill.
<i>Stellaria nemorum</i>	Wood Stichwort	L.
<i>Tamus communis</i>	Black Bryony	L.
<i>Taraxacum</i> agg.	Dandelion	
<i>Tripleurospermum inodorum</i>	Scentless Mayweed	Schultz Bip.
<i>Tussilago farfara</i>	Colt's-foot	L.
<i>Urtica dioica</i>	Stinging Nettle	L.
<i>Veronica chamaedrys</i>	Germander Speedwell	L.
<i>Veronica hederifolia</i>	Ivy-leaf Speedwell	L.
<i>Veronica persica</i>	Persian Speedwell	Poiret
<i>Vicia sepium</i>	Bush Vetch	L.
<i>Vicia tetrasperma</i>	Smooth Tare	(L.) Schreb.
<i>Viola arvensis</i>	Field Pansy	Murray
<i>Viola hirta</i>	Hairy violet	L.
<i>Viola reichenbachiana</i>	Wood violet	Reichenb.
<i>Viola riviniana</i>	Common Dog Violet	Reichenb.

1.2 Scientific and common names for plant species within this thesis: tree and shrub species

Scientific name	Common name	Authority
<i>Acer campestre</i>	Field Maple	L.
<i>Alnus glutinosa</i>	Alder	(L.) Gaertner
<i>Betula</i> spp.	Birch	
<i>Cornus sanguinea</i>	Dogwood	L.
<i>Corylus avellana</i>	Hazel	L.
<i>Crataegus monogyna</i>	Hawthorn Common	Jacq.
<i>Euonymus europaeus</i>	Spindle	L.
<i>Fagus sylvatica</i>	Beech	L.
<i>Fraxinus excelsior</i>	Ash	L.
<i>Larix decidua</i>	European Larch	Mill.
<i>Larix kaempferi</i>	Japanese Larch	(Lindl.) Carrière
<i>Ligustrum vulgare</i>	Privet	L.
<i>Picea abies</i>	Norway Spruce	(L.) H. Karst.
<i>Picea sitchensis</i>	Sitka Spruce	(Bong.) Carrière
<i>Populus serotina</i>	Black Italian Poplar	?
<i>Prunus spinosa</i>	Blackthorn	L.
<i>Pseudotsuga menziesii</i>	Douglas fir	(Mirb.) Franco
<i>Quercus</i> spp.	Oak	
<i>Rhamnus cathartica</i>	Buckthorn	L.
<i>Rosa canina</i>	Dog Rose	L.
<i>Rubus</i> agg.	Brambles	
<i>Sorbus aucuparia</i>	Rowan	L.
<i>Viburnum lantana</i>	Wayfaring Tree	L.

Appendix 2 The maintenance and development of plant species diversity

Definitions of terms immigration, colonization, survival and establishment from four Dictionaries

	The Concise Oxford Dictionary of Botany (Allaby 1992)	The Concise Oxford Dictionary of Ecology (Allaby 1994)	The Concise Oxford Dictionary Allen (1990)	The New Universal Dictionary Meredith (unknown)
Immigration	"In genetics, the movement or flow of genes into a population, caused by immigrating individuals which interbreed with residents"		Not listed	"To go permanently from one's or its place to another."
Immigrate	Not listed	Not listed	"Come as a permanent resident to a country other than one's native land; to bring in as an immigrant."	" To plant or establish a colony in; to make into a colony."
Colonization	Not listed	"The successful establishment of an invading species in a habitat"	Not listed	"The act of colonising; the condition of being colonised."
Colonize	Not listed	Not listed	"Establish a colony; settle as colonists; become established."	" To plant or establish a colony, to make into a colony."
Survivor	"Natural selection: ("survival of the fittest"): A complex process in which the total environment determines which members of a species survive to reproduce and so pass on their genes to the next generation. This need not involve a struggle between organisms."		"A person who survives or has survived."	"One who outlives another, one who escapes from disaster."
Survive			"Continue to live or exist, be still alive or exist longer than, to remain alive after going through danger, or accident."	" To live longer, one who outlives another; one who escapes from disaster."
Survival	"Survivorship curve: A graphical description of the survival of individuals in a population from birth to the maximum age attained by one member. Usually it is plotted as the logarithm of the number of survivors – as a function of age. If a population has a constant mortality rate, the graph will be a straight line"		"The process or an instance of surviving, result of natural selection."	"Surviving or living after; to last longer than; a process, custom carried on to a new state of society, continued existence after death."
Establishment	Not listed	Not listed	"A place of business, a residence, any organised body permanently maintained for a purpose."	"The act of settling; a residence; style of living; place of business."
Establish	Not listed	Not listed	"To set up or consolidate on a permanent basis, settle oneself in some capacity, to achieve permanence."	" to make firm, fix; settle."

Appendix 3 Distribution of plant species across ten woodland-hedgerow transition zones

3.1 Compass bearing, aspect and orientation of the ten Enclosure Act hedgerows

Transect	Hedge	Orientation: compass bearing	Orientation Away from woodland	Aspect Compass bearing	Aspect
1	1	159	SSE	249	WSW
	2			69	ENE
2	3	167	SSE	77	ENE
	4			257	WSW
3	5	131	ESE	221	SSW
	6			41	NNE
4	7	137	SSE	227	WSW
	8			47	ENE
5	9	302	WNW	212	SSW
	10			32	NNE
6	11	294	WNW	204	SSW
	12			24	NNE
7	13	294	WNW	204	SSW
	14			24	NNE
8	15	05	NNE	95	ESE
	16			275	WNW
9	17	318	NNW	48	ENE
	18			228	WSW
10	19	93	ESE	183	SSW
	20			03	NNE

3.2 Glossary of autoecological terms (Hodgson *et al.* 1995)

Soil pH:

Modal class within the stated range within:

1pH unit = a

2 pH units = b

3 pH units = c

4 pH units = d

Life history:

A = annual

As = summer annual

Aw = winter annual

B = usually biennial

M = monocarpic perennial

P = polycarpic perennial

Establishment strategies:

Primary: C = competitor, R = ruderal, S = stress-tolerant

Secondary: CR = competitive-ruderal, SC = stress-tolerant competitor, SR = stress-tolerant ruderal

Tertiary: CSR = overall strategist

Leaf phenology:

Canopy seasonal:

Sa = aestival (spring-autumn)

Sh = hibernal (autumn-early summer)

Sv = vernal (winter-spring)

Canopy evergreen:

Ea = always evergreen

Ep = partially evergreen

Life form:

Ph = phanerophyte (woody/buds>250mm)

Ch = chamaephyte (buds <250mm)

G = geophyte (buds below soil)

H = hemicryptophyte (buds at soil level)

Th = therophyte (surviving unfavourable periods as seeds)

Regenerative strategies:

S = seasonal-seed

Sv = seasonal-vegetative

Bs = persistent seed-bank

V = vegetative

W = widely dispersed seeds

? = unknown

Seed bank:

Transient = rarely persisting more than one year

Intermediate = persisting 1-5years

Persistent = persisting at least 5 years

Modes of dispersal:

Anim = animal dispersed: a = awn, b = burr, e = elaisome (ants), i = ingested, m = adhesive mucilage

Aquat = water

Wind = wind dispersed: c = small seeds from capsule, p = plumed, w = winged

Dispersule weight:

S = spore

1 = <0.20mg

2 = 0.21-0.50mg

3 = 0.51-1.00mg

4 = 1.01-2.00mg

5 = 2.01-10.00mg

6 = >10.00mg

3.3 Transect profiles for herbaceous plant species

Transect 1: Hedge 1 & 2: Geddington Chase

Quadrat Location	Wood										Hedge									
	10	9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9	10
<i>Achillea millefolium</i>																				
<i>Aegopodium podagraria</i>																				
<i>Alliaria petiolata</i>																				
<i>Allium ursinum</i>																				
<i>Ajuga reptans</i>																				
<i>Angelica sylvestris</i>																				
<i>Anthriscus sylvestris</i>																				
<i>Arum maculatum</i>																				
<i>Bryonia dioica</i>																				
<i>Calyptegia sepium</i>																				
<i>Capsella bursa-pastoris</i>																				
<i>Cardamine flexuosa</i>																				
<i>Centaurea nigra</i>																				
<i>Cerastium holosteoides</i>																				
<i>Chaerophyllum temulentum</i>																				
<i>Chamaenerion angustifolium</i>																				
<i>Circaea lutetiana</i>																				
<i>Cirsium arvense</i>																				
<i>Cirsium vulgare</i>																				
<i>Conopodium majus</i>																				
<i>Convolvulus arvensis</i>																				
<i>Dactylorhiza fuchsii</i>																				
<i>Filipendula ulmaria</i>																				
<i>Galium aparine</i>																				
<i>Galium mollugo</i>																				
<i>Geranium dissectum</i>																				
<i>Geranium molle</i>																				
<i>Geranium robertianum</i>																				
<i>Geum urbanum</i>																				
<i>Glechoma hederacea</i>																				
<i>Hedera helix</i>																				
<i>Heracleum sphondylium</i>																				
<i>Hyacinthoides non-scripta</i>																				
<i>Hypericum hirsutum</i>																				
<i>Hypericum perforatum</i>																				
<i>Lamium galeobdolon</i>																				
<i>Lapsana communis</i>																				
<i>Lonicera periclymenum</i>																				
<i>Mercurialis perennis</i>																				
<i>Moehringia trinervia</i>																				
<i>Myosotis arvensis</i>																				
<i>Myosotis sylvatica</i>																				
<i>Petasites hybridus</i>																				
<i>Plantago lanceolata</i>																				
<i>Potentilla reptans</i>																				
<i>Potentilla sterilis</i>																				
<i>Primula vulgaris</i>																				
<i>Ranunculus repens</i>																				
<i>Rumex obtusifolius</i>																				
<i>Rumex sanguineus</i>																				
<i>Scrophularia auriculata</i>																				
<i>Scrophularia nodosa</i>																				
<i>Sisymbrium officinale</i>																				
<i>Solanum dulcamara</i>																				
<i>Stachys sylvatica</i>																				
<i>Stellaria media</i>																				
<i>Stellaria nemorum</i>																				
<i>Tamus communis</i>																				
<i>Taraxacum spp.</i>																				
<i>Tussilago farfara</i>																				
<i>Urtica dioica</i>																				
<i>Veronica chamaedrys</i>																				
<i>Veronica hederifolia</i>																				
<i>Veronica persica</i>																				
<i>Vicia tetrasperma</i>																				
<i>Vicia sepium</i>																				
<i>Viola arvensis</i>																				
<i>Viola hirta</i>																				
<i>Viola reichenbachiana</i>																				
<i>Viola riviniana</i>																				
Totals	4	3	0	1	3	3	1	4	9	4	4	3	9	4	8	7	5	8	5	4

Woodland: species total = 14

Hedge species total = 18

Transect 2: Hedge 4 & 3: Geddington Chase

Quadrat Location	Wood										Hedge									
	10	9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9	10
<i>Achillea millefolium</i>																				
<i>Aegopodium podagraria</i>	■																			
<i>Alliaria petiolata</i>																				
<i>Allium ursinum</i>																				
<i>Ajuga reptans</i>																				
<i>Angelica sylvestris</i>																				
<i>Anthriscus sylvestris</i>										■	■	■	■		■	■	■	■	■	■
<i>Arum maculatum</i>																				
<i>Bryonia dioica</i>																				
<i>Calystegia sepium</i>														■	■	■				
<i>Capsella bursa-pastoris</i>																				
<i>Cardamine flexuosa</i>																				
<i>Centaurea nigra</i>																				
<i>Cerastium holosteoides</i>																				
<i>Chaerophyllum temulentum</i>										■	■	■	■	■				■	■	■
<i>Chamaenerion angustifolium</i>										■	■				■					■
<i>Circaea lutetiana</i>																				
<i>Cirsium arvense</i>										■	■	■	■	■	■	■				■
<i>Cirsium vulgare</i>																				
<i>Conopodium majus</i>																				
<i>Convolvulus arvensis</i>																				
<i>Dactylorhiza fuchsii</i>																				
<i>Filipendula ulmaria</i>																				
<i>Galium aparine</i>						■				■	■	■	■	■	■	■	■	■	■	■
<i>Gallium mollugo</i>																				
<i>Geranium dissectum</i>																				
<i>Geranium molle</i>																				
<i>Geranium robertianum</i>																				
<i>Geum urbanum</i>																				
<i>Glechoma hederacea</i>				■						■	■	■	■	■	■	■	■	■	■	■
<i>Hedera helix</i>				■																
<i>Heracleum sphondylium</i>				■						■	■									
<i>Hyacinthoides non-scripta</i>																				
<i>Hypericum hirsutum</i>						■	■	■	■	■										
<i>Hypericum perforatum</i>																				
<i>Lamium galeobdolon</i>																				
<i>Lapsana communis</i>																				
<i>Lonicera periclymenum</i>																				
<i>Mercurialis perennis</i>	■	■	■							■	■	■	■	■	■	■	■	■	■	■
<i>Moehringia trinervia</i>																				
<i>Myosotis arvensis</i>																				
<i>Myosotis sylvatica</i>																				
<i>Petasites hybridus</i>																				
<i>Plantago lanceolata</i>																				
<i>Potentilla reptans</i>																				
<i>Potentilla sterilis</i>																				
<i>Ranunculus repens</i>																			■	■
<i>Rumex obtusifolius</i>	■	■	■							■	■	■	■	■	■	■	■	■	■	■
<i>Rumex sanguineus</i>																				
<i>Scrophularia auriculata</i>						■														
<i>Scrophularia nodosa</i>				■	■				■											
<i>Sisymbrium officinale</i>																				
<i>Solanum dulcamara</i>										■										
<i>Stachys sylvatica</i>										■	■	■	■	■	■	■	■	■	■	■
<i>Stellaria media</i>																				
<i>Stellaria nemorum</i>																				
<i>Tamus communis</i>																				
<i>Taraxacum spp.</i>																				
<i>Tussilago farfara</i>																				
<i>Urtica dioica</i>			■																	
<i>Veronica chamaedrys</i>																				
<i>Veronica hederifolia</i>																				
<i>Veronica persica</i>																				
<i>Vicia tetrasperma</i>																				
<i>Vicia sepium</i>																				
<i>Viola arvensis</i>																				
<i>Viola hirta</i>																				
<i>Viola reichenbachiana</i>																				
<i>Viola riviniana</i>																				
Totals	3	2	4	0	3	3	2	2	9	7	7	10	7	6	7	7	5	4	7	8

Woodland: species total = 17

Hedgerow: species total = 16

Transect 3: Hedge 5 & 6: Geddington Chase

Quadrat Location	Wood										Hedge										
	10	9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9	10	
<i>Achillea millefolium</i>												■	■								
<i>Aegopodium podagraria</i>																					
<i>Alliaria petiolata</i>																■	■				
<i>Allium ursinum</i>																					
<i>Ajuga reptans</i>																					
<i>Angelica sylvestris</i>																					
<i>Anthriscus sylvestris</i>																					
<i>Arum maculatum</i>									■	■											
<i>Bryonia dioica</i>												■	■	■	■	■	■	■	■	■	
<i>Calystegia sepium</i>																					
<i>Capsella bursa-pastoris</i>																					
<i>Cardamine flexuosa</i>																					
<i>Centaurea nigra</i>																					
<i>Cerastium holosteoides</i>																					
<i>Chaerophyllum temulentum</i>																					
<i>Chamaenerion angustifolium</i>																					
<i>Circaea lutetiana</i>																					
<i>Cirsium arvense</i>																					
<i>Cirsium vulgare</i>																					
<i>Conopodium majus</i>																					
<i>Convolvulus arvensis</i>																					
<i>Dactylorhiza fuchsii</i>																					
<i>Filipendula ulmaria</i>																					
<i>Galium aparine</i>																					
<i>Gallium mollugo</i>																					
<i>Geranium dissectum</i>																					
<i>Geranium molle</i>																					
<i>Geranium robertianum</i>																					
<i>Geum urbanum</i>																					
<i>Glechoma hederacea</i>																					
<i>Hedera helix</i>																					
<i>Heracleum sphondylium</i>																					
<i>Hyacinthoides non-scripta</i>																					
<i>Hypericum hirsutum</i>																					
<i>Hypericum perforatum</i>																					
<i>Lamium galeobdolon</i>																					
<i>Lapsana communis</i>																					
<i>Lonicera periclymenum</i>																					
<i>Mercurialis perennis</i>																					
<i>Moehringia trinervia</i>																					
<i>Myosotis arvensis</i>																					
<i>Myosotis sylvatica</i>																					
<i>Petasites hybridus</i>																					
<i>Plantago lanceolata</i>																					
<i>Potentilla reptans</i>																					
<i>Potentilla sterilis</i>																					
<i>Primula vulgaris</i>																					
<i>Ranunculus repens</i>																					
<i>Rumex obtusifolius</i>																					
<i>Rumex sanguineus</i>																					
<i>Scrophularia auriculata</i>																					
<i>Scrophularia nodosa</i>																					
<i>Sisymbrium officinale</i>																					
<i>Solanum dulcamara</i>																					
<i>Stachys sylvatica</i>																					
<i>Stellaria media</i>																					
<i>Stellaria nemorum</i>																					
<i>Tamus communis</i>																					
<i>Taraxacum spp.</i>																					
<i>Tussilago farfara</i>																					
<i>Urtica dioica</i>																					
<i>Veronica chamaedrys</i>																					
<i>Veronica persica</i>																					
<i>Vicia sepium</i>																					
<i>Vicia tetrasperma</i>																					
<i>Viola arvensis</i>																					
<i>Viola hirta</i>																					
<i>Viola reichenbachiana</i>																					
<i>Viola riviniana</i>																					
Total	0	0	3	0	1	0	1	2	6	6	6	11	9	7	9	9	10	7	8	9	8

Woodland: species total = 10

Hedgerow: species total = 22

Transect 4: Hedge 7 & 8: Geddington Chase

Quadrat Location	Wood										Hedge									
	10	9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9	10
<i>Achillea millefolium</i>																				
<i>Aegopodium podagraria</i>																				
<i>Alliaria petiolata</i>																				
<i>Allium ursinum</i>																				
<i>Ajuga reptans</i>																				
<i>Angelica sylvestris</i>																				
<i>Anthriscus sylvestris</i>																				
<i>Arum maculatum</i>																				
<i>Bryonia dioica</i>																				
<i>Calystegia sepium</i>																				
<i>Capsella bursa-pastoris</i>																				
<i>Cardamine flexuosa</i>																				
<i>Centaurea nigra</i>																				
<i>Cerastium holosteoides</i>																				
<i>Chaerophyllum temulentum</i>																				
<i>Chamaenerion angustifolium</i>																				
<i>Circaea lutetiana</i>																				
<i>Cirsium arvense</i>																				
<i>Cirsium vulgare</i>																				
<i>Conopodium majus</i>																				
<i>Convolvulus arvensis</i>																				
<i>Dactylorhiza fuchsii</i>																				
<i>Filipendula ulmaria</i>																				
<i>Galium aparine</i>																				
<i>Gallium mollugo</i>																				
<i>Geranium dissectum</i>																				
<i>Geranium molle</i>																				
<i>Geranium robertianum</i>																				
<i>Geum urbanum</i>																				
<i>Glechoma hederacea</i>																				
<i>Hedera helix</i>																				
<i>Heracleum sphondylium</i>																				
<i>Hyacinthoides non-scripta</i>																				
<i>Hypericum hirsutum</i>																				
<i>Hypericum perforatum</i>																				
<i>Lamiastrum galeobdolon</i>																				
<i>Lapsana communis</i>																				
<i>Lonicera periclymenum</i>																				
<i>Mercurialis perennis</i>																				
<i>Moehringia trinervia</i>																				
<i>Myosotis arvensis</i>																				
<i>Myosotis sylvatica</i>																				
<i>Petasites hybridus</i>																				
<i>Plantago lanceolata</i>																				
<i>Potentilla reptans</i>																				
<i>Potentilla sterilis</i>																				
<i>Dactylorhiza fuchsii</i>																				
<i>Ranunculus repens</i>																				
<i>Rumex obtusifolius</i>																				
<i>Rumex sanguineus</i>																				
<i>Scrophularia auriculata</i>																				
<i>Scrophularia nodosa</i>																				
<i>Sisymbrium officinale</i>																				
<i>Stachys sylvatica</i>																				
<i>Stellaria holostea</i>																				
<i>Stellaria media</i>																				
<i>Stellaria nemorum</i>																				
<i>Tamus communis</i>																				
<i>Taraxacum spp.</i>																				
<i>Tussilago farfara</i>																				
<i>Urtica dioica</i>																				
<i>Veronica chamaedrys</i>																				
<i>Veronica persica</i>																				
<i>Vicia tetrasperma</i>																				
<i>Vicia sepium</i>																				
<i>Viola arvensis</i>																				
<i>Viola hirta</i>																				
<i>Viola reichenbachiana</i>																				
<i>Viola riviniana</i>																				
Total																				

Woodland: species total = 11

Hedgerow: species total = 21

Transect 5: Hedge 9 & 10: Fineshade

Quadrat Location	Wood										Hedge									
	10	9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9	10
<i>Achillea millefolium</i>																				
<i>Aegopodium podagraria</i>																				
<i>Alliaria petiolata</i>																				
<i>Allium ursinum</i>																				
<i>Ajuga reptans</i>																				
<i>Angelica sylvestris</i>																				
<i>Anthriscus sylvestris</i>																				
<i>Arum maculatum</i>																				
<i>Bryonia dioica</i>																				
<i>Calystegia sepium</i>																				
<i>Capsella bursa-pastoris</i>																				
<i>Cardamine flexuosa</i>																				
<i>Centaurea nigra</i>																				
<i>Cerastium holosteoides</i>																				
<i>Chaerophyllum temulentum</i>																				
<i>Chamaenerion angustifolium</i>																				
<i>Circaea lutetiana</i>																				
<i>Cirsium arvense</i>																				
<i>Cirsium vulgare</i>																				
<i>Conopodium majus</i>																				
<i>Convolvulus arvensis</i>																				
<i>Dactylorhiza fuchsii</i>																				
<i>Filipendula ulmaria</i>																				
<i>Galium aparine</i>																				
<i>Galium mollugo</i>																				
<i>Geranium dissectum</i>																				
<i>Geranium molle</i>																				
<i>Geranium robertianum</i>																				
<i>Geum urbanum</i>																				
<i>Glechoma hederacea</i>																				
<i>Hedera helix</i>																				
<i>Heracleum sphondylium</i>																				
<i>Hyacinthoides non-scripta</i>																				
<i>Hypericum hirsutum</i>																				
<i>Hypericum perforatum</i>																				
<i>Lamium galeobdolon</i>																				
<i>Lapsana communis</i>																				
<i>Lonicera periclymenum</i>																				
<i>Mercurialis perennis</i>																				
<i>Moehringia trinervia</i>																				
<i>Myosotis arvensis</i>																				
<i>Myosotis sylvatica</i>																				
<i>Petasites hybridus</i>																				
<i>Plantago lanceolata</i>																				
<i>Potentilla reptans</i>																				
<i>Potentilla sterilis</i>																				
<i>Primula vulgaris</i>																				
<i>Ranunculus repens</i>																				
<i>Rumex obtusifolius</i>																				
<i>Rumex sanguineus</i>																				
<i>Scrophularia auriculata</i>																				
<i>Scrophularia nodosa</i>																				
<i>Sisymbrium officinale</i>																				
<i>Solanum dulcamara</i>																				
<i>Stachys sylvatica</i>																				
<i>Stellaria media</i>																				
<i>Stellaria nemorum</i>																				
<i>Tamus communis</i>																				
<i>Taraxacum spp.</i>																				
<i>Tussilago farfara</i>																				
<i>Urtica dioica</i>																				
<i>Veronica chamaedrys</i>																				
<i>Veronica persica</i>																				
<i>Vicia sepium</i>																				
<i>Vicia tetrasperma</i>																				
<i>Viola arvensis</i>																				
<i>Viola hirta</i>																				
<i>Viola reichenbachiana</i>																				
<i>Viola riviniana</i>																				
Total	1	0	0	2	0	0	0	0	1	2	7	7	9	8	11	8	9	8	9	8

Woodland: species total =11

Hedgerow: species total =23

Transect 6: Hedge 11 & 12: Fineshade

Herbaceous plant species	Wood										Hedge									
	10	9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9	10
<i>Achillea millefolium</i>																■	■			
<i>Aegopodium podagraria</i>																				
<i>Alliaria petiolata</i>																				
<i>Allium ursinum</i>																				
<i>Ajuga reptans</i>																				
<i>Angelica sylvestris</i>																				
<i>Anthriscus sylvestris</i>																				
<i>Arum maculatum</i>										■	■					■	■		■	■
<i>Bryonia dioica</i>																				■
<i>Calystegia sepium</i>																				
<i>Capsella bursa-pastoris</i>																				
<i>Cardamine flexuosa</i>																				
<i>Centaurea nigra</i>																				
<i>Cerastium holsteoides</i>																				
<i>Chaerophyllum temulentum</i>																				
<i>Chamaenerion angustifolium</i>																				
<i>Circaea lutetiana</i>																				
<i>Cirsium arvense</i>																				
<i>Cirsium vulgare</i>																				
<i>Conopodium majus</i>																				
<i>Convolvulus arvensis</i>																				
<i>Dactylorhiza fuchsii</i>																				
<i>Filipendula ulmaria</i>																				
<i>Galium aparine</i>																				
<i>Gallium mollugo</i>																				
<i>Geranium dissectum</i>																				
<i>Geranium molle</i>																				
<i>Geranium robertianum</i>																				
<i>Geum urbanum</i>																				
<i>Glechoma hederacea</i>																				
<i>Hedera helix</i>																				
<i>Heracleum sphondylium</i>																				
<i>Hyacinthoides non-scripta</i>																				
<i>Hypericum hirsutum</i>																				
<i>Hypericum perforatum</i>																				
<i>Lamium galeobdolon</i>																				
<i>Lapsana communis</i>																				
<i>Lonicera periclymenum</i>																				
<i>Mercurialis perennis</i>																				
<i>Moehringia trinervia</i>																				
<i>Myosotis arvensis</i>																				
<i>Myosotis sylvatica</i>																				
<i>Petasites hybridus</i>																				
<i>Plantago lanceolata</i>																				
<i>Potentilla reptans</i>																				
<i>Potentilla sterilis</i>																				
<i>Primula vulgaris</i>																				
<i>Ranunculus repens</i>																				
<i>Rumex obtusifolius</i>																				
<i>Rumex sanguineus</i>																				
<i>Scrophularia auriculata</i>																				
<i>Scrophularia nodosa</i>																				
<i>Sisymbrium officinale</i>																				
<i>Solanum dulcamara</i>																				
<i>Stachys sylvatica</i>																				
<i>Stellaria media</i>																				
<i>Stellaria nemorum</i>																				
<i>Tamus communis</i>																				
<i>Taraxacum spp.</i>																				
<i>Tussilago farfara</i>																				
<i>Urtica dioica</i>																				
<i>Veronica chamaedrys</i>																				
<i>Veronica persica</i>																				
<i>Vicia sepium</i>																				
<i>Vicia tetrasperma</i>																				
<i>Viola arvensis</i>																				
<i>Viola hirta</i>																				
<i>Viola reichenbachiana</i>																				
<i>Viola riviniana</i>																				
Total	4	4	2	0	1	2	3	2	6	5	7	7	5	5	4	7	7	5	7	7

Woodland : species total =12

Hedgerow: species total =18

Transect 7: Hedge 13 & 14: Fineshade

Quadrat Location	Wood										Hedge									
	10	9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9	10
<i>Achillea millefolium</i>																				
<i>Aegopodium podagraria</i>																				
<i>Alliaria petiolata</i>																				
<i>Allium ursinum</i>																				
<i>Ajuga reptans</i>																				
<i>Angelica sylvestris</i>																				
<i>Anthriscus sylvestris</i>																				
<i>Arum maculatum</i>																				
<i>Bryonia dioica</i>																				
<i>Calystegia sepium</i>																				
<i>Capsella bursa-pastoris</i>																				
<i>Cardamine flexuosa</i>																				
<i>Centaurea nigra</i>																				
<i>Cerastium holosteoides</i>																				
<i>Chaerophyllum temulentum</i>																				
<i>Chamaenerion angustifolium</i>																				
<i>Circaea lutetiana</i>																				
<i>Cirsium arvense</i>																				
<i>Cirsium vulgare</i>																				
<i>Conopodium majus</i>																				
<i>Convolvulus arvensis</i>																				
<i>Dactylorhiza fuchsii</i>																				
<i>Filipendula ulmaria</i>																				
<i>Gaium aparine</i>																				
<i>Gallium mollugo</i>																				
<i>Geranium dissectum</i>																				
<i>Geranium molle</i>																				
<i>Geranium robertianum</i>																				
<i>Geum urbanum</i>																				
<i>Glechoma hederacea</i>																				
<i>Hedera helix</i>																				
<i>Heracleum sphondylium</i>																				
<i>Hyacinthoides non-scripta</i>																				
<i>Hypericum hirsutum</i>																				
<i>Hypericum perforatum</i>																				
<i>Lamium galeobdolon</i>																				
<i>Lapsana communis</i>																				
<i>Lonicera periclymenum</i>																				
<i>Mercurialis perennis</i>																				
<i>Moehringia trinervia</i>																				
<i>Myosotis arvensis</i>																				
<i>Myosotis sylvatica</i>																				
<i>Petasites hybridus</i>																				
<i>Plantago lanceolata</i>																				
<i>Potentilla reptans</i>																				
<i>Potentilla sterilis</i>																				
<i>Primula vulgaris</i>																				
<i>Ranunculus repens</i>																				
<i>Rumex obtusifolius</i>																				
<i>Rumex sanguineus</i>																				
<i>Scrophularia auriculata</i>																				
<i>Scrophularia nodosa</i>																				
<i>Sisymbrium officinale</i>																				
<i>Solanum dulcamara</i>																				
<i>Stachys sylvatica</i>																				
<i>Stellaria media</i>																				
<i>Stellaria nemorum</i>																				
<i>Tamus communis</i>																				
<i>Taraxacum spp.</i>																				
<i>Tussilago farfara</i>																				
<i>Urtica dioica</i>																				
<i>Veronica chamaedrys</i>																				
<i>Veronica persica</i>																				
<i>Vicia sepium</i>																				
<i>Vicia tetrasperma</i>																				
<i>Viola arvensis</i>																				
<i>Viola hirta</i>																				
<i>Viola reichenbachiana</i>																				
<i>Viola riviniana</i>																				
Total	5	10	9	5	5	6	7	0	2	6	8	8	6	8	4	3	3	2	2	2

Woodland: species total = 22

Hedgerow: species total = 16

Transect 8: Hedge 15 & 16: Geddington

Herbaceous plant species	Wood										Hedge										
	10	9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9	10	
<i>Achillea millefolium</i>																					
<i>Aegopodium podagraria</i>																					
<i>Alilaria petiolata</i>																					
<i>Allium ursinum</i>																					
<i>Ajuga reptans</i>																					
<i>Angelica sylvestris</i>																					
<i>Anthriscus sylvestris</i>																					
<i>Arum maculatum</i>																					
<i>Bryonia dioica</i>																					
<i>Calystegia sepium</i>																					
<i>Capsella bursa-pastoris</i>																					
<i>Cardamine flexuosa</i>																					
<i>Centaurea nigra</i>																					
<i>Cerastium holosteoides</i>																					
<i>Chaerophyllum temulentum</i>																					
<i>Chamaenerion angustifolium</i>																					
<i>Circaea lutetiana</i>																					
<i>Cirsium arvense</i>																					
<i>Cirsium vulgare</i>																					
<i>Conopodium majus</i>																					
<i>Convolvulus arvensis</i>																					
<i>Dactylorhiza fuchsii</i>																					
<i>Filipendula ulmaria</i>																					
<i>Galium aparine</i>																					
<i>Gallium mollugo</i>																					
<i>Geranium dissectum</i>																					
<i>Geranium molle</i>																					
<i>Geranium robertianum</i>																					
<i>Geum urbanum</i>																					
<i>Glechoma hederacea</i>																					
<i>Hedera helix</i>																					
<i>Heracleum sphondylium</i>																					
<i>Hyacinthoides non-scripta</i>																					
<i>Hypericum hirsutum</i>																					
<i>Hypericum perforatum</i>																					
<i>Lamiastrum galeobdolon</i>																					
<i>Lapsana communis</i>																					
<i>Lonicera periclymenum</i>																					
<i>Mercurialis perennis</i>																					
<i>Moehringia trinervia</i>																					
<i>Myosotis arvensis</i>																					
<i>Myosotis sylvatica</i>																					
<i>Petasites hybridus</i>																					
<i>Plantago lanceolata</i>																					
<i>Potentilla reptans</i>																					
<i>Potentilla sterilis</i>																					
<i>Primula vulgaris</i>																					
<i>Ranunculus repens</i>																					
<i>Rumex obtusifolius</i>																					
<i>Rumex sanguineus</i>																					
<i>Scrophularia auriculata</i>																					
<i>Scrophularia nodosa</i>																					
<i>Sisymbrium officinale</i>																					
<i>Solanum dulcamara</i>																					
<i>Stachys sylvatica</i>																					
<i>Stellaria media</i>																					
<i>Stellaria nemorum</i>																					
<i>Tamus communis</i>																					
<i>Taraxacum spp.</i>																					
<i>Tussilago farfara</i>																					
<i>Urtica dioica</i>																					
<i>Veronica chamaedrys</i>																					
<i>Veronica persica</i>																					
<i>Vicia tetrasperma</i>																					
<i>Vicia sepium</i>																					
<i>Viola arvensis</i>																					
<i>Viola hirta</i>																					
<i>Viola reichenbachiana</i>																					
<i>Viola riviniana</i>																					
Total	2	7	4	4	4	4	3	3	1	2	6	6	6	4	10	6	6	3	8	5	3

Woodland: species total = 14

Hedgerow: species total = 16

Transect 9: Hedge 18 & 17: Geddington

Quadrat Location Herbaceous plant species	Wood										Hedge									
	10	9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9	10
<i>Achillea millefolium</i>																				
<i>Aegopodium podagraria</i>																				
<i>Alliaria petiolata</i>																				
<i>Allium ursinum</i>																				
<i>Ajuga reptans</i>																				
<i>Angelica sylvestris</i>																				
<i>Anthriscus sylvestris</i>																				
<i>Arum maculatum</i>																				
<i>Bryonia dioica</i>																				
<i>Calystegia sepium</i>																				
<i>Capsella bursa-pastoris</i>																				
<i>Cardamine flexuosa</i>																				
<i>Centaurea nigra</i>																				
<i>Cerastium holosteoides</i>																				
<i>Chaerophyllum temulenum</i>																				
<i>Chamaenerion angustifolium</i>																				
<i>Circaea lutetiana</i>																				
<i>Cirsium arvense</i>																				
<i>Cirsium vulgare</i>																				
<i>Conopodium majus</i>																				
<i>Convolvulus arvensis</i>																				
<i>Dactylorhiza fuchsii</i>																				
<i>Filipendula ulmaria</i>																				
<i>Galium aparine</i>																				
<i>Galium mollugo</i>																				
<i>Geranium dissectum</i>																				
<i>Geranium molle</i>																				
<i>Geranium robertianum</i>																				
<i>Geum urbanum</i>																				
<i>Glechoma hederacea</i>																				
<i>Hedera helix</i>																				
<i>Heracleum sphondylium</i>																				
<i>Hyacinthoides non-scripta</i>																				
<i>Hypericum hirsutum</i>																				
<i>Hypericum perforatum</i>																				
<i>Lamium galeobdolon</i>																				
<i>Lapsana communis</i>																				
<i>Lonicera periclymenum</i>																				
<i>Mercurialis perennis</i>																				
<i>Moehringia trinervia</i>																				
<i>Myosotis arvensis</i>																				
<i>Myosotis sylvatica</i>																				
<i>Petasites hybridus</i>																				
<i>Plantago lanceolata</i>																				
<i>Potentilla reptans</i>																				
<i>Potentilla sterilis</i>																				
<i>Frimula vulgaris</i>																				
<i>Ranunculus repens</i>																				
<i>Rumex obtusifolius</i>																				
<i>Rumex sanguineus</i>																				
<i>Scrophularia auriculata</i>																				
<i>Scrophularia nodosa</i>																				
<i>Sisymbrium officinale</i>																				
<i>Solanum dulcamara</i>																				
<i>Stachys sylvatica</i>																				
<i>Stellaria media</i>																				
<i>Stellaria nemorum</i>																				
<i>Tamus communis</i>																				
<i>Taraxacum spp.</i>																				
<i>Tussilago farfara</i>																				
<i>Urtica dioica</i>																				
<i>Veronica chamaedrys</i>																				
<i>Veronica hederifolia</i>																				
<i>Veronica persica</i>																				
<i>Vicia sepium</i>																				
<i>Vicia tetrasperma</i>																				
<i>Viola arvensis</i>																				
<i>Viola hirta</i>																				
<i>Viola reichenbachiana</i>																				
<i>Viola riviniana</i>																				
Total	1	1	2	2	2	1	1	5	2	2	6	11	10	9	8	12	9	7	5	6

Woodland: species total =7

Hedgerow: species total =20

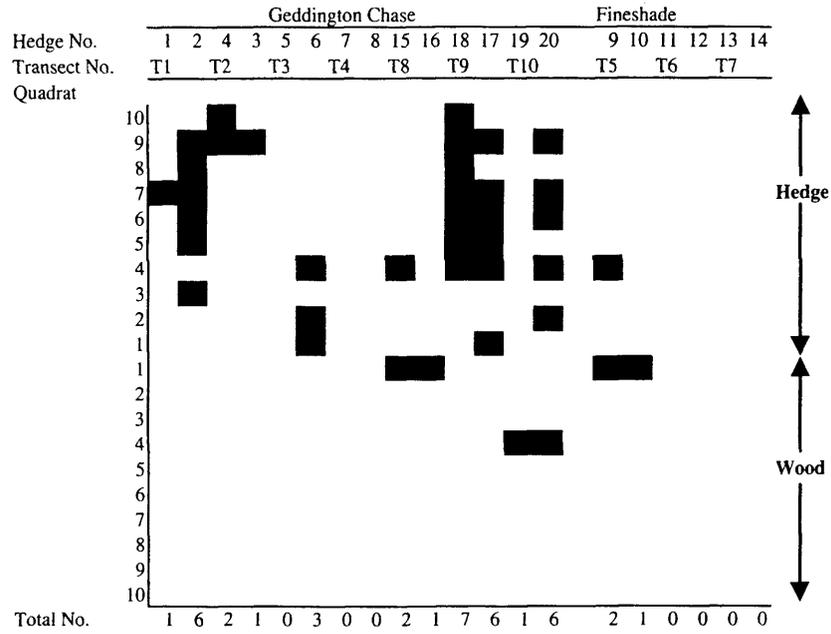
Transect 10: Hedge 19 & 20: Geddington

Quadrat Location	Wood										Hedge									
	10	9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9	10
<i>Achillea millefolium</i>																				
<i>Aegopodium podagraria</i>																				
<i>Alliaria petiolata</i>																				
<i>Allium ursinum</i>																				
<i>Ajuga reptans</i>																				
<i>Angelica sylvestris</i>																				
<i>Anthriscus sylvestris</i>																				
<i>Arum maculatum</i>																				
<i>Bryonia dioica</i>																				
<i>Calystegia sepium</i>																				
<i>Capsella bursa-pastoris</i>																				
<i>Cardamine flexuosa</i>																				
<i>Centaurea nigra</i>																				
<i>Cerastium holosteoides</i>																				
<i>Chaerophyllum temulentum</i>																				
<i>Chamaenerion angustifolium</i>																				
<i>Circaea lutetiana</i>																				
<i>Cirsium arvense</i>																				
<i>Cirsium vulgare</i>																				
<i>Conopodium majus</i>																				
<i>Convolvulus arvensis</i>																				
<i>Dactylorhiza fuchsii</i>																				
<i>Filipendula ulmaria</i>																				
<i>Galium aparine</i>																				
<i>Gallium mollugo</i>																				
<i>Geranium dissectum</i>																				
<i>Geranium molle</i>																				
<i>Geranium robertianum</i>																				
<i>Geum urbanum</i>																				
<i>Glechoma hederacea</i>																				
<i>Hedera helix</i>																				
<i>Heracleum sphondylium</i>																				
<i>Hyacinthoides non-scripta</i>																				
<i>Hypericum hirsutum</i>																				
<i>Hypericum perforatum</i>																				
<i>Lamium galeobdolon</i>																				
<i>Lapsana communis</i>																				
<i>Lonicera periclymenum</i>																				
<i>Mercurialis perennis</i>																				
<i>Moehringia trinervia</i>																				
<i>Myosotis arvensis</i>																				
<i>Myosotis sylvatica</i>																				
<i>Petasites hybridus</i>																				
<i>Plantago lanceolata</i>																				
<i>Potentilla reptans</i>																				
<i>Potentilla sterilis</i>																				
<i>Primula vulgaris</i>																				
<i>Ranunculus repens</i>																				
<i>Rumex obtusifolius</i>																				
<i>Rumex sanguineus</i>																				
<i>Scrophularia auriculata</i>																				
<i>Scrophularia nodosa</i>																				
<i>Sisymbrium officinale</i>																				
<i>Solanum dulcamara</i>																				
<i>Stachys sylvatica</i>																				
<i>Stellaria nemorum</i>																				
<i>Stellaria media</i>																				
<i>Tamus communis</i>																				
<i>Taraxacum spp.</i>																				
<i>Tussilago farfara</i>																				
<i>Urtica dioica</i>																				
<i>Veronica chamaedrys</i>																				
<i>Veronica hederifolia</i>																				
<i>Veronica persica</i>																				
<i>Vicia sepium</i>																				
<i>Vicia tetrasperma</i>																				
<i>Viola arvensis</i>																				
<i>Viola hirta</i>																				
<i>Viola reichenbachiana</i>																				
<i>Viola riviniana</i>																				
Total	0	0	3	0	2	1	4	3	3	2	7	12	4	6	6	6	5	4	7	4

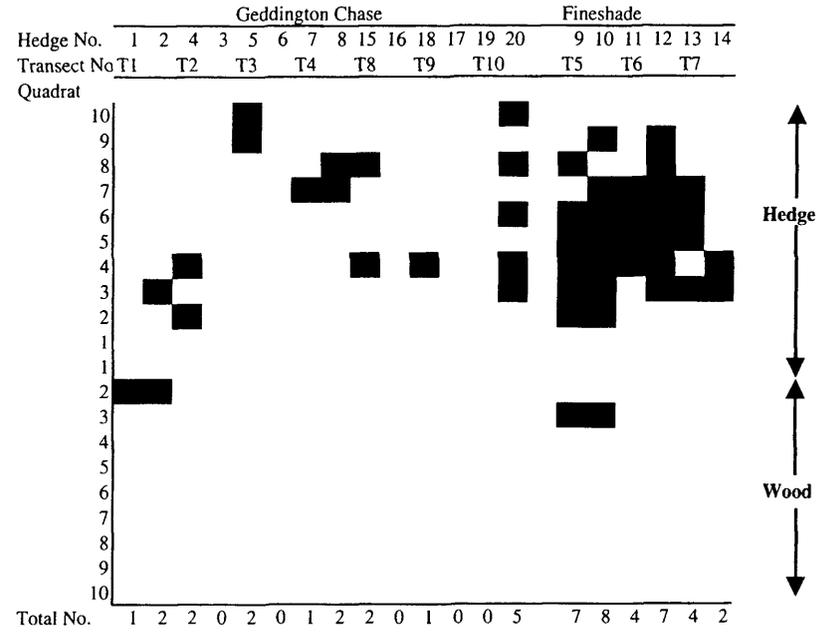
Woodland: species total =7

Hedgerow: species total = 17

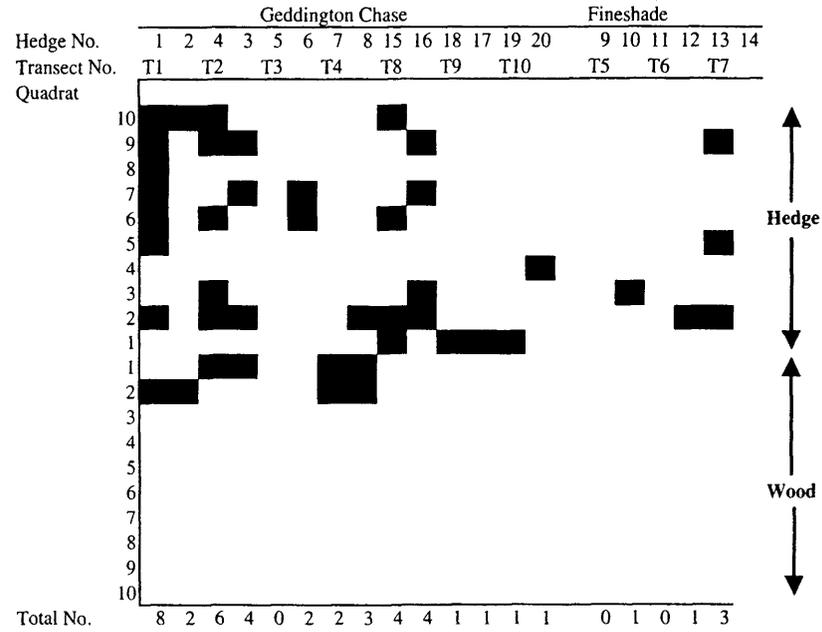
a) Location of quadrats containing *Stellaria media* in hedge and woodland transects.



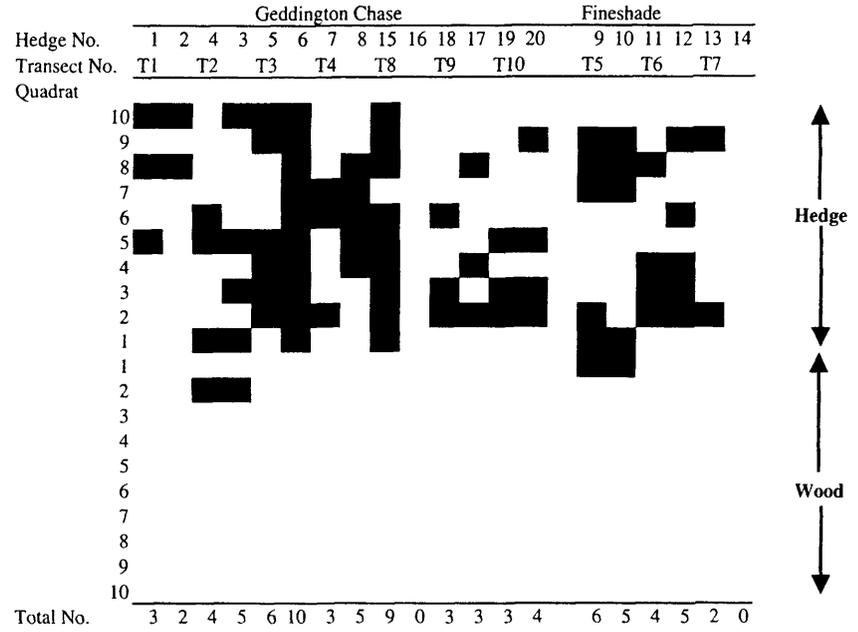
b) Location of quadrats containing *Tamus communis* in hedge and woodland transects.



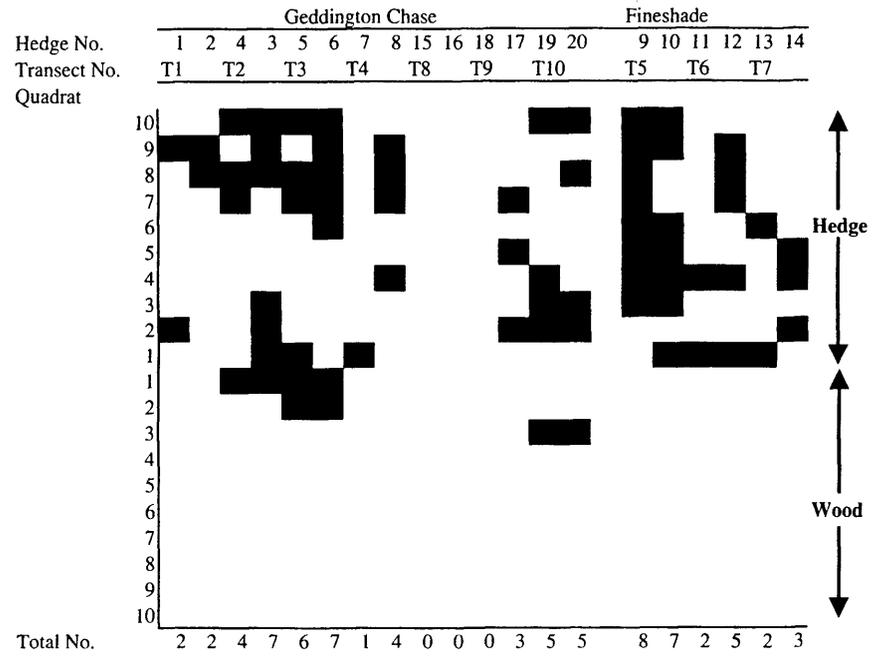
c) Location of quadrats containing *Anthriscus sylvestris* in hedge and woodland transects.



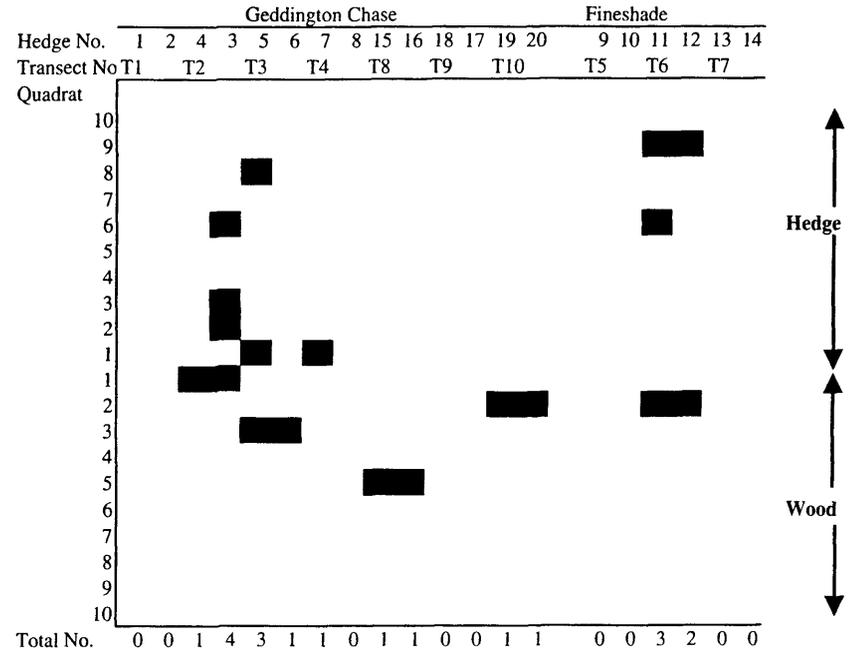
d) Location of quadrats containing *Cirsium arvense* in hedge and woodland transects.



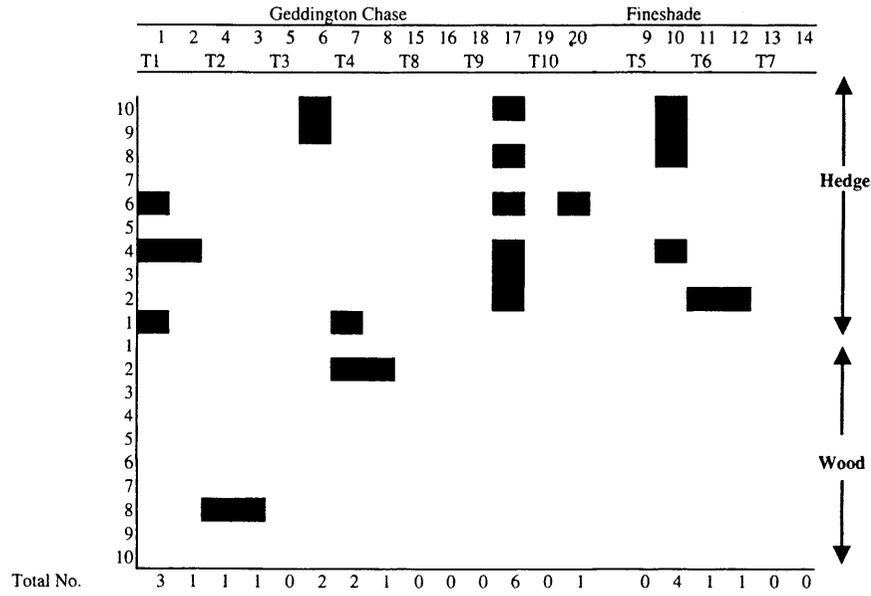
e) Location of *Chaerophyllum temulentum* in hedge and woodland transects.



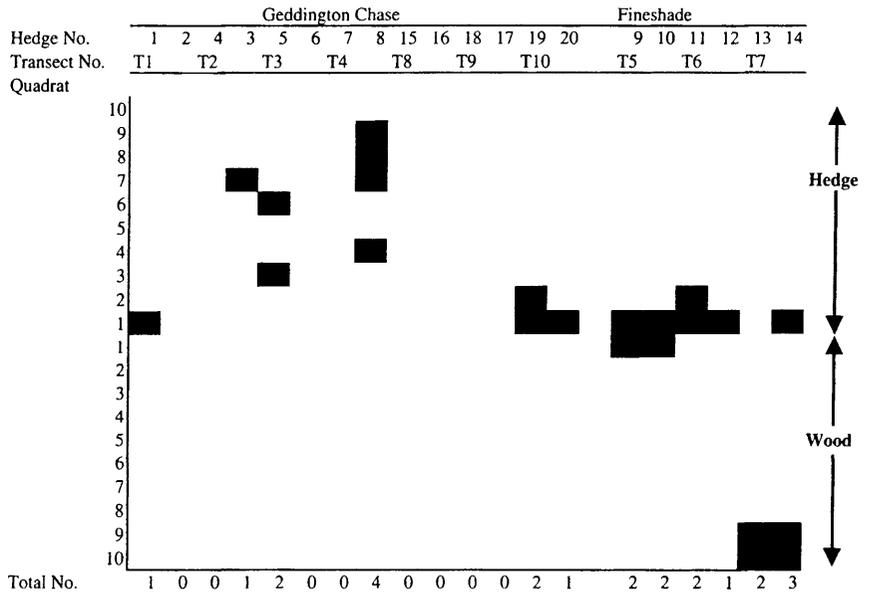
f) Location of quadrats containing *Arum maculatum* in hedge and woodland transects.



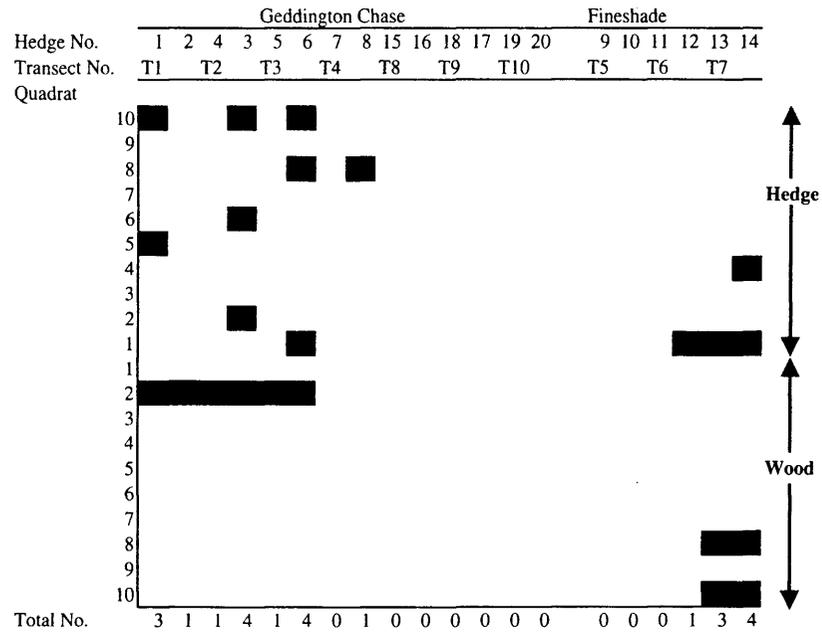
k) Location of quadrats containing *Heracleum sphondylium* in hedge and woodland quadrats.



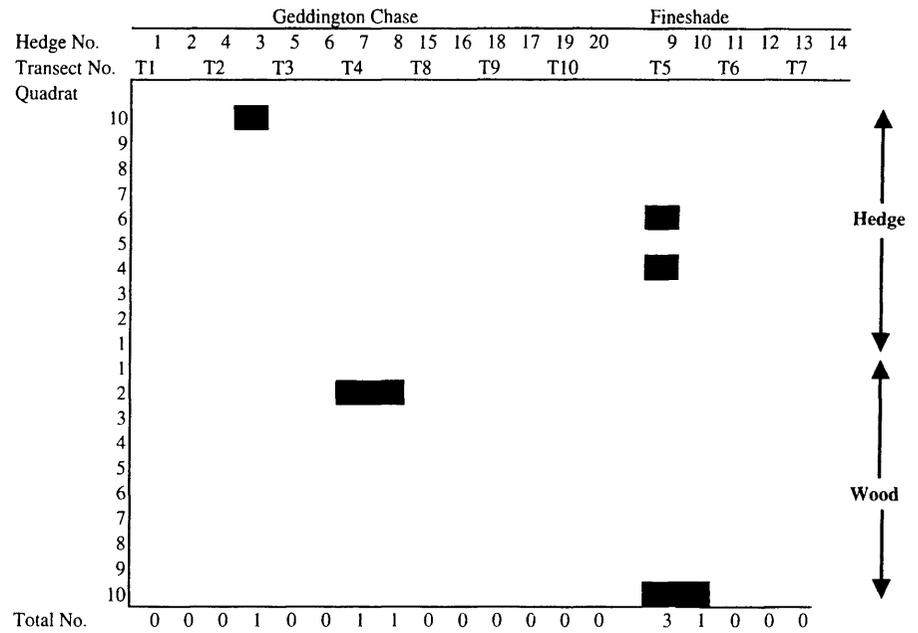
l) Location of quadrats containing *Ranunculus repens* in hedge and woodland transects.



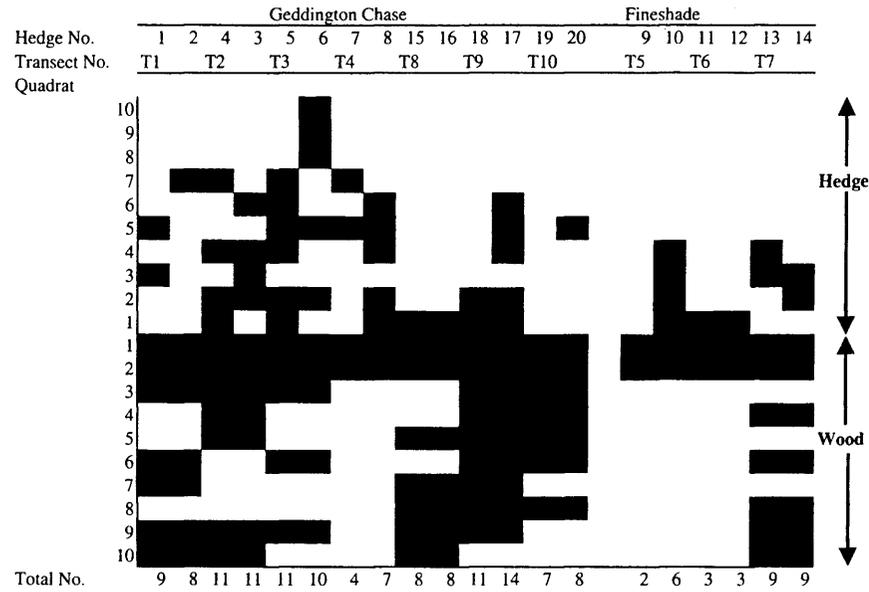
m) Location of quadrats containing *Stachys sylvatica* in hedge and woodland transects.



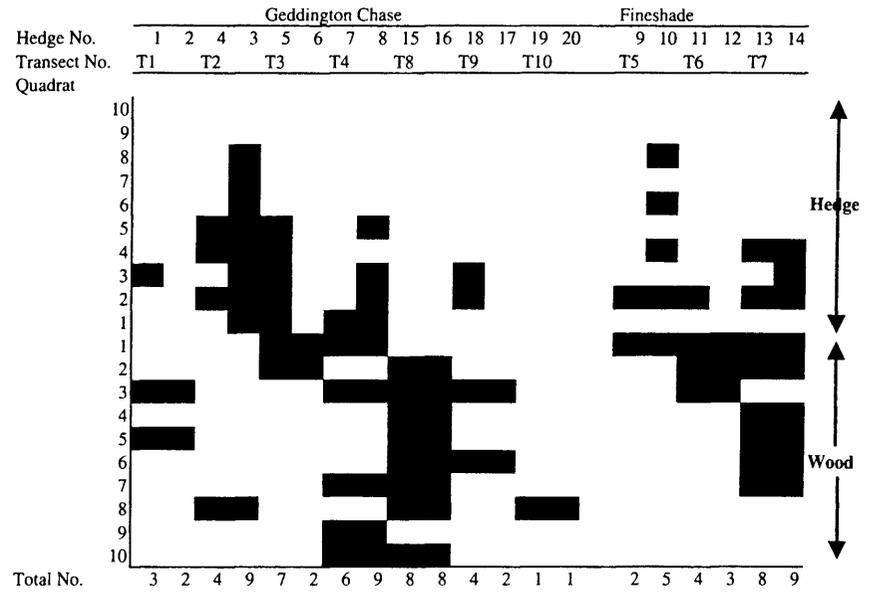
n) Location of quadrats containing *Potentilla reptans* in hedge and woodland transects.



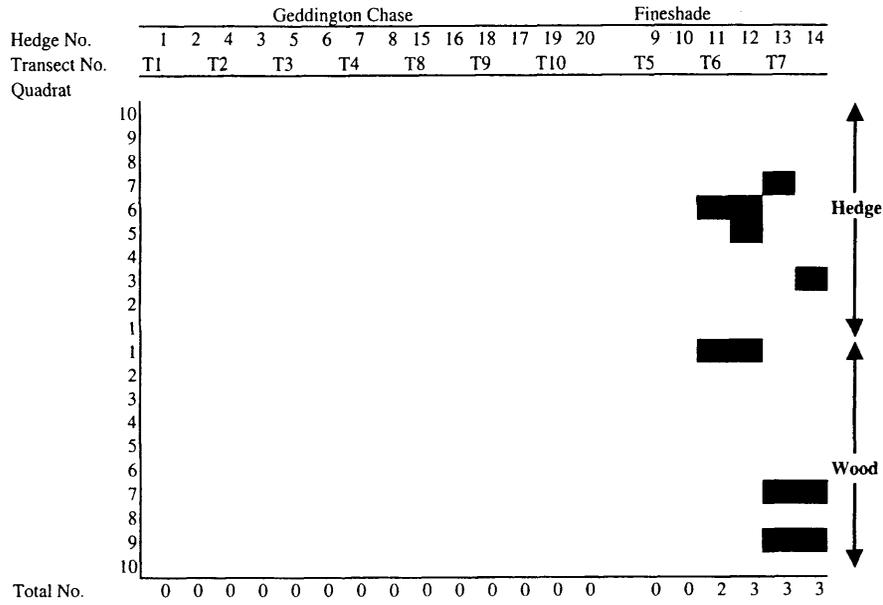
o) Location of quadrats containing *Mercurialis perennis* in hedge and woodland transects.



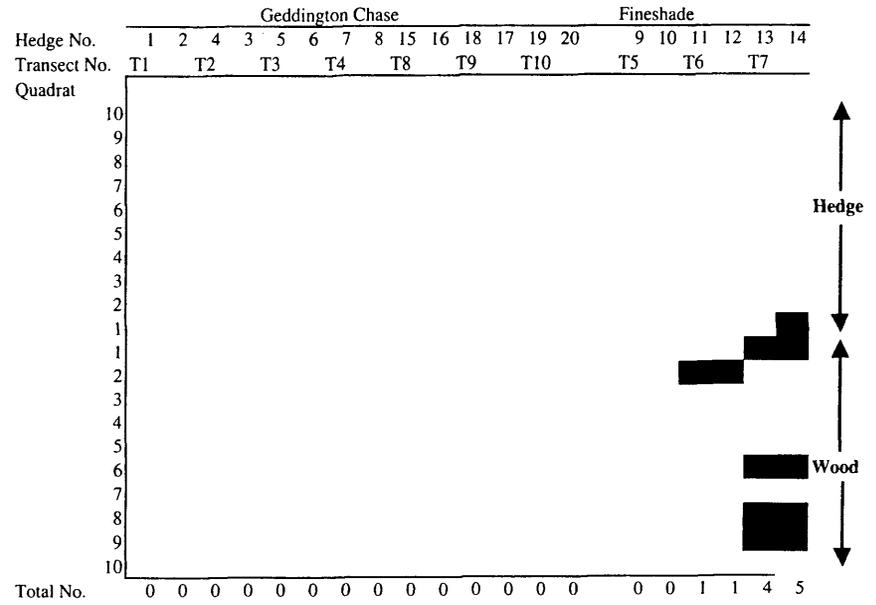
p) Location of quadrats containing *Glechoma hederacea* in hedge and woodland transects.



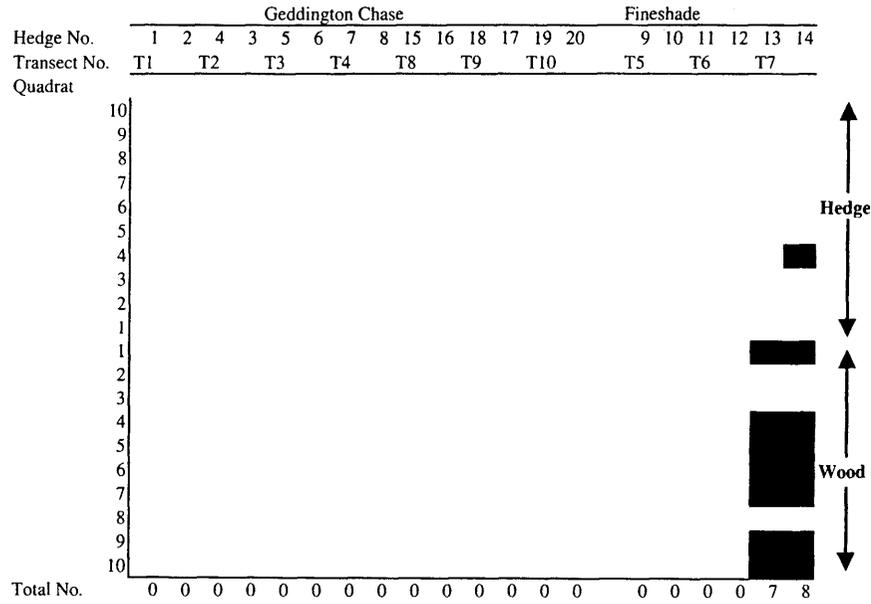
q) Location of quadrats containing *Hedera helix* in hedge and woodland quadrats.



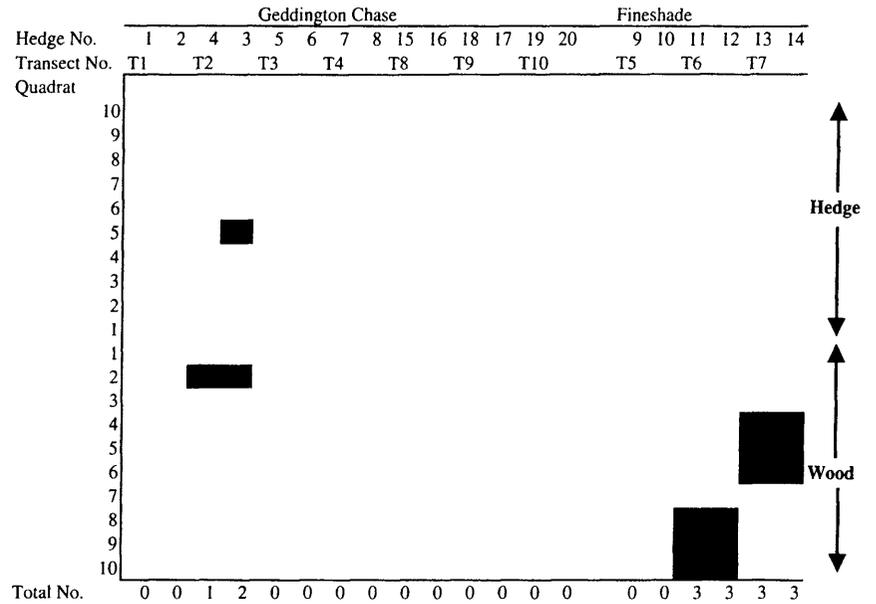
r) Location of quadrats containing *Geum urbanum* in hedge and woodland transects.



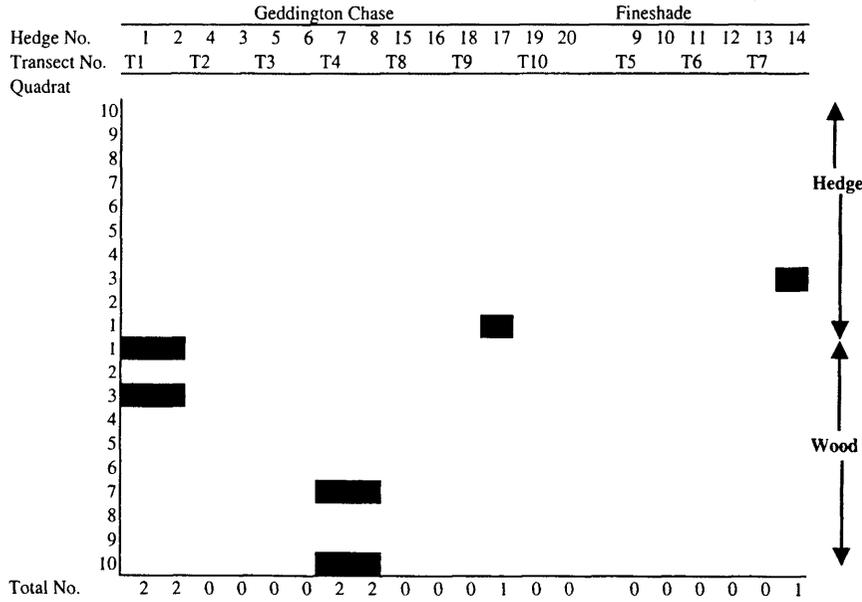
s) Location of quadrats containing *Geranium robertianum* in hedge and woodland transects.



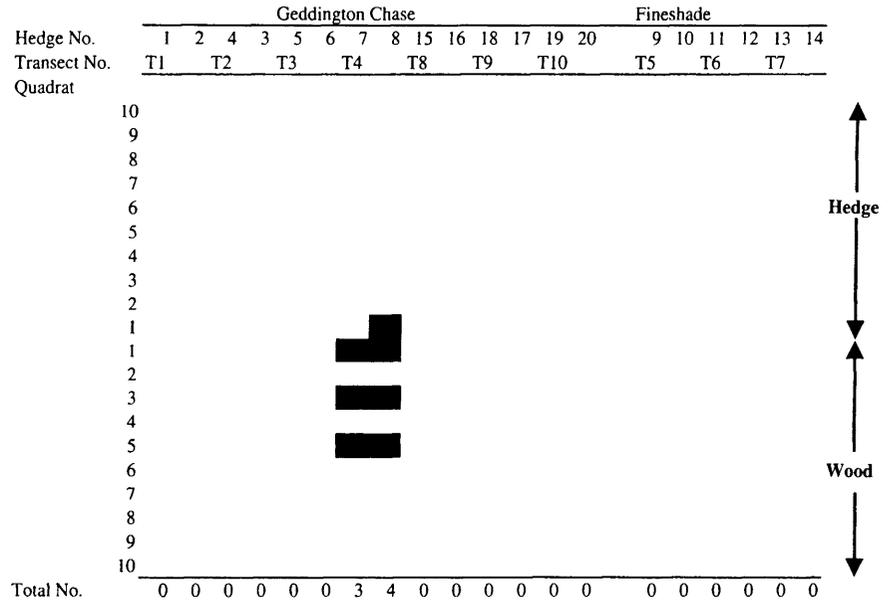
t) Location of quadrats containing *Chamaenerion angustifolium* in hedge and woodland transects.



u) Location of quadrats containing *Viola riviniana* in hedge and woodland transects.

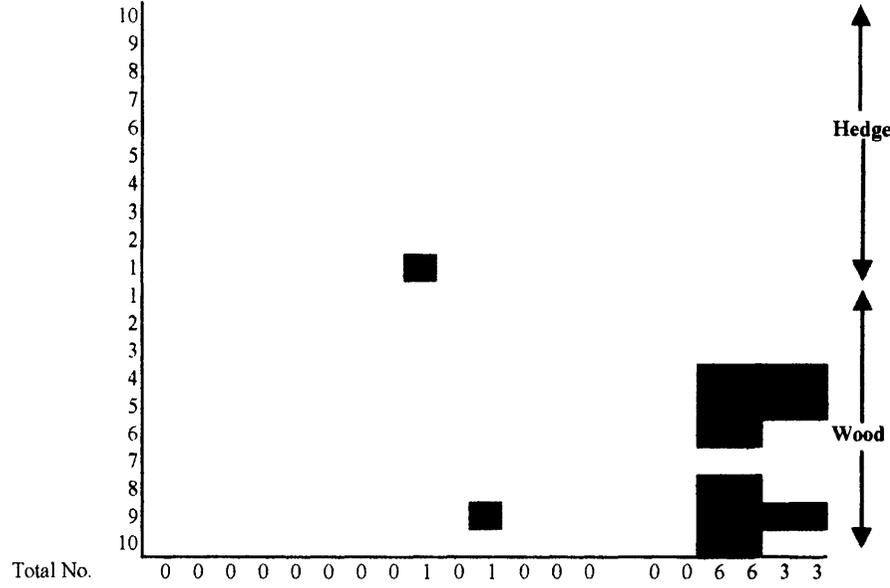


v) Location of quadrats containing *Lamium galeobdolon* in hedge and woodland transects.



w) Location of quadrats containing *Circaea lutetiana* in hedge and woodland transects.

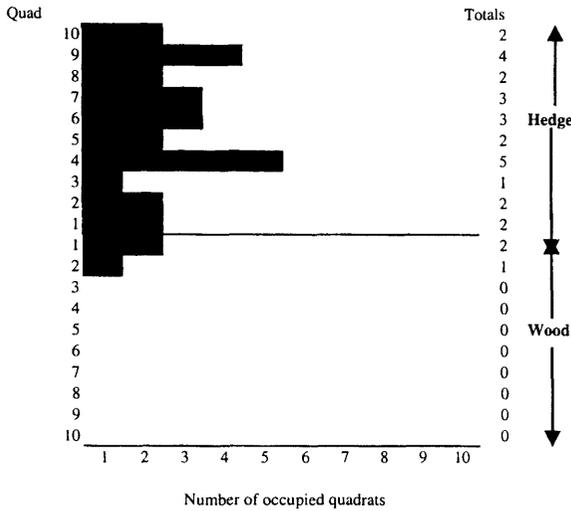
	Geddington Chase										Fineshade									
Hedge No.	1	2	4	3	5	6	7	8	15	16	18	17	19	20	9	10	11	12	13	14
Transect No.	T1	T2	T3	T4	T8	T9	T10	T5	T6	T7										



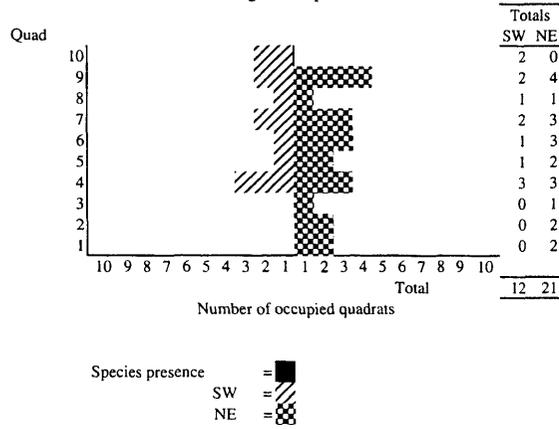
3.5 Combined transect data: herbaceous plant species

a) *Stellaria media*

Combined transect data in hedgerows and woodland

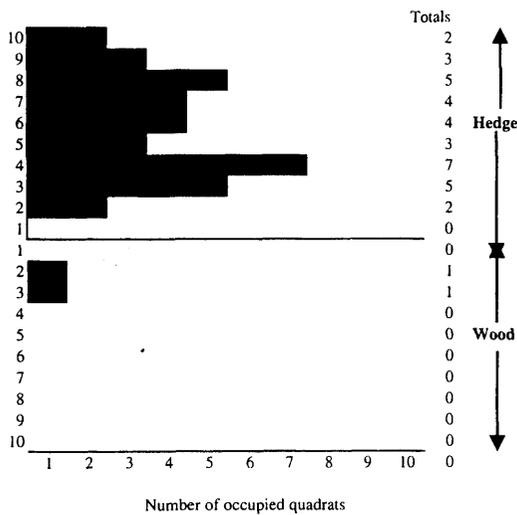


Combined transect data for hedgerow aspect.

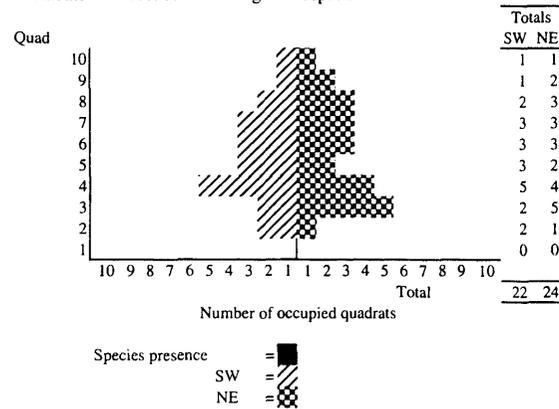


b) *Tamus communis*

Combined transect data in hedgerows and woodland

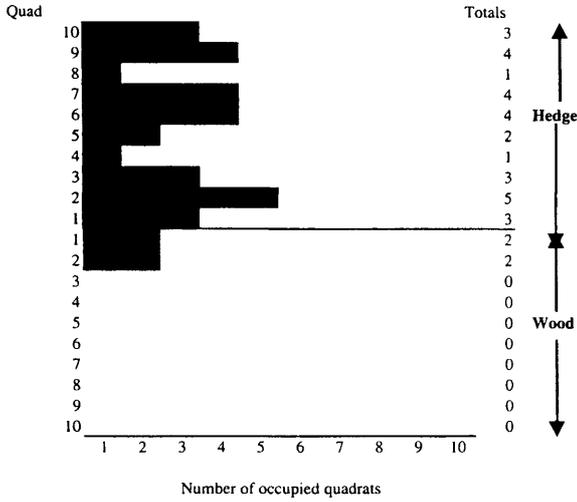


Combined transect data for hedgerow aspect.

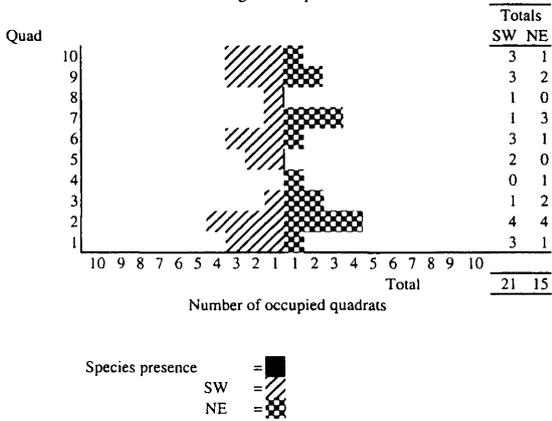


c) *Anthriscus sylvestris*

Combined transect data in hedgerows and woodland

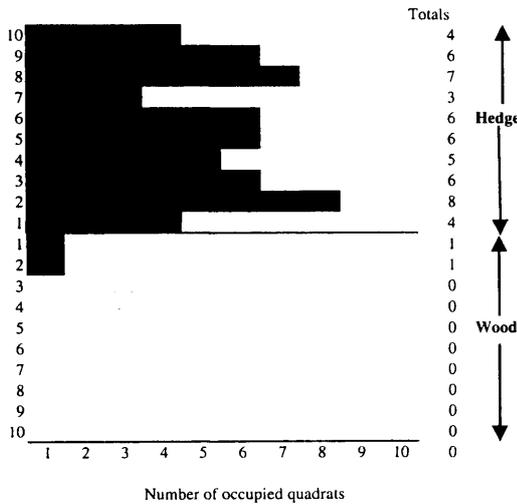


Combined transect data for hedgerow aspect.

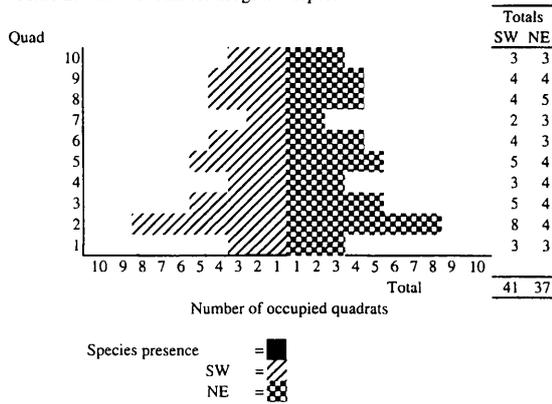


d) *Cirsium arvense*

Combined transect data in hedgerows and woodlands

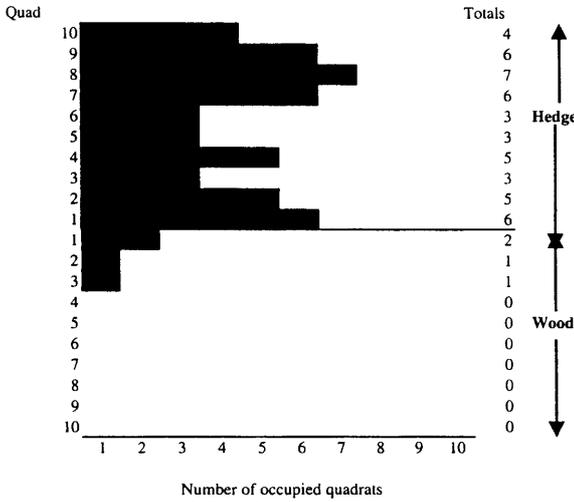


Combined transect data for hedgerow aspect.

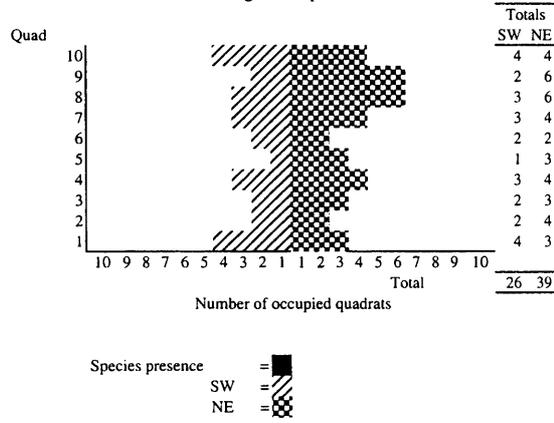


e) *Chaerophyllum temulentum*

Combined transect data in hedgerows and woodland

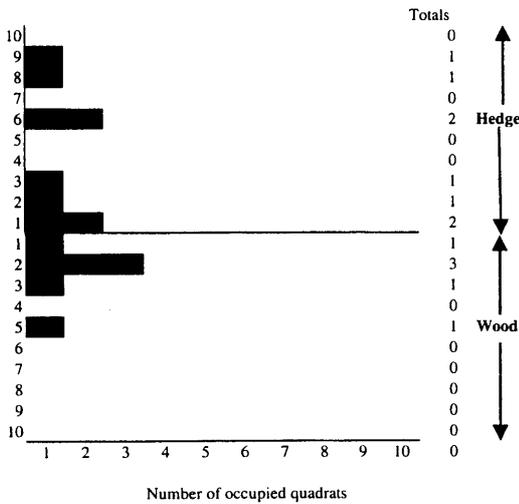


Combined transect data for hedgerow aspect.

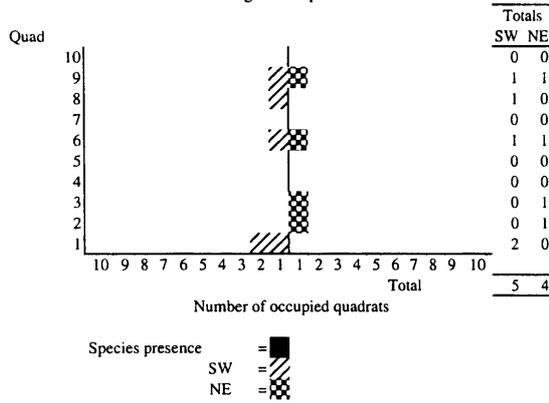


f) *Arum maculatum*

Combined transect data in hedgerows and woodland

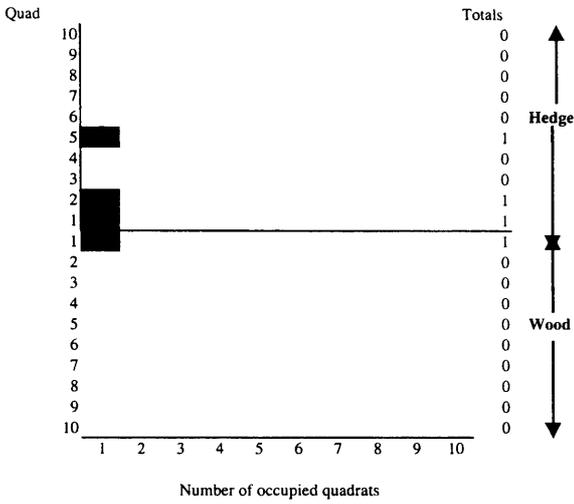


Combined transect data for hedgerow aspect.

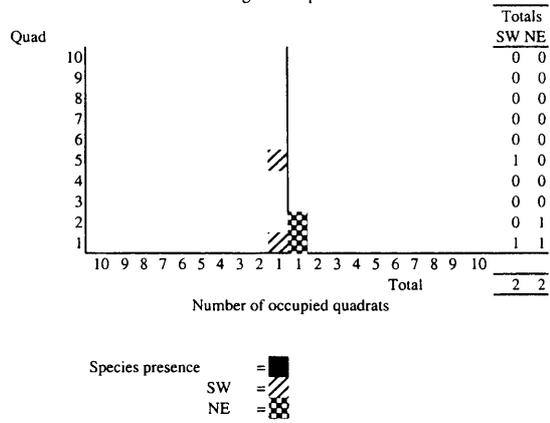


g) *Petasites hybridus*

Combined transect data in hedgerows and woodland

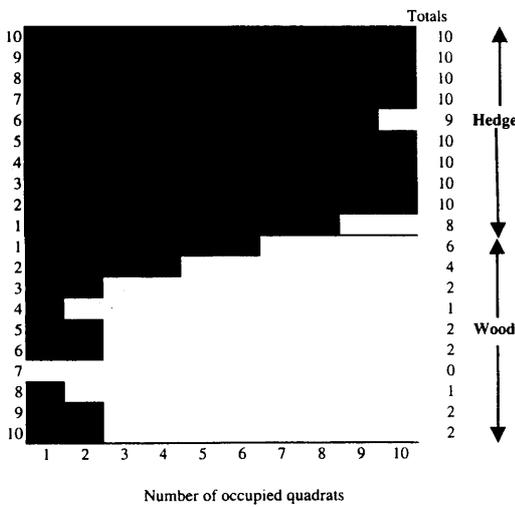


Combined transect data for hedgerow aspect.

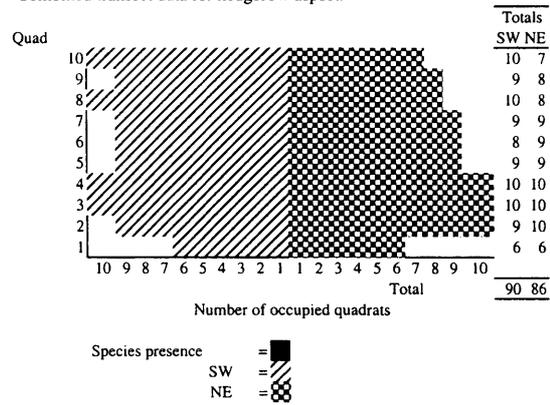


h) *Galium aparine*

Combined transect data in hedgerows and woodland

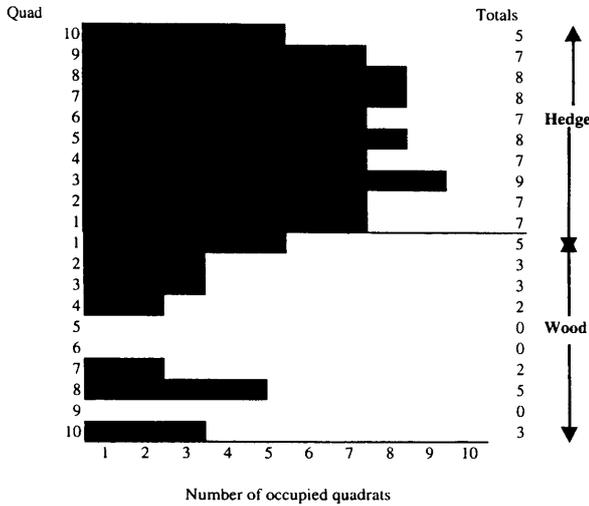


Combined transect data for hedgerow aspect.

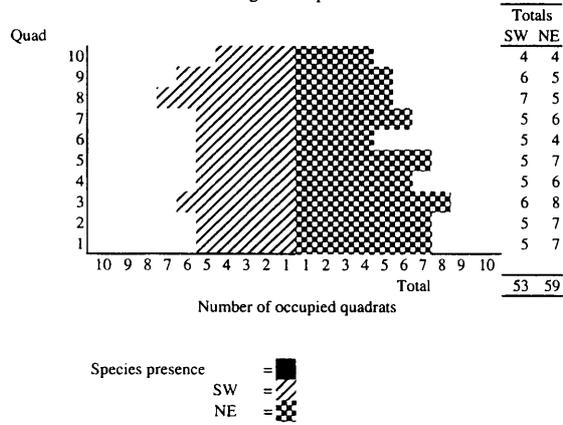


i) *Urtica dioica*

Combined transect data in hedgerows and woodland

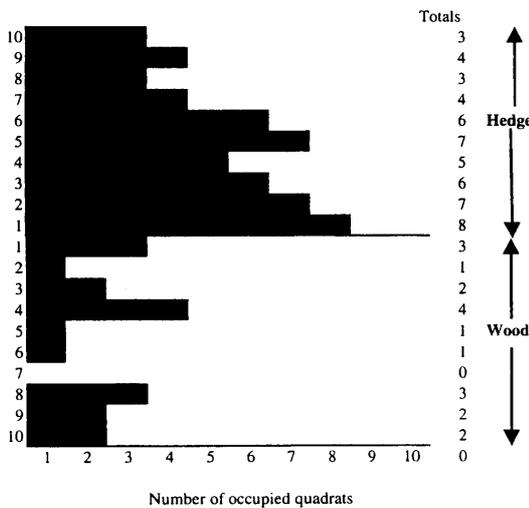


Combined transect data for hedgerow aspect.

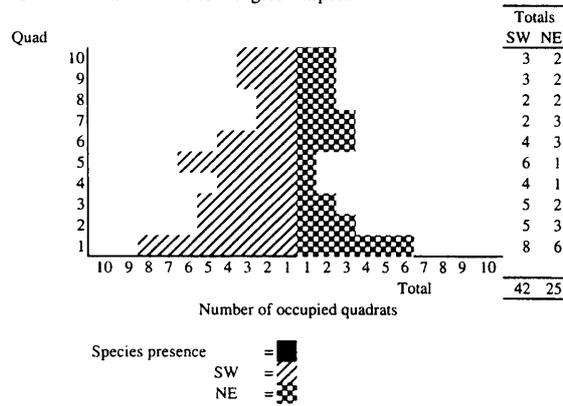


j) *Rumex obtusifolius*

Combined transect data in hedgerows and woodland

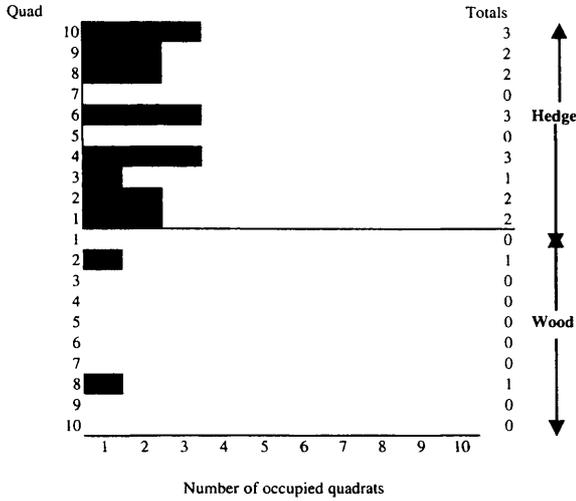


Combined transect data for hedgerow aspect.

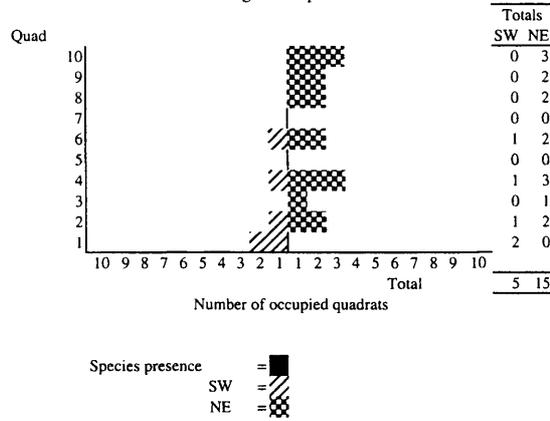


k) *Heracleum sphondylium*

Combined transect data in hedgerows and woodland

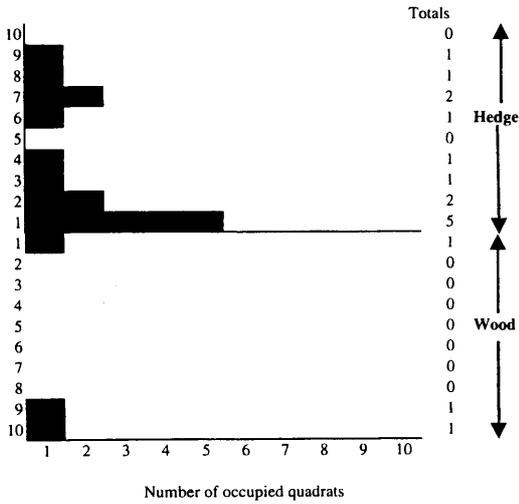


Combined transect data for hedgerow aspect.

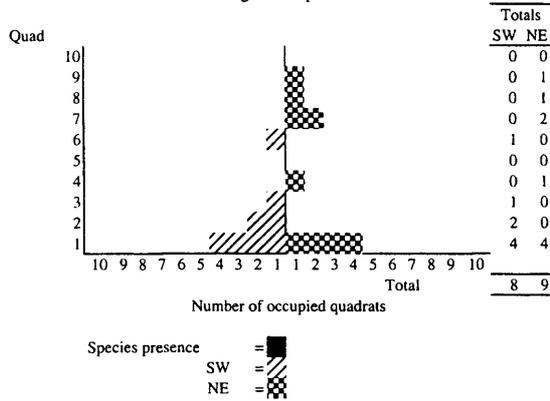


l) *Ranunculus repens*

Combined transect data in hedgerows and woodland

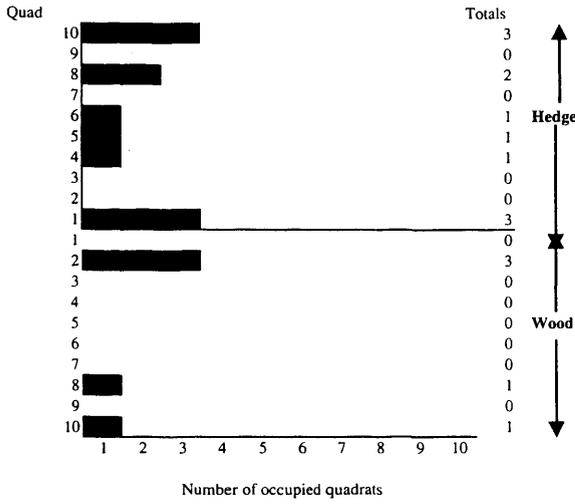


Combined transect data for hedgerow aspect.

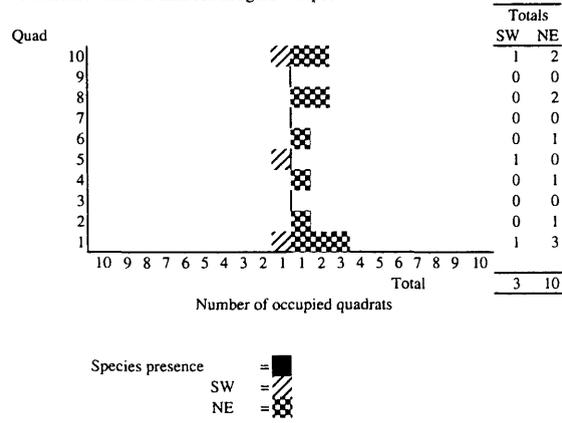


m) *Stachys sylvatica*

Combined transect data in hedgerows and woodland

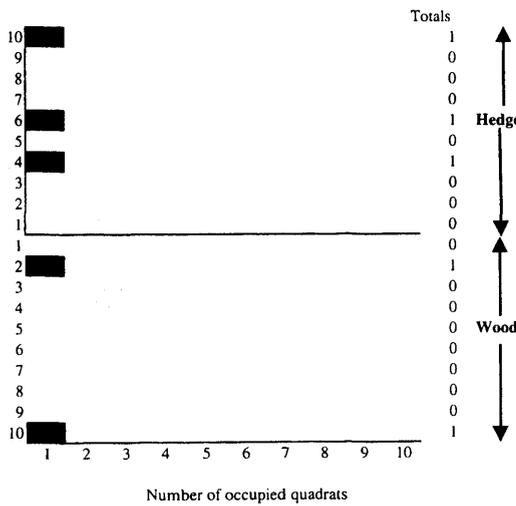


Combined transect data for hedgerow aspect.

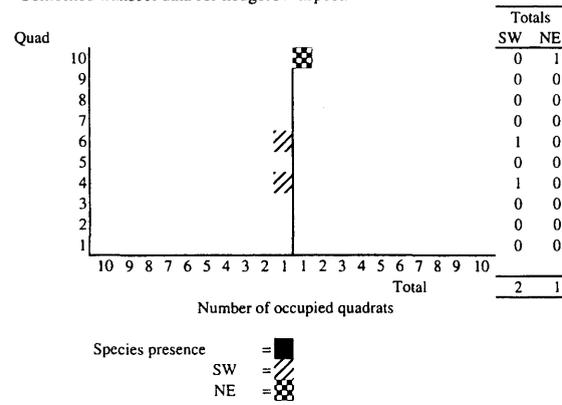


n) *Potentilla reptans*

Combined transect data in hedgerows and woodland

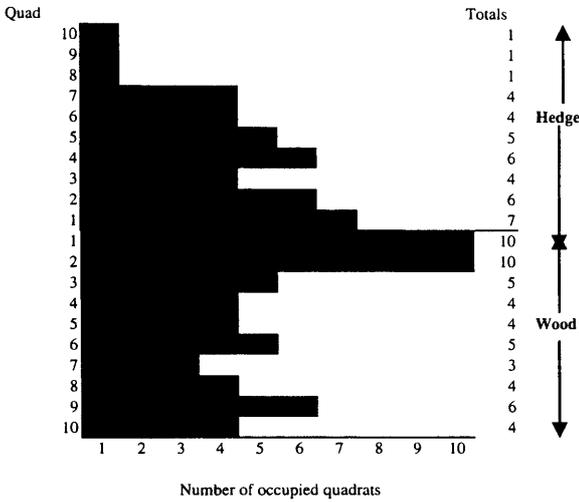


Combined transect data for hedgerow aspect.

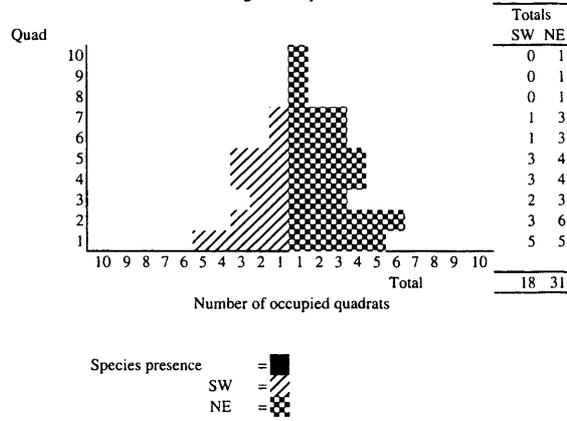


o) *Mercurialis perennis*

Combined transect data in hedgerows and woodland

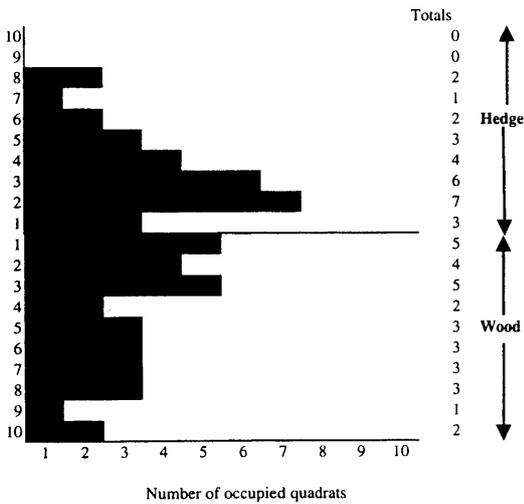


Combined transect data for hedgerow aspect.

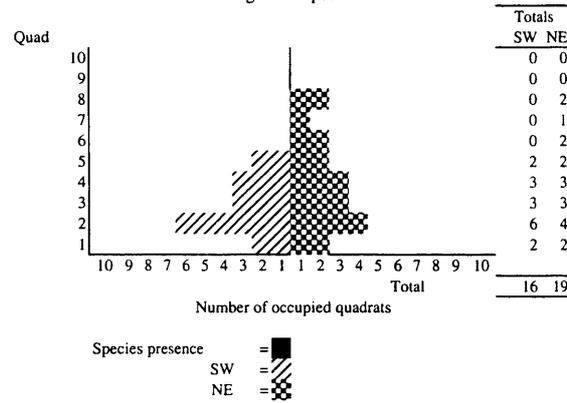


p) *Glechoma hederacea*

Combined transect data in hedgerows and woodland

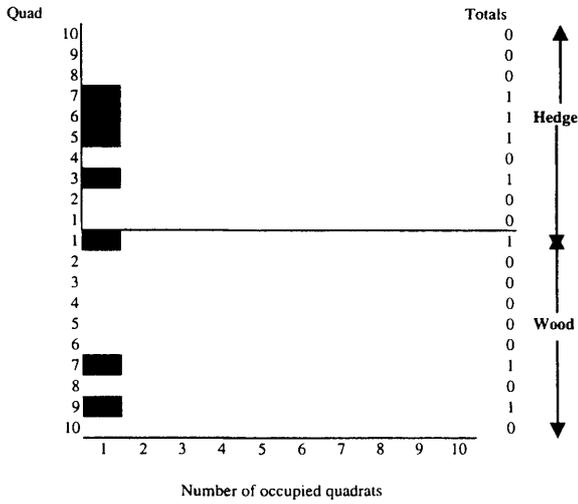


Combined transect data for hedgerow aspect.

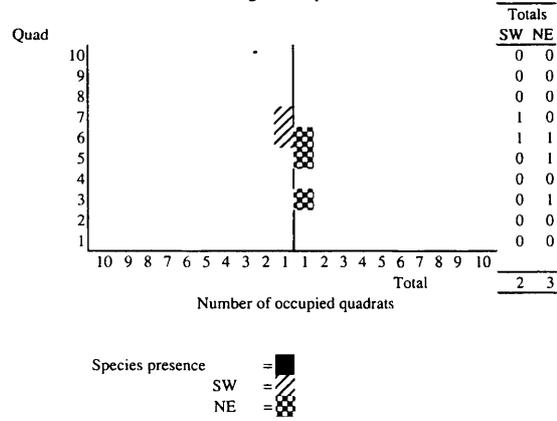


q) *Hedera helix*

Combined transect data in hedgerows and woodland

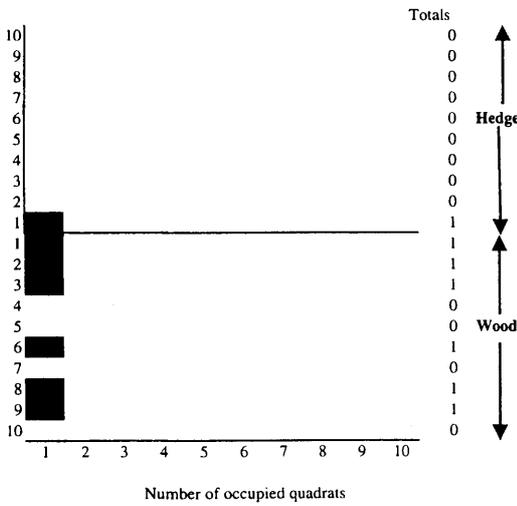


Combined transect data for hedgerow aspect.

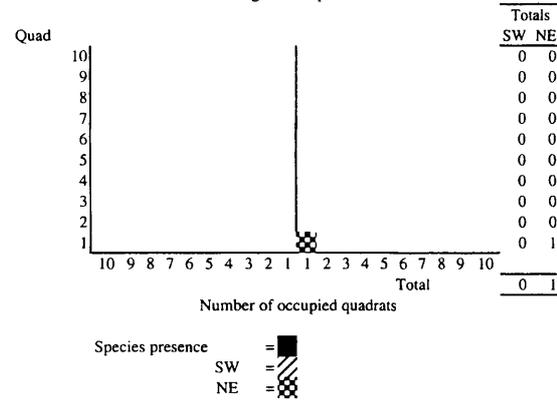


r) *Geum urbanum*

Combined transect data in hedgerows and woodland

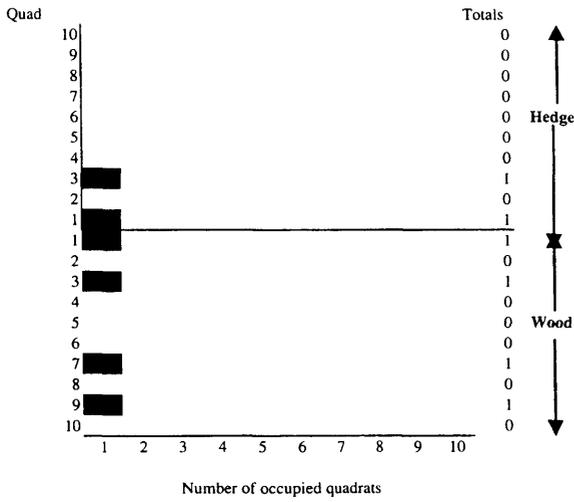


Combined transect data for hedgerow aspect.

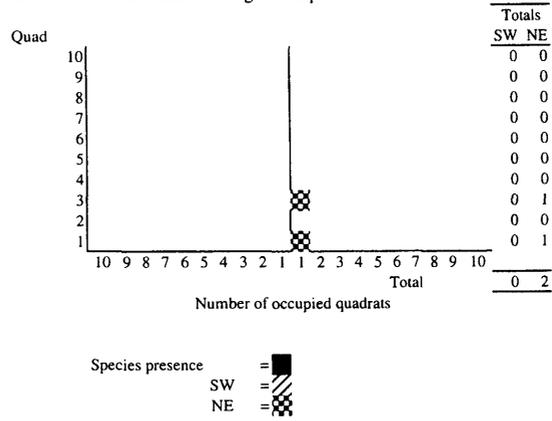


u) *Viola riviniana*

Combined transect data in hedgerows and woodland

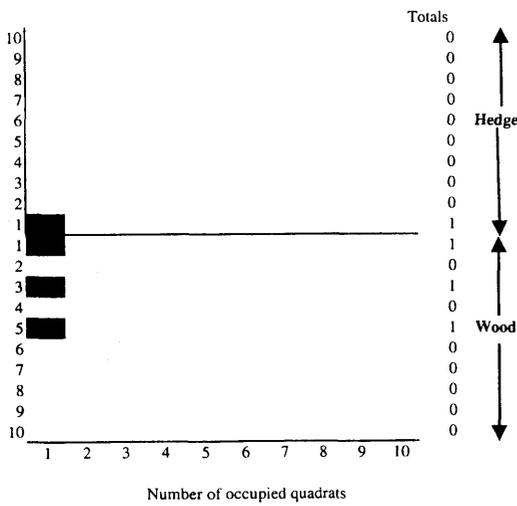


Combined transect data for hedgerow aspect.

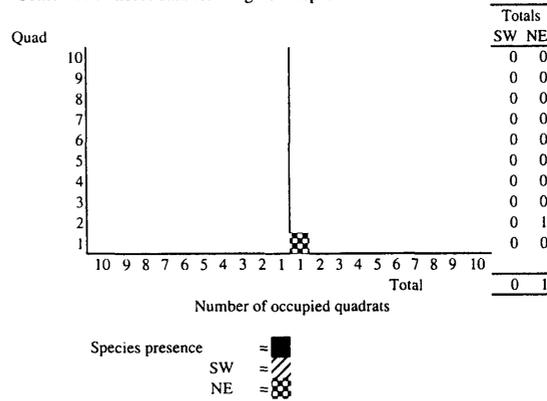


v) *Lamium galeobdolon*

Combined transect data in hedgerows and woodland

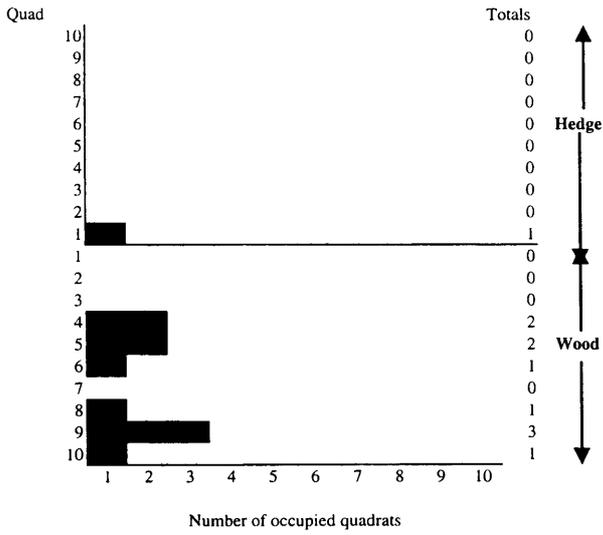


Combined transect data for hedgerow aspect.

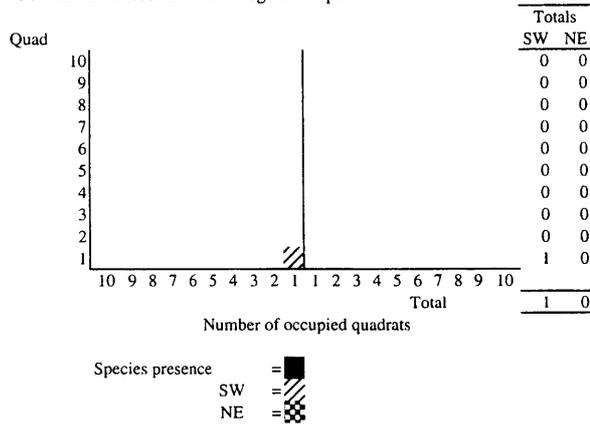


w) *Circaea lutetiana*

Combined transect data in hedgerows and woodland



Combined transect data for hedgerow aspect.



3.6 Autoecological characteristics of herbaceous plant species in the three community groups

a) Herbaceous species in woodland transects only: life history strategies.

	Commonest habitat	Soil pH	Present status	Life history	Established strategy	Life form	Leaf phenology	Regenerative strategies	Seed bank	Agency of dispersal	Dispersule/germinule form	Dispersule weight
Hedge												
<i>Stellaria holostea</i>	HEDGE	3d	-	P	CSR	Ch	Ea	V	1	UNSPc	Sd	5
Wood												
<i>Allium ursinum</i>	WOODl	6b	-	P	SR/CSR	G	Sv	V,S	1	UNSP	Sd	5
<i>Hyacinthoides non-scripta</i>	PLANTb	4b	?	P	SR	G	Sv	V,S	1	UNSP	Sd	5
<i>Lonicera periclymenum</i>	WOODl	4a	?	P	SC	Ph	Ep	V,S	1	ANIMi	F/S	5
<i>Moehringia trinervia</i>	WOODl	4a	+	A/P	SR	Th/Ch	Sa	?	2	UNSPc	Sd	2
<i>Myosotis sylvatica</i>	unlisted											
<i>Primula vulgaris</i>	SCRUB	6d	-	P	S/CSR	H	Ea	Bs	3	ANIME	Sd	2
<i>Viola reichenbachiana</i>	unlisted											
Mire												
<i>Cardamine flexuosa</i>	MIREs	6b	+	A-P	R/SR	H	Ea	S,Bs	3	WINDw	Sd	1
<i>Filipendula ulmaria</i>	MIREs	5c	-	P	C/SC	H	Sa	V	1	AQUAT	Fr	3
<i>Solanum dulcamara</i>	MIREs	7c	?	P	C/CSR	Ch/Ph	Sa	(V),S	2	ANIMi	F/S	4
Pasture												
<i>Dactylorhiza fuchsii</i>	PASTl	7c	?	P	S/CSR	G	Sa	W	?	WINDem	Sd	S
<i>Potentilla sterilis</i>	PASTl	5c	-	P	S	H	Ea	V, Bs	3	UNSP	Fr	3
<i>Viola riviniana</i>	PASTl	5d	-	P	S	H	Ea	V,S	1	ANIME	Sd	4
Disturbance												
<i>Aegopodium podagraria</i>	SOIL	6b	+	P	CR/CSR	H	Sa	V,S	1	*UNSP	Fr	4
<i>Hypericum hirsutum</i>	SCREE	7b	-	P	SR/CSR	H	Ep	V, Bs	3	WINDc	Sd	1
<i>Hypericum perforatum</i>	WASTEI	7c	+	P	CR/CSR	H	Ep	V, Bs	3	WINDc	Sd	1
<i>Tussilago farfara</i>	QRYI	7b	+	P	CR	G	Sa	(V),W	1	*WINDp	Fr	2
<i>Vicia sepium</i>	SOIL	5c	-	P	C/CSR	H	Sa	V	1	UNSP	Sd	6
Riverbank												
<i>Scrophularia auriculata</i>	RIVBNK	6c	?	P	CR	H	Sa	S, Bs	3	AQ/WIc	Sd	1
Meadow												
<i>Cerastium fontanum</i>	MEADOW	5c	+	P/A	R/CSR	Ch/Th	Ea	(V), Bs	3	UNSPc	Sd	1
Scrub												
<i>Ajuga reptans</i>	SCRUB	6b	-	P	CSR	H	Ea	V	2	*ANIME	Fr	4
<i>Scrophularia nodosa</i>	SCRUB	6c	+	P	CR	H	Sa	Bs	3	WINDc	Sd	1

b) Herbaceous species found in woodland and adjoining hedgerow transects : life history strategies

	Commonest habitat	Soil pH	Present status	Life history	Established strategy	Life form	Leaf phenology	Regenerative strategies	Seed bank	Agency of dispersal	Dispersule/germinule form	Dispersule weight
Hedge species												
<i>Chaerophyllum temulentum</i>	HEDGE	6b	?	M	R/CSR	H	Sh	S	1	UNSP	Fr	5
<i>Galium aparine</i>	HEDGE	7c	+	Aws	CR	Th	Sh	S	1	ANIMb	Fr	5
<i>Glechoma hederacea</i>	HEDGE	6c	?	P	CSR	H	Ea	V	2	*UNSP	Fr	3
<i>Stachys sylvatica</i>	HEDGE	6b	+	P	C/CR	H	Sa	(V), Bs	3	*ANIMa	Fr	4
<i>Tamus communis</i>	HEDGE	7a	-	P	C/CR	G	Sa	S	1	ANIMi	F/S	6
Wood species												
<i>Arum maculatum</i>	WOOD1	6c	?	P	SR/CSR	G	Sv	V,S	1	ANIMi	F/S	6
<i>Geum urbanum</i>	WOOD1	5c	?	P	S/CSR	H	Ea	S	2	ANIMa	Fr	3
<i>Hedera helix</i>	WOOD1	7d	?	P	SC	Ch/Ph	Ea	V	1	ANIMi	F/S	6
<i>Lamium galeobdolon</i>	WOOD1	4d	-	P	S/SC	Ch	Ea	V,S	1	ANIME	Fr	4
<i>Mercurialis perennis</i>	WOOD1	7c	-	P	SC	H	Ep	V,S	1	ANIME	Sd	5
Mire												
<i>Circaea lutetiana</i>	MIREs	6b	+	P	CR	G	Sa	(V),S	1	*ANIMb	F/S	3
Road-verge												
<i>Anthriscus sylvestris</i>	RDVRGE	7c	?	P	CR	H	Sh	Sv,S	1	UNSP	Fr	5
<i>Potentilla reptans</i>	RDVRGE	6c	+	P	CR/CSR	H	Ep	V,Bs	3	*UNSP	Fr	2
Pasture												
<i>Viola riviniana</i>	PAST1	5d	-	P	S	H	Ea	V,S	1	ANIME	Sd	4
Disturbed												
<i>Chamerion angustifolium</i>	CINDER	4d	+	P	C	G	Sa	V,W	1	WINDp	Sd	1
<i>Cirsium arvense</i>	COAL	5c	+	P	C	G	Sa	V,W, Bs	3	*WINDp	Fr	4
<i>Geranium robertianum</i>	SCREE	7b	+	B-P	R/CSR	Th/H	Ea	?	2	ANIMa	f/S	4
<i>Heracleum sphondylium</i>	WASTE1	5c	+	P/M	CR	H	Sa	S	1	WINDw	Fr	5
<i>Rumex obtusifolius</i>	SOIL	7c	+	P	CR	H	Ea	Bs	3	ANIMa	Fr	4
<i>Urtica dioica</i>	SOIL	6c	+	P	C	Ch/H	Ep	V, Bs	3	*ANIMa	Fr	1
Riverbank												
<i>Petasites hybridus</i>	RIVBNK	6b	?	P	C	G	Sa	V,W	1	*WINDp	Fr	2
Meadow												
<i>Ranunculus repens</i>	MEADOW	6c	+	P	CR	H	Ea	(V), Bs	3	*AQ/AN	Fr	5
Arable												
<i>Stellaria media</i>	ARABLE	6c	+	Aws	R	Th	Ep	Bs	3	UNSPag	Sd	2

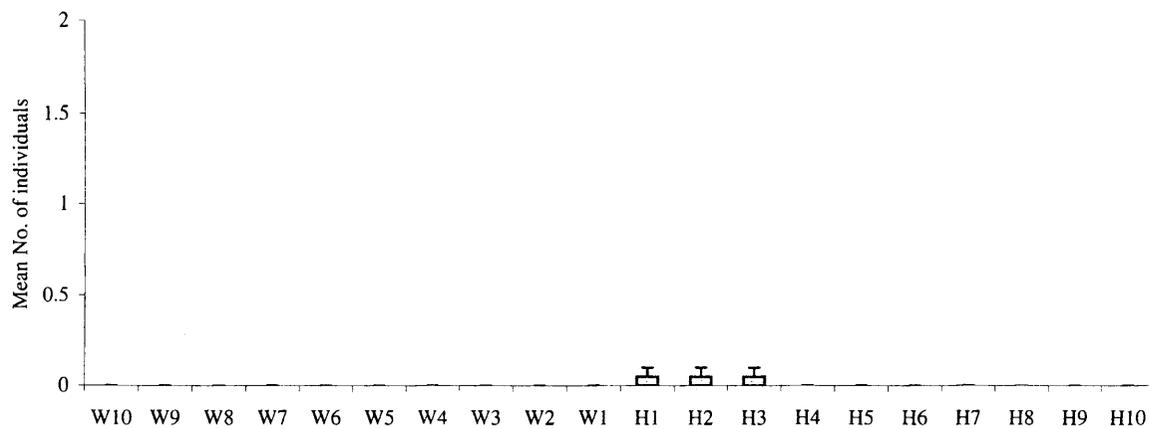
c) Herbaceous species found in hedgerow transects only: life history strategies

	Commonest habitat	Soil pH	Present status	Life history	Established strategy	Life form	Leaf phenology	Regenerative strategies	Seed bank	Agency of dispersal	Dispersule/germinule form	Dispersule weight
Hedge species												
<i>Bryonia dioica</i>	unlisted											
<i>Galium mollugo</i>	unlisted											
Wood speicies												
<i>Veronica hederifolia</i>	WOODI	6c	+	As	R/SR	Th	Sv	Bs	3	ANIMe	Sd	5
Road-verge												
<i>Geranium dissectum</i>	RDVRGE	7c	+	Aws	R/SR	Th	Sh	S	2	ANIMa	f/S	5
<i>Sisymbrium officinale</i>	RDVRGE	6b	+	A/B	R/CR	Th	Ep	Bs	3	WINDw	Sd	2
Pasture												
<i>Achillea millefolium</i>	PASTE	5c	?	P	CR/CSR	Ch	Ea	V,?S	1	WINDw	Fr	1
<i>Cirsium vulgare</i>	PASTI	5c	+	M	CR	H	Ea	W	2	WINDp	Fr	5
<i>Conopodium majus</i>	PASTI	6c	-	P	SR	G	Sv	S	2	UNSP	Fr	5
<i>Veronica chamaedrys</i>	PASTI	7c	-	P	CSR	Ch	Ea	V, Bs	3	UNSPcw	Sd	1
<i>Viola hirta</i>	PASTI	7c	-	P	S	H	Ea	V,?S	2	ANIMe	Sd	5
Disturbed												
<i>Centaurea nigra</i>	WASTEI	7c	?	P	CSR	H	Sa	V,S	2	UNSP	Fr	5
<i>Geranium molle</i>	OUTCRP	7b	?	Aws	R/SR	Th	Sh	S	2	ANIMa	f/S	4
Riverbank												
<i>Alliaria petiolata</i>	RIVBNK	6b	+	A/M	CR	H	Sh	S	2	UNSP	Sd	5
<i>Angelica sylvestris</i>	RIVBNK	5d	?	M/P	C/CR	H	Sa	S	1	AQUAT	Fr	4
<i>Calystegia sepium</i>	RIVBNK	7b	+	P	C/CR	G	Sa	(V),Bs	3	*UNSP	Sd	6
Meadow												
<i>Plantago lanceolata</i>	MEADOW	7c	+	P	CSR	H	Ea	V, Bs	3	ANIMm	Sd	4
<i>Taraxacum agg.</i>	MEADOW	7b	+	P	R/CSR	H	Ea	W	2	*WINDp	Fr	3
Arable												
<i>Capsella bursa-pastoris</i>	ARABLE	7c	+	Asw	R	Th	Ep	Bs	3	WINDw	Sd	1
<i>Convolvulus arvensis</i>	ARABLE	7c	?	P	CR	G	Sa	(V), Bs	3	*UNSP	Sd	6
<i>Lapsana communis</i>	ARABLE	6c	?	Aws	R/CR	Th	Ep	S, Bs	3	UNSPag	Fr	4
<i>Myosotis arvensis</i>	ARABLE	6b	?	Aw	R/SR	Th	Sh	S, Bs	3	ANIMa	Fr	2
<i>Veronica persica</i>	ARABLE	6b	-	Aws	R	Th	Ep	Bs	3	UNSPag	Sd	3
<i>Vicia tetrasperma</i>												
<i>Viola arvensis</i>	ARABLE	5c	?	As	R	Th	Ep	Bs	3	UNSPag	Sd	2
Scrub												
<i>Rumex sanguineus</i>	SCRUB	6c	+	P	CSR	H	Ea	Bs	3	UNSP	Fr	4

3.7 Spatial distribution of woody plant species not displayed in the text

a) Spatial distribution of *Cornus sanguinea* (bar = SE)

Established individuals

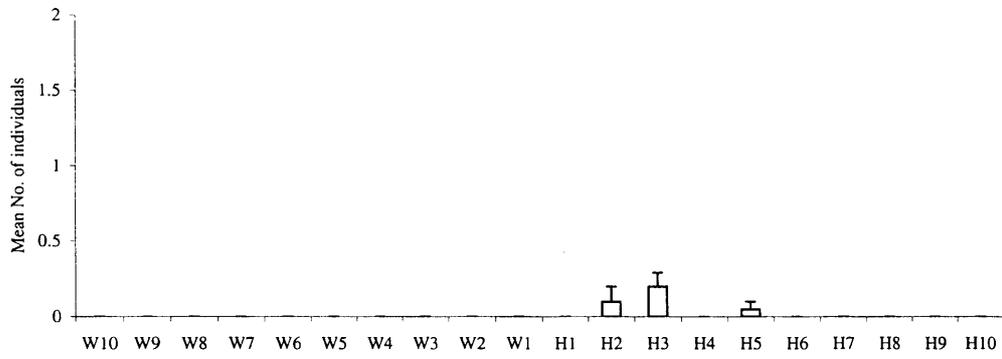


Saplings: none found

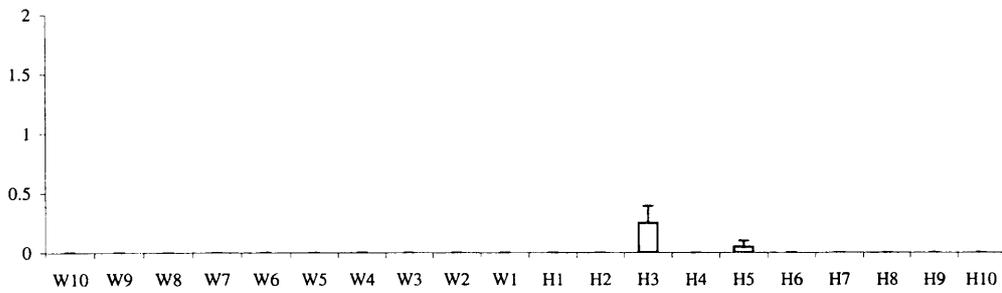
Seedlings: none found

b) Spatial distribution of *Euonymus europaeus* (bar = SE)

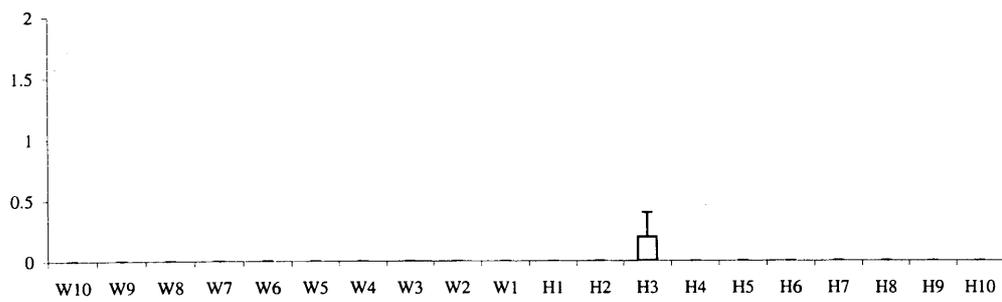
Established individuals



Saplings

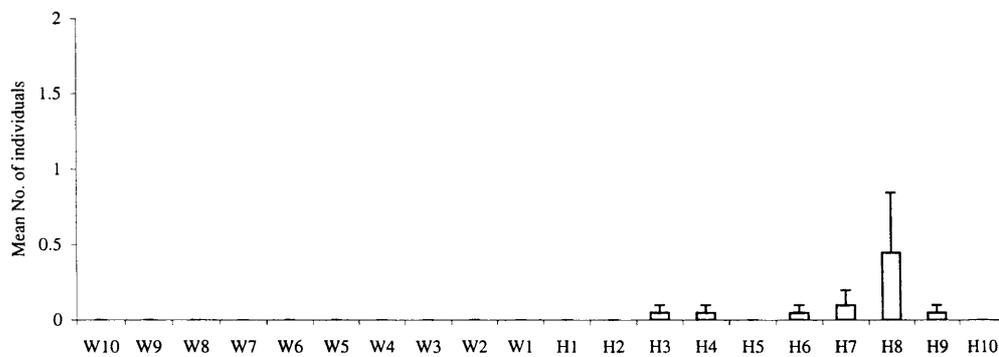


Seedlings

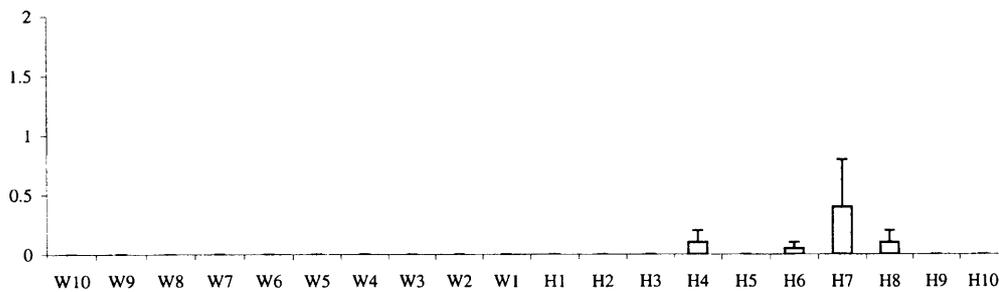


c) Spatial distribution of *Ligustrum vulgare* (bar = SE)

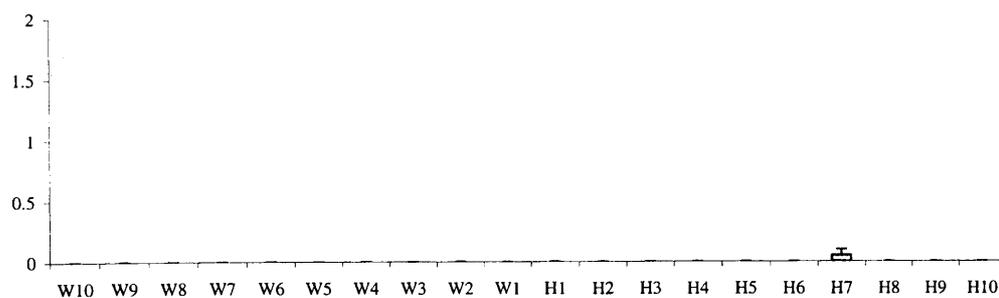
Established individuals



Saplings

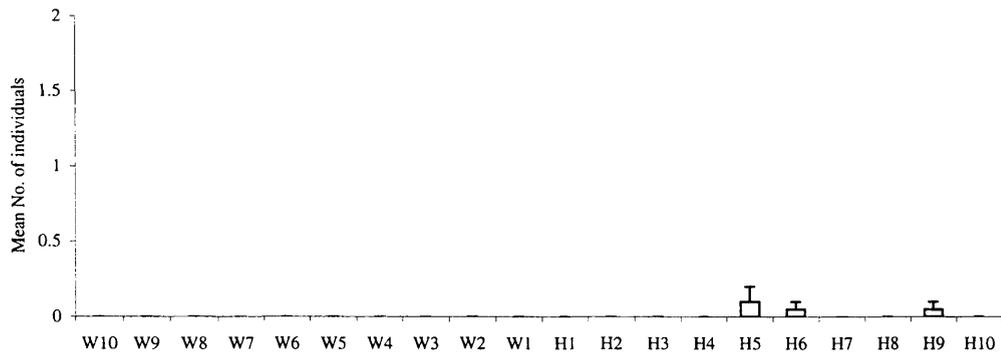


Seedlings

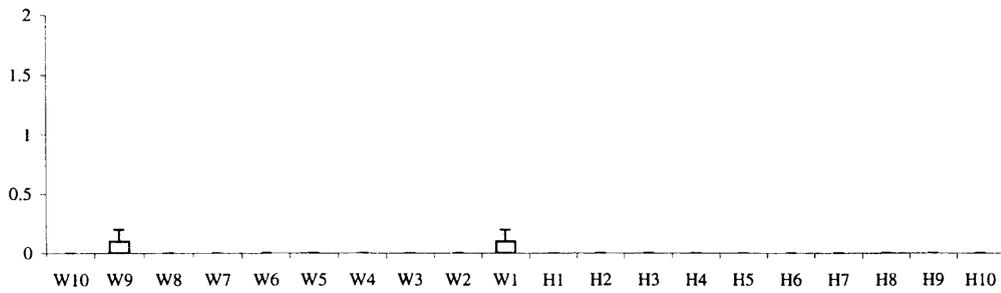


d) Spatial distribution of *Rhamnus catharticus* (bar = SE)

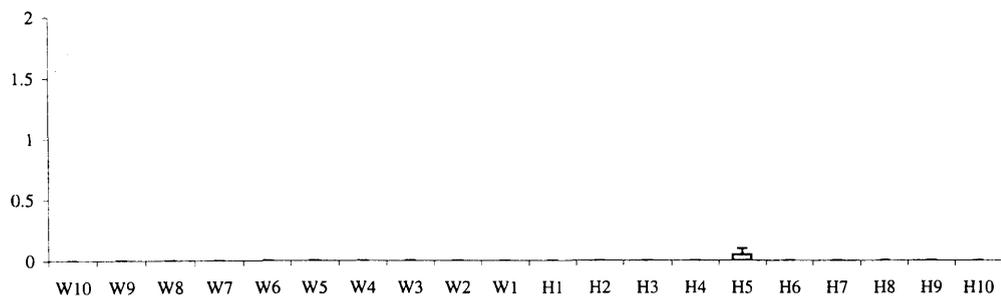
Established individuals



Saplings



Seedlings



4.2 Further autoecological accounts of herbaceous species

a) Herbaceous species in the seed bank only.

Chenopodium polyspermum L. (All-seed) is a native plant common to waste and cultivated ground (Stace 1991). Species of the same Genus produce numerous flowers grouped in small clusters on inflorescence spikes; each of these form individual fruits containing one seed (Sutton 1995). *Chenopodium polyspermum* is able to persist within the seed bank (Type 2-3 (Thompson *et al.* 1997)).

Cicerbita macrophylla (Willd.) (Common Blue-sow-thistle) is a strongly rhizomatous naturalised plant of rough or waste ground and roadsides (Stace 1991). Since it was first recorded in 1915, it has spread throughout most of the British Isles (Stace 1991). This implies an efficient method of dispersal and successful colonization and establishment in areas of disturbance. As with many species of the family of Asteraceae, the seeds are adapted for wind dispersal with persistent pappi (plumes attached) (Stace 1991).

Epilobium spp. (Willowherb) are perennial plants that produce seeds with hairy plumes (Stace 1991). Numerous seeds are released when the fruit capsule split into four segments (Sutton 1995). This group of species is known to be able to disperse their seeds widely, be retained for intermediate period within the seed bank and able to colonize a wide variety of habitats (Grime *et al.* 1988). *Equilobium angustifolium* often colonizes recently opened woodland and can propagate itself by the growth of underground runners (Tansley 1949).

The seeds of *Gnaphalium uliginosum* (Cudweed) are adapted for wind dispersal (plumes) and are able to persist within the seed bank (Grime *et al.* 1988); this species is classified as seed bank types 2-3 (Thompson *et al.* 1997).

Hypericum spp. (St John's worts) release small wind-dispersed seeds from seed capsules that remain persistently in the seed bank (Grime *et al.* 1988) (Seed bank type 2-3 (Thompson *et al.*

1997)). Numerous finely pitted seeds are released when the fruit capsule split into three segments (Sutton 1995). *H.perforatum*, *H. montanum* and *H. hirsutum* are commonly found in woodland in most of the British Isles (Stace 1991) and are frequently associated with disturbed habitats (Grime *et al.* 1988).

Plantago major L. (Rat's-tail Plantain) is abundant throughout the British Isles and it is commonly found in open rough ground, either cultivated or in grassy places (Stace 1991). This rosette-forming herb is resistant to trampling and is often associated with paths, tracks and gateways (Grime *et al.* 1988). Vegetative reproduction is limited to the production of side shoots, particularly after mechanical damage (Grime *et al.* 1988). The inflorescence consists of a spike each containing many flowers, which produces a capsule containing two elliptical and flattened seeds (Sutton 1995). Consequently, seed production may be prolific. The seed coating becomes mucilaginous when wet; adhering to mud and are then dispersed by shoes, vehicles and on the feet of birds and mammals (Grime *et al.* 1988). The main regenerative strategy is the retention of persistent seed bank (Grime *et al.* 1988) (Seed bank type 2-3 (Thompson *et al.* 1997)

Scrophularia auricalata L. (Water Figwort) is found in damp open and shady places throughout most of the British Isles (Stace 1991). Although *S. auriculata* commonly occurs in wetland habitats it is frequently found with *S. nodosa* (Common Figwort) in damp woodlands. The main regenerative strategy is considered to produce numerous seeds, which are able to persistent within the seed bank (Grime *et al.* 1988). (Seed bank type 2-3 (Thompson *et al.* 1997)). Many small oblong-pitted seeds are released from egg-shaped capsules (Sutton 1995). These seeds are then thought to be wind-dispersed (Grime *et al.* 1988).

Veronica chamaedrys ssp. *chamaedrys* L. (Germander Speedwell) is a native species commonly found in woodlands, hedgerows and damp grasslands (Stace 1991). This species is able to colonize bare ground by the growth of creeping stolons, which have the capacity to root along

their entire length or regenerate if they become detached (Grime *et al.* 1988). *Veronica chamaedrys* exhibits a degree of shade tolerance and is able to subsist in shaded woodland or tall grassland (Grime *et al.* 1988). Seeds are released from heart-shaped capsules (Sutton 1995) but seed production is thought to be infrequent in areas of low soil fertility (Grime *et al.* 1988). This species releases seed from capsules and dispersal is thought to be wind assisted. The seed bank types for this species range from transient to short-term persistent (Seed bank type 2-3 (Thompson *et al.* 1997)).

b) Herbaceous plant species located in the vegetation and seed bank.

Anthriscus sylvestris L. (Cow Parsley) is a perennial winter-green herbaceous plant species (Grime *et al.* 1988). Native to the British Isles, it is abundant in most grassy places, hedgerows and woodland margins (Stace 1991). This species provides a common feature in the British countryside, as many roadsides are coloured in the early spring by its profuse white flower heads. It is tolerant of partial shade and can compete in taller grass, within hedgerows and open woodland (Grime *et al.* 1988). However, this species is intolerant of regular cutting, heavy grazing and droughty or waterlogged soils (Grime *et al.* 1988). Little is known about the dispersal mechanism. Grime *et al.* (1988) list *Anthriscus sylvestris* as having an unspecified dispersal. The compact flower heads (Umbellifer) are composed of many single flowers, each producing one long fruit containing two seeds (Sutton 1995). These seed are not permanently retained within the seed bank. (Seed bank type 1-2 (Thompson *et al.* 1997)).

Arctium lappa L (Burdock) is a tall (1.5m) erect herbaceous biennial with a scattered distribution across south and central parts of the British Isles (Stace 1991). It is a native species associated with waysides, wood-clearings and wasteland. *Arctium lappa* have a characteristic spiked seed coating (burr) which attaches readily to clothing and mammals fur. This is thought to be the main mode of dispersal (Grime *et al.* 1988). The seeds can be persistent within the seed bank (Grime *et al.* 1988) (Seed bank type 3 (Thompson *et al.* 1997)).

Bryonia dioica L. (White Bryony) is a dioecious (single sexed) perennial with tuberous roots, and finds support from other shrubs and plants by the growth of climbing stems with simple tendrils (Stace 1988). This species has a limited geographical distribution in the British Isles as it is absent in the north and southwest England and is rare in Wales (except in the east) (Stace 1988). The 3-6 seeds are retained within a smooth red berry (Sutton 1995). Little is known about the mode of dispersal and this species is not listed by Grime *et al* (1998). The production of a coloured fruit suggests an adaptation for consumer/disperser interactions.

Capsella bursa-pastoris L. (Shepherd's Purse) is an annual-biennial herbaceous plant species, characteristic of cultivated or open bare ground (Stace 1991) and is often found on continuously disturbed land (Grime *et al.* 1988). The seeds (12-24) are enclosed in a heart-shaped capsule (siliqua) (Sutton 1995). The seed coating (testa) becomes mucilaginous when wet, and transported in mud that sticks to footwear, farm machinery and the feet of birds and mammals (Grime *et al.* 1988). These seeds are noted by Grime *et al.* (1988) as being exceptionally persistent within the seed bank formed in the soil.

Cirsium arvense L. Scop. (Creeping Thistle) is common throughout the British Isles and is customarily found in grassland, hedgerows, arable, waste and rough ground (Stace 1991). It is noted as a competitive perennial and designated as a noxious weed by the Weeds Act 1959 (Grime *et al.* 1988). This species can regenerate by aggressive vegetative reproduction particularly when the extensive systems of branched lateral roots are broken, for example by farm machinery (Grime *et al.* 1988). The seeds are adapted for wind dispersal by having plumes (pappus) attached. Grime *et al.* (1988) reported that these pappi detach quite easily which may reduce the effectiveness of this dispersal adaptation. The longevity of the seeds within the seed bank can vary (Seed bank types 1-3 (Thompson *et al.* 1997)).

Galium aparine L. (Goosegrass or Cleavers) is cosmopolitan weed, associated with maritime beaches, fen communities, river and stream banks, cultivated land, hedgerows and scrub

throughout the British Isles (Stace 1991, Taylor 1999). *Galium aparine* is occasionally scarce in some woodland communities (Taylor 1999). This scrambling annual plant is a competitive ruderal and is able to colonize habitats when the soils are highly fertile (Grime *et al.* 1988). The stems and fruits are covered in hooked bristles that adhere to clothing or mammal fur, thus facilitating this species' mode of dispersal (Ridley 1930). Once dry, the fruits split into two halves, each half containing one seed (Sutton 1995). The seeds of *Galium aparine* form a transient seed bank (Thompson *et al.* 1997, rarely persisting for more than two years (Grime *et al.* 1988); germinating in the autumn or the following spring (Taylor 1999).

Glechoma hederacea L. (Ground Ivy) is a native perennial common (except in the North of Scotland) in woodlands and rough ground, particularly on heavy soils (Stace 1991). It is also frequent within hedgerows and shaded roadsides (Grime *et al.* 1988). This species is also associated with secondary woodland habitats (Peterken and Game 1984). *Glechoma hederacea* can form carpets of vegetative mass as long creeping stems spread (Grime *et al.* 1988) and root into the soil. Vegetative spread is thought to be the main regenerative strategy, while transport of vegetative fragments is also important for long-distance dispersal (Grime *et al.* 1988). There is no clear explanation of how this species arrives and colonizes recent woodlands. The fruit of *Glechoma hederacea* splits into four nut-like parts each containing a single seed (Sutton 1995). It is uncertain as to how these seeds are dispersed. Once within the seed bank the seeds are retained in a viable condition for a limited period (Seed bank type 1-2 (Thompson *et al.* 1997)).

Moehringia trinervia L. (Three-veined Sandwort) is a native plant of woodland and hedgerow throughout most of the British Isles (Stace 1991). Grime *et al.* (1988) regard this species as one that is exclusively found in woodland. Peterken and Game (1984) considers the species as characteristic of secondary woodland flora. *Moehringia trinervia* is typical of many annual plants producing prolific numbers of seeds (Grime *et al.* 1988). The seeds are transient to short-term persistent within the seed bank (Seed bank type 1-2 (Thompson *et al.* 1997)). *Moehringia trinervia* can successfully colonize areas of bare ground within woodlands, where rabbit scraps

or tree falls disturb the soil (a woodland opportunist) (Grime *et al.* 1988). The seeds contain elaisome, which acts as an attractant to ants thereby facilitating dispersal (Grime *et al.* 1988).

Myosotis arvensis L. (Field Forget-me-not) is an annual herb common in well-drained open ground (Stace 1991). This species particularly favours disturbed artificial habitats and exploits transient habitats like waste ground or disturbance in woodlands (Grime *et al.* 1988). The fruits of *Myosotis arvensis* are nut-like capsules that split into four segments, each containing a single seed. The sepals of the former flower are covered in hooked hairs and enclose the fruit (Sutton 1995). These hairs aid the fruit and seeds to be dispersed by human clothing or in fur on animals (Ridley 1930). The seed bank strategy is of short-term persistence (Seed bank type 2 (Thompson *et al.* 1997)).

Potentilla sterilis L. (Barren Strawberry) is a perennial herbaceous species that can spread vegetatively by the extension of creeping stems (stolons) (Grime *et al.* 1988). Native to the British Isles, this species is found within woodland margins, woodland clearings and hedgerows (Stace 1991). *Potentilla sterilis* can be distinguished from a similar species, *Fragaria vesca* (Wild Strawberry) by a nut-like fruit and the absence of the fleshy pulped fruit with pip-like seeds (Sutton 1995). The seeds are retained for a short period in the seed bank (Thompson *et al.* 1997) and seed regeneration is associated with disturbance events within woodlands. Little is known about its mode of dispersal. This species is noted for its poor colonizing ability outside woodland of ancient origin and is known as one of the suite of species that are indicative of woodlands of antiquity (Peterken and Game 1984).

Rumex obtusifolius L. (Broad-leaved Dock) is a native perennial commonly found by roads and rivers, on waste and cultivated ground throughout the British Isles (Stace 1991). Sutton (1995) also regards *Rumex obtusifolius* as a plant common to field margins and hedgerows and it is noted as an agricultural weed in the Weeds Act 1959 (Grime *et al.* 1988). The outer coating of the former flower (perianth) encloses the maturing fruit and develops spiny teeth (Sutton 1995).

This outer coating facilitates seed dispersal because it can attach to human clothing or mammal fur (Grime *et al.* 1988). The seeds are persistent in the seed bank (Seed bank type 2-3 (Thompson *et al.* 1997)). This species also has a limited capacity for vegetative reproduction (Grime *et al.* 1988).

Stachys sylvatica L. (Hedge Woundwort) is native plant, which is common in most of the British Isles (Stace 1991) and is characteristic of hedgerows, road-verges, riverbanks, and the edge of woodland rides and floodplains (Grime *et al.* 1988). It forms strong surface rhizomes (Stace 1991) and has a capacity for intensive vegetative growth from root fragments (Grime *et al.* 1988). The species is noted as being a successful in secondary woodlands (Peterken 1977), yet evidence to support long-distance dispersal is lacking (Grime *et al.* 1988). This genus possesses nut-like fruits that split into four segments, each containing one seed (Sutton 1995). The bases of the flower sepals form a tube which has teeth that are sharply pointed (Sutton 1995). This structure may encase the fruit, and acts like a burr to aid dispersal. The seeds of *Stachys sylvatica* are able to persist within the seed bank, particularly in unshaded habitats (Grime *et al.* 1988) (Seed bank types 1-2 (Thompson *et al.* 1997)).

Stellaria media L. (Common Chickweed) is a sprawling, much branched, annual herb (Stace 1991). Although primarily an arable weed it also occurs in a wide range of habitats typically associated with disturbance and high soil fertility (Grime *et al.* 1988). *Stellaria media* has limited vegetative capacity for regeneration but produces a profusion of small seeds (Grime *et al.* 1988). The seeds are held within a capsule (Sutton 1995) and once released are persistent within the seed bank (Grime *et al.* 1988) (Seed bank types 2-3 (Thompson *et al.* 1997)). The seeds are widely dispersed in the faeces of bird and animals and are often transported by farm machinery or with crops (Grime *et al.* 1988).

Tripleurospermum inodorum Schultz Bip. (Scentless Mayweed) is a short-lived annual/perennial, which exploits a wide range of habitats associated with disturbed and fertile

soil (Grime *et al.* 1988). It is intolerant of dense shade and waterlogging but like many ruderals, this species flourishes on recently opened ground (Grime *et al.* 1988). As a prolific seed producer, its widespread distribution is thought to be facilitated by dispersal by human and animal agencies (Grime *et al.* 1988). The seeds are nut-like in appearance with no adaptation for wind dispersal (Sutton 1995) and are persistently retained in the seed bank (Grime *et al.* 1988).

Urtica dioica L. (Stinging Nettle) is a common species typically associated with woodlands, fens and fertile cultivated ground (Stace 1991). This species is strongly rhizomatous, with the ability to form dense clonal dioecious patches. As well as arising well from repeated cutting, it can regenerate rapidly from rhizome fragments (Grime *et al.* 1988). Although dioecious, it is known produce numerous seeds which are able to persist in the seed bank (Thompson *et al.* 1997). The seeds of *Urtica dioica* are nut-like in appearance and enclosed by the withered flowers (Sutton 1995). These seeds are thought to be ingested and dispersed by a variety of animals, and transported in soil (Grime *et al.* 1988).

Veronica persia Poiret (Common Field-speedwell) is a naturalized non-native species and is depicted by Stace (1991) as a species that occurs casually or scattered in cultivated ground and rough wasteland in England and Wales. Grime *et al.* (1988), however are of the opinion that this species is on the increase and is common throughout the British Isles. As a high seed producer, this annual can exploit both transient and semi permanent disturbed habitats and is now regarded as an arable and garden weed (Grime *et al.* 1988). The seeds of *Veronica persia* are released from a capsule and are thought to be ant dispersed, but human transportation via agricultural and horticultural activity is also thought to play an important part its the wide spread dispersion (Grime *et al.* 1988). The ability of shoot fragments to regenerate is also regarded as a potential process of colonization in frequently disturbed areas (Grime *et al.* 1988).

c) *Species present in the vegetation only*

Aegopodium podagraria L. (Ground Elder) was an introduction to the British flora and is now common in waste places, cultivated land or other open ground (Stace 1991). Fruits are ridged capsules, which split into two, containing one seed per half (Sutton 1995). There is a paucity of information about regeneration strategies and means of long distance dispersal of this species, but it is thought to be rhizomatous.

Alliaria petiolata Bieb. (Hedge Garlic) is a herbaceous plant characteristic of riverbanks, woodland and hedgerows, particularly on moist fertile soils (Grime et al. 1988). Around 3-18 seeds are released from elongated pods (Sutton 1995). A long period of chilling is required for germination and seeds can remain dormant for 18 months or more (Grime et al. 1988). *Alliaria petiolata* can reproduce vegetatively by the formation of adventitious buds but this is thought to be infrequent (Grime et al. 1988).

Arum maculatum L. (Lords and Ladies) is a monocotyledonous herbaceous plant found frequently in woodland and hedgerows on relatively fertile soils (Grime et al. 1988). Vegetative propagation occurs by the production of daughter tubers, but seed dispersal by birds is regarded as equally important (Grime et al. 1988). The fruits of *Arum maculatum* are produced on upright spikes (Sutton 1997). These fruits (berries) are bright red and contain 1-3 globular pitted seeds (Sutton 1995). The released seeds are slow to establish (up to 2-3 years) and are highly dependent upon mycorrhizal association (Grime et al. 1988).

Circaea lutetiana L. (Enchanters Nightshade) is a perennial rhizomatous and/or stoloniferous herbaceous plant is common in woodlands and hedgerows throughout the British Isles, except in the north of Scotland (Stace 1991). The ability to produce rapid growing stolons (300mm) enables this species to achieve local dominance during the formation of secondary woodland or disturbed sites in established woodlands (Grime et al. (1988). *Circaea lutetiana* is virtually restricted to shaded sites and is capable of surviving under deep shade (Grime et al. (1988). The

ovoid fruit capsule contains 1-2 seeds and is covered with dense hooked bristles, which attach easily to clothing and mammal fur (Sutton 1995).

Galium mollugo L. (Hedge Bedstraw) is a smooth upright perennial herbaceous plant (Stace 1991), without the scrambling habit and hooked hairs of *Galium aparine*. *Galium mollugo* is a native species of grassy places and hedgerows on well drained base-rich soils (Stace 1991). No further information could be found about vegetative reproduction or seed characteristics in this species.

Geranium molle L. (Dove's-foot Crane's-bill) is a characteristic plant of cultivated and waste land and is commonly distributed throughout the British Isles (Stace 1991). Tolerant of frequent disturbance, droughted soils and nutrient stress, *Geranium molle* is able to exploit rock outcrops, sandy wasteland and recently formed bare ground and road-sides (Grime *et al.* 1988). This species is absent in woodlands and wetland (Grime *et al.* 1988) suggesting an intolerance to shade and waterlogged soils. Regeneration is dependent upon seed production and a prolonged flowering period may allow more than one cohort of seeds to be produced in one season (Grime *et al.* 1988). The seeds are contained in a long-beaked capsule and are released by the coiling of capsule segments as it dries out (Sutton 1995).

Geum urbanum L. (Wood Avens) is native in British woodlands and hedgerows. Although its distribution is constrained in the far north (Stace 1991), it is common in *Fraxinus excelsior* - *Acer campestre* - *Mercurialis perennis* woodland (NVC W8) particularly in the *Primula vulgaris*-*Glechoma hederacea* subcommunity, which is well represented over base-rich soil in the East Midlands (Taylor 1997). *Geum urbanum* is regarded as a semi-shade species, with increased flowering and seed-set in unshaded conditions (Grime *et al.* 1988). It is only able to become dominant in areas where recent disturbance has occurred (Grime *et al.* 1988). The rhizome system of *Geum urbanum* is not well developed: ramets have a relative short length of rhizome with adventitious roots (Taylor 1997). The flowering-heads produce numerous fruits

each carrying hooked hairs at the tip (Sutton 1995). It is these hooks which enable the seeds to be dispersed on clothing and mammalian fur (Grime *et al.* 1988).

Hedera helix L. (Ivy) is a woody climbing species frequently found on trees, banks and walls. (Stace 1991). Long stems attach by numerous short roots and climb either vertically up tree trunks or grow horizontally to form carpets upon the woodland floor (Grime *et al.* 1988). Only the vertical stems are able to produce fruits and do so in relatively unshaded places (Grime *et al.* 1988). Large (6-8mm) leathery green-black fruits contain 2-5 seeds (Sutton 1995). Birds frequently disperse these seeds and, once deposited, the retention of this species in the seed-bank is limited (Grime *et al.* 1988).

Heracleum sphondylium L. (Hogweed) is a robust tap-rooted herbaceous plant characteristic of rough grassland and wasteland, particularly on moist fertile soils (Grime *et al.* 1988). The species has no capacity for vegetative reproduction and its regeneration is dependent upon the production of flattened winged fruits, dispersed short distances by wind (Grime *et al.* 1988).

Hyacinthoides non-scripta L. (Bluebell) is frequently found on shaded-banks and grasslands in wetter regions (Stace 1991). Peterken and Game (1984) considers this species as having an affinity for woodlands with ancient origin. *Hyacinthoides non-scripta* is a bulb forming, monocotyledonous herbaceous plant that exhibits vernal phenology in that it exploits the light phase of the woodland canopy (Grime *et al.* 1988) in late winter and early spring. *Hyacinthoides non-scripta* is intolerant of trampling, grazing and cutting and vulnerable to waterlogging (Grime *et al.* 1988). Bulblets are produced when the plant reaches maturity, but this method of vegetative reproduction is considered to be of a minor importance in the regeneration strategy of this species (Wilson 1959, Grime *et al.* 1988). Several seeds are released when the globular capsules, up the flowering stem, split into three segments (Sutton 1995).

Mercurialis perennis L. (Dog's Mercury) is a herbaceous plant species regarded by Peterken and Game (1981) as having a weak affinity with ancient woodland in Lincolnshire and is often found in woodland relict hedgerows (Rackham 1969, Pollard *et al.* 1974, Peterken and Game 1984). *Mercurialis perennis* is common over much of the British Isles (Stace 1991), often forming dense ground cover in woodlands, spreading rhizomatous roots and forming new shoots in the autumn (Grime *et al.* 1988). These highly cloned patches are mainly composed of plants producing diecious reproductive parts that rarely produce seeds. When mating is successful, broad hairy capsules develop two seeds (Sutton 1995). These seeds contain an oily substance (elaiosome) which acts as an attractant to ants therefore facilitating dispersal (Ridley 1930).

Primula vulgaris Hudson (Primrose) is perennial native herbaceous species found in woodland and hedgerows (Stace 1991). *Primula vulgaris* is able to duplicate forming large clumps of daughter plants. Numerous seeds are held in a capsule and dispersed by ants (Valverde and Silvertown 1995, 1997).

Viola rivinianna Reichb. (Common Dog Violet) is native to a wide range of woodland and grassland and is common throughout the British Isles (Stace 1991). *Viola riviniana* can reproduce vegetatively through adventitious sprouting from the roots. Flowers are both insect pollinated and cleistogamous (self pollinating) and seeds are shed by an explosive action as the seed capsule dries out (dehiscence) and subsequently dispersed by ants (Beattie and Lyons 1975). Ants can disperse *Viola rivinianna* seeds for distances up to 75cm (Culver and Beattie 1978).

**Appendix 5 Immigration, colonization and establishment of woody plant species in three
Experimental Hawthorn Hedgerows under three differing management regimes**

5.1 Historical Background of the Hawthorn Hedge Field

The Nature Conservancy Council purchased the ancient woodland, Monks Wood in the 1950s; subsequently the woodland was classified as National Nature Reserve. Monks Wood (ITE) Experimental Station was formally opened in 1963 (Steele 1973).

The Hawthorn Hedge Field has been grazed or mown on an annual basis and has had little or no agricultural chemicals applied (Sparks, pers. com. 1997). Calcareous clays with loamy and sandy drift (Hodge *et al.* 1973) underlie the experimental field. Former enclosures within the experimental field were known as Little Sand (the western section of the field) and Twelve Acres (the eastern part of the field). Twelve acres was possibly once part of an early Romano-British settlement around AD 0-300 (Hooper 1973). Evidence of later ridge and furrow cultivation is present in the southern edge of the nature reserve (Peterken 1973). This land may have fallen out of production during the period when the Black Death struck the country. Hooper (1973) found documentary evidence which implies that Monks Wood (NNR) increased in size by the middle of the sixteenth century. Clearance of the secondary woodlands from the field, between Judith's hedge and Monks Wood boundary banks, is thought to have occurred in the seventeenth or eighteenth century, but Pollard *et al.* (1974) had difficulty dating this event with any precision.

5.2 Planting scheme for the Experimental Hawthorn Hedgerows (1962): a) planting density, b) summary statistics.

a) Planting densities

Hedge No.	1	2	3	4	5	6	7	8	9
Number of plants	1084	1054	998	862	666	646	602	568	ND
Hedge length (ft)	813	792	750	646	500	486	452	427	ND

b) Summary statistics

Total plants	6480
Total hedge length (ft)	4866
Distance from Monks Wood NNR	30yds
Turning space (Judith's Hedge end)	10yds
Distance between hedgerows	50yds

ND = no data

5.3 Original Experimental design for the Experimental Hawthorn Hedgerows

The hedgerow experiment was designed with Latin Square randomised plots. This method of randomisation prevented bias towards those plots near to the edges of the field. Statistical analyses were intended to determine the effects of management on the structure and woody plant species composition. The hedgerows were left unmanaged until the winter of 1969-1970.

Four types of management were replicated five times. The treatments consisted of:

- A. coppiced on a 10 year cycle;
- B. trimmed annually to 5 feet;
- C. trimmed every 3 years to 5 feet;
- D. trimmed every 3 years to 9feet;

Apart from "Treatment A" the other treatments were carried out with a mechanical cutter-bar.

5.4 Bird species in the Hawthorn Hedgerow Field observed by researchers at ITE Monks Wood

Latin name	English name	Latin name	English name
<i>Aegithalos caudatus</i>	Long tailed tit	<i>Pica pica</i>	Magpie
<i>Columba palumbus</i>	Wood pigeon	<i>Prunella modularis</i>	Dunnock
<i>Corvus corone</i>	Carrion crow	<i>Regulus regulus</i>	Goldcrest
<i>Emberiza citrinella</i>	Yellow hammer	<i>Sylvia atricapilla</i>	Blackcap
<i>Erithacus rubecula</i>	Robin	<i>Sylvia communis</i>	Whitethroat
<i>Fringilla coelebs</i>	Chaffinch	<i>Troglodytes troglodytes</i>	Wren
<i>Garrulus glandarius</i>	Jay	<i>Turdus iliacus</i>	Redwing
<i>Parus ater</i>	Coal tit	<i>Turdus merula</i>	Blackbird
<i>Parus caeruleus</i>	Blue tit	<i>Turdus philomelos</i>	Songthrush
<i>Parus major</i>	Great tit	<i>Turdus pilaris</i>	Fieldfare
<i>Pyrrhula pyrrhula</i>	Bullfinch	<i>Turdus viscivorus</i>	Mistle thrush
<i>Phylloscopus trochilus</i>	Willow warbler		

5.5 Additional autoecological information of woody plant species

Cornus sanguinea is a shrub that grows to around 4m in height and is commonly found in woods or scrubland on base-rich soils or clays (Stace 1991). This species is associated with: *Fraxinus excelsior-Acer campestre-Mercurialis perennis* woodland, (NVC: W8), *Fagus sylvatica-Mercurialis perennis* woodland (NVC: W12), and *Crataegus monogyna-Hedera helix* scrub (NVC: W21) (Rodwell 1991). Seeds of *Cornus sanguinea* are contained within green berries small (6-8mm in diameter (Clapham *et al.* 1964)), when ripe turn purple-black (Stokoe 1970). The berries are consumed and dispersed by birds (Pollard *et al.* 1974). This species is thought to have some ability to reproduce vegetatively (Pollard *et al.* 1974).

Crataegus monogyna L. (Common Hawthorn) is native woody species can grow up to 10-15m high and is commonly associated with woodland borders, scrub and hedgerows (Stace 1991). *Crataegus monogyna* is a rapid colonizer of pasture, and forms scrub where grazing by livestock has ceased (1969, Merton 1970). Rodwell (1991) classifies scrub of this kind as *Crataegus monogyna-Hedera helix* community (NVC: W21). The red fruits or berries of *Crataegus monogyna* (Haws) contain a single nut-like seed, where the fruits of the less common woodland species *Crataegus laevigata* (Midland Hawthorn) contain two or three seeds (Beckett and Beckett 1979).

Euonymus europaeus is associated with hedgerows of antiquity (Pollard *et al.* 1974) and a relict shrub of ancient woodland. It is a native shrub species of hedgerow, scrub and woodland, where soils are calcareous or base rich (Stace 1991). This species typically located in the following woodland communities: *Fraxinus excelsior-Acer campestre-Mercurialis perennis* (W8), *Fagus sylvatica-Mercurialis perennis* (W12), *Taxus baccata* (Yew) woodland (W13), and *Crataegus monogyna- Hedera helix* scrub (W21). Stokoe (1970) describes the fruit of *Euonymus europaeus* as a deeply lobed capsule that ripens in the autumn, turning a crimson hue. The lobes are marked with grooves, which indicate future divisions that disclose the four

orange coloured seeds within. Once released, animals transport the seeds after ingestion or by the activities of ants (Hodgson *et al.* 1995).

Fraxinus excelsior is one of the most common native trees of woodlands, scrub and hedgerows in the British Isles, especially on damp or base rich soils (Stace 1991). The seeds of this species are adapted for wind dispersal. Ash 'keys' (samaras) are produced in bunches, and each contains a single seed. These seed capsules are elongated and twisted to form a "wing" (Stokoe 1970). This adaptation increases the distance the seed disperses away from the parent plant with the aid of the wind. *Fraxinus excelsior* is a prolific seed producer in most years, many of which germinate successfully (Rackham 1980). The keys first begin to fall from the parent plant in the autumn and can continue to be released until the following spring (Beckett and Beckett 1979). Germination can take between two-six years, although most seeds germinate the second spring after released (Stokoe 1970), and around 5% appear in the first year (Beckett and Beckett 1979).

In a woodland habitat, under normal shade conditions, the seedlings of *Fraxinus excelsior* grow a few inches high and then remain in a "suppressed" state for many years until a gap within the canopy allows rapid growth (Rackham 1980). Seedlings are sensitive to heavy shade, failing to develop and even dying (Beckett and Beckett 1979). Seedlings are also vulnerable to grazing (Grime *et al.* 1988). The cessation of livestock grazing leads to the development of secondary ash-woods with hawthorn (Merton 1970) or the sub-climax scrub community of *Crateagus monogyna-Hedera helix* (W12) (Rodwell 1991). There is an indication that *Fraxinus excelsior* easily disperses into and colonizes newly formed habitats effectively (Rodwell 1991). In hedgerows, *Fraxinus excelsior* occurs much more frequently as a timber tree although is able to persist if saplings are controlled by hedge cutting (Pollard *et al.* 1974).

Ligustrum vulgare is a native erect shrub is semi-deciduous, with many green leaves remaining throughout the year, grows 3-5m high and is commonly found in hedgerows and scrub throughout most of the British Isles on base rich soils (Stace 1991). Rodwell (1991) revealed

that *Ligustrum vulgare* is associated with seven NVC community types. These communities include: wet woodland type plant communities, Alder carr, (W5: *Alnus glutinosa-Carex paniculata*), Hawthorn Scrub (W21: *Crataegus monnogyne-Hedera helix scrub*), and five other woodland community types (W8, W10, W12, W13, and W14). *Ligustrum vulgare* is able to colonize young hedgerows, but is relatively scarce in established hawthorn hedgerows (Pollard *et al.* 1974). Beckett and Beckett (1979) describe the flowers of *Ligustrum vulgare* as small, funnel shaped structures that are clustered tightly forming a conical inflorescence. The small shiny black berries ripen between September and October. They also state that *Ligustrum vulgare* produce vegetative shoots and can form dense growth, which can provide good cover for birds.

This climbing *Rosa* species is commonly associated with hedgerows, scrub and the edges of woodland (Stace 1991, Sutton 1995). The red berry-like fruits or “hips” form in the late summer and fully ripen in the autumn (October-November). These fruits are attractive to many bird species (Beckett and Beckett 1979). Each hip contains numerous nut-like fruits (Sutton 1995).

The majority of the sub group *Rubus* form an extremely complex apomictic group, collectively known as *Rubus fruticosus* L agg. (Stace 1991). Whilst surveying the experimental hedgerows it was noted that the forms of the “Bramble group” were varied. It was acknowledged that the identification of hybridised subgroups and microspecies is time consuming and require specialist skills. Over 400 microspecies have been recognised in the British Isles (Stace 1991). All members of the above group, located in this study, are treated as one.

Rubus fruticosus L agg. are robust, spiny shrub woody perennials, producing long arching stems (Grime *et al.* 1988). Birds and mammals are considered to be important dispersal vectors and the main explanation for this species group arrival a newly colonized sites (Grime *et al.* 1988). In

dense perennial communities regeneration is less frequently the result of seed production and more commonly derived from extensive vegetative spread (Grime *et al.* 1988).

5.6 Total number of individuals and woody plant species located in the three Experimental Hawthorn Hedgerows.

Hedge No. Aspect	1. (Coppiced)			4. (Laid)			8. (Control)		
	West	East	Total	West	East	Total	West	East	Total
Size Class 1									
<i>Cornus sanguinea</i>	48	24	72	10	8	18	3	1	4
<i>Euonymus europaeus</i>	24	13	37	24	13	37	3	1	4
<i>Fraxinus excelsior</i>	2	-	2	2	-	2	1	2	3
<i>Ligustrum vulgare</i>	2	-	2	3	2	5	16	3	19
<i>Lonicera periclymenum</i>	-	-	-	3	-	3	9	11	20
<i>Prunus spinosa</i>	23	16	39	12	14	26	27	18	45
<i>Quercus robur</i>	3	1	4	2	-	2	2	2	4
<i>Rosa canina</i>	244	343	587	228	122	350	204	92	296
<i>Rubus</i> agg.	331	656	987	468	553	1021	416	346	762
<i>Sambus nigra</i>	-	-	-	-	1	1	-	-	-
<i>Viburnum lantana</i>	-	1	1	-	1	1	-	-	-
No. of tree and shrub species	6	5	7	6	6	8	6	6	6
Number of climbers	2	2	2	3	2	3	3	3	3
Total No. of woody plant spp.	8	7	9	9	8	11	9	9	9
Size Class 2									
<i>Cornus sanguinea</i>	31	29	60	6	4	10	-	-	-
<i>Euonymus europaeus</i>	20	17	37	14	5	19	1	-	1
<i>Fraxinus excelsior</i>	3	-	3	3	3	6	-	1	1
<i>Ligustrum vulgare</i>	-	-	-	-	-	-	14	5	19
<i>Lonicera periclymenum</i>	-	-	-	2	2	4	-	3	3
<i>Prunus spinosa</i>	35	14	49	17	8	25	2	4	6
<i>Quercus robur</i>	5	1	6	-	4	4	-	-	-
<i>Rosa canina</i>	625	417	1042	335	76	411	33	10	43
<i>Rubus</i> agg.	597	828	1425	491	442	933	228	243	471
<i>Sambus nigra</i>	-	-	-	-	-	-	-	-	-
<i>Viburnum lantana</i>	-	-	-	-	-	-	-	-	-
No. of tree and shrub species	5	4	5	4	5	5	3	3	4
Number of climbers	2	2	2	3	3	3	2	3	3
Total No. of woody plant spp.	7	6	7	7	8	8	5	6	7
Size Class 3									
<i>Cornus sanguinea</i>	12	9	21	-	-	-	-	-	-
<i>Euonymus europaeus</i>	4	2	6	5	-	5	-	-	-
<i>Fraxinus excelsior</i>	-	-	-	2	1	3	-	-	-
<i>Ligustrum vulgare</i>	-	-	-	-	-	-	6	8	14
<i>Lonicera periclymenum</i>	1	1	2	-	-	-	3	6	9
<i>Prunus spinosa</i>	13	11	24	5	1	6	3	-	3
<i>Quercus robur</i>	-	-	-	-	-	-	-	-	-
<i>Rosa canina</i>	207	139	346	143	44	187	110	75	185
<i>Rubus</i> agg.	341	447	788	431	227	658	82	96	178
<i>Sambus nigra</i>	-	-	-	-	-	-	-	-	-
<i>Viburnum lantana</i>	-	-	-	-	-	-	-	-	-
No. of tree and shrub species	3	3	3	3	2	3	2	1	2
Number of climbers	3	3	3	2	2	2	3	3	3
Total No. of woody plant spp.	6	6	6	5	4	5	5	4	5

5.7 Mean abundance of individual woody plant species in the three EHH.

The highest mean abundance for *Cornus sanguinea*, in each size class, was found within the coppiced hedgerow (Hedge 1) (Figure A5.7a). Individuals in the second size class were absent in Hedge 8, and individuals in the establishment phase (size class 3) were not present in either the laid (Hedge 4) or the unmanaged (Hedge 8) EHH.

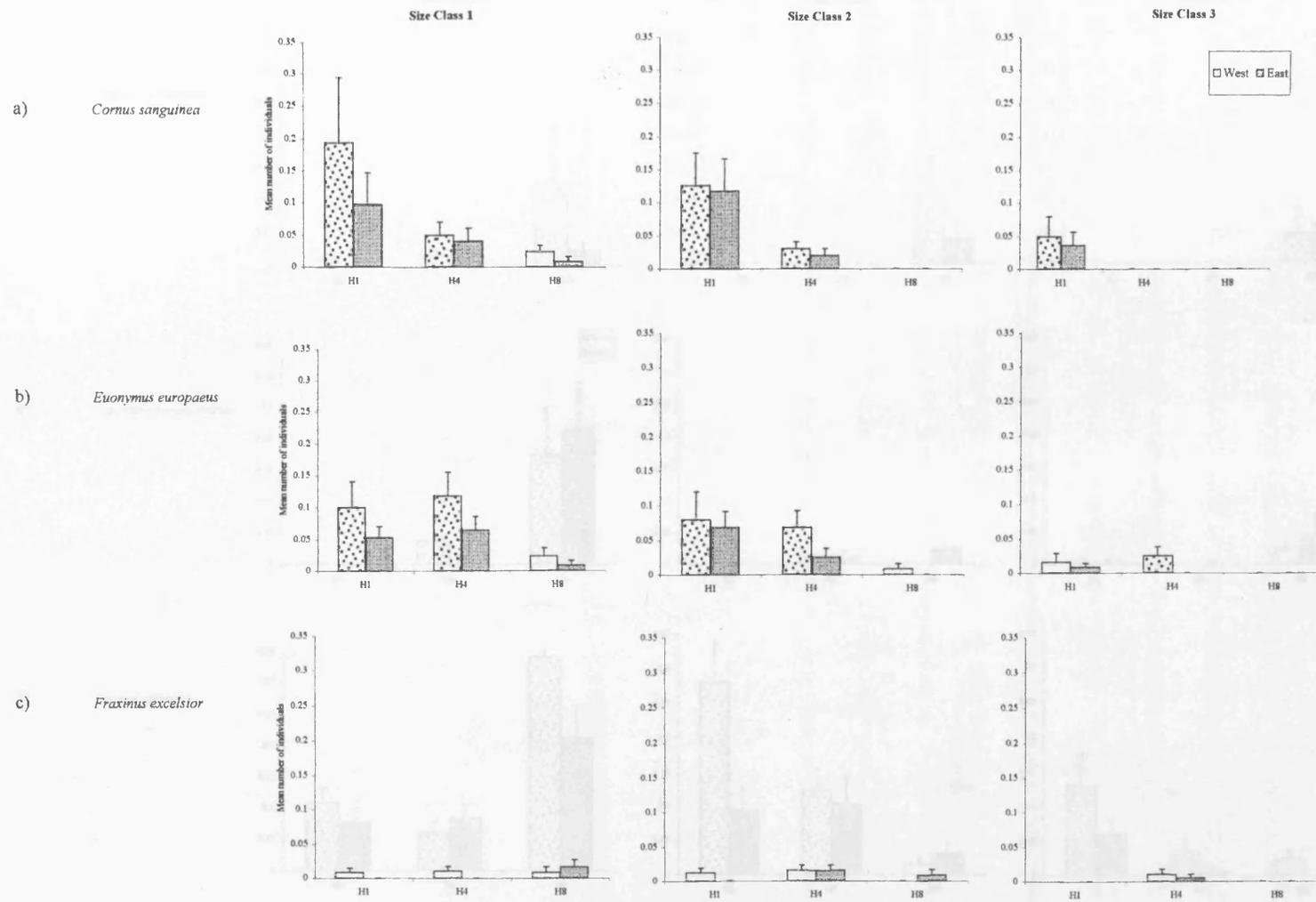
Overall *Euonymus europaeus* mean abundance values were similar to *Cornus sanguinea* (Figure A5.7b). However, mean values for this species were lower on the western side of Hedge 1, and higher mean values in the layered hedgerow were found. Individuals that fit into the establishment size class category were also located on the western side of the layered hedgerow. Some degree of variation in hedge aspect was detected.

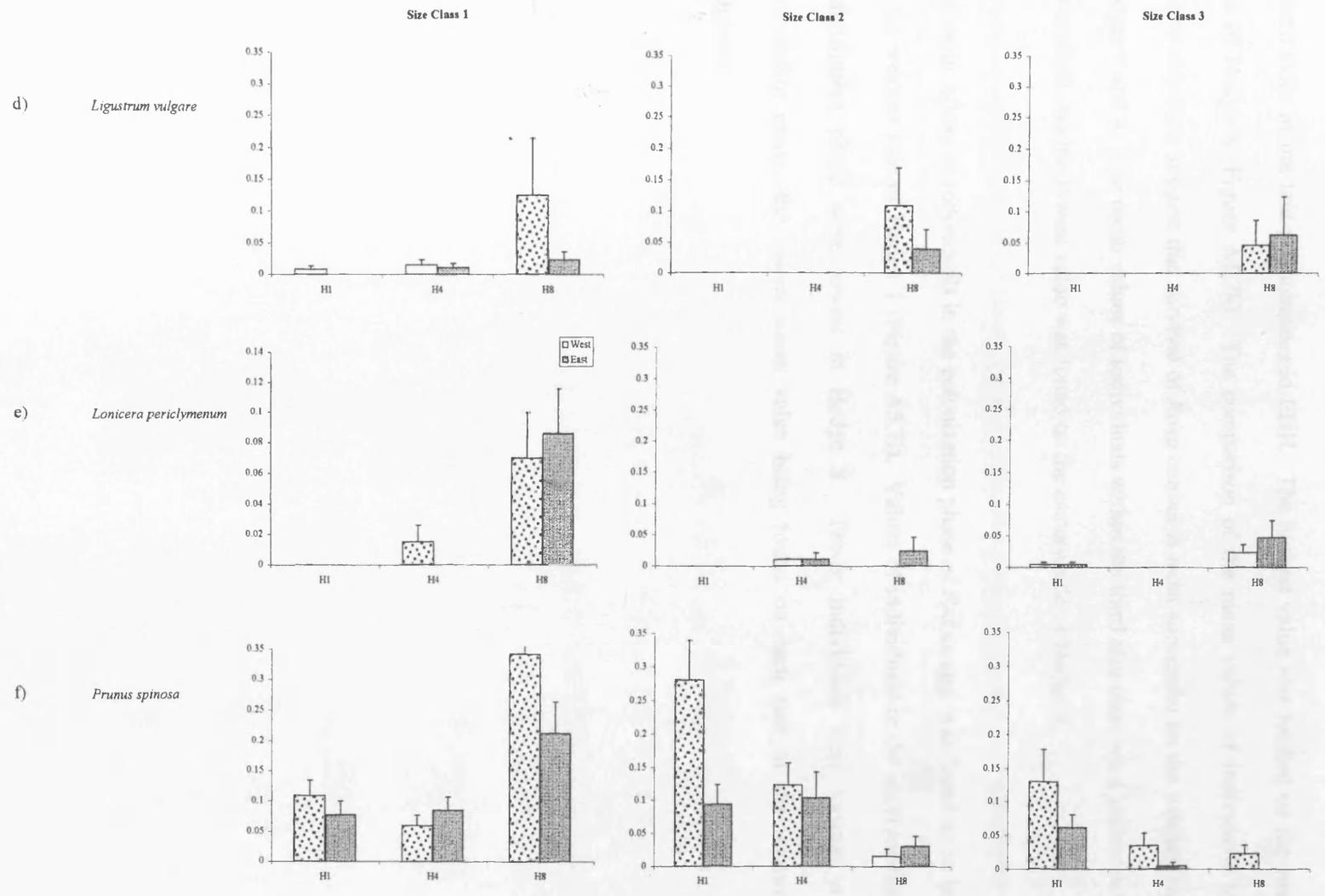
Low mean values were found for the individuals of *Fraxinus excelsior* (Figure 5.7c). Colonization was found to on each side of the unmanaged hedgerow (Hedge 8) and survivorship on each side of the laid hedgerow (Hedge 4). Establishing individuals were only located in Hedge 4.

The mean values of colonizing individuals of *Ligustrum vulgare*, *Lonicera periclymenum* and *Prunus spinosa* were highest in the unmanaged hedgerow (Hedge 8) (Figure A5.7d-f). Individuals of both *Ligustrum vulgare* and *Lonicera periclymenum* had reached the survival and establishment phases in this taller unmanaged EHH. However individuals of *Prunus spinosa* had not developed so well under these conditions. The mean abundance values for *Prunus spinosa* in size class 2 and 3 were highest in the one the western side of Hedge 1.

Similar to *Fraxinus excelsior*, the mean number of colonizing individuals of *Quercus robur* was low in each EHH, although was found to be slightly higher within the unmanaged hedgerow

Figure A5.7 Mean abundance of individual woody plant species



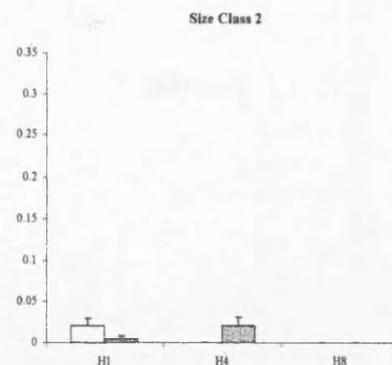
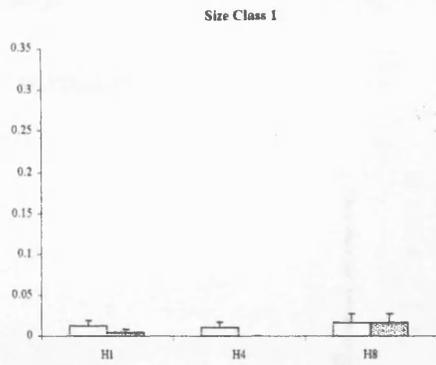


(Figure A5.7g) higher mean values for surviving individuals was found in Hedge 4. No established individuals were identified in any of the EHH.

The lowest mean abundance values colonizing individuals of *Rosa canina* was found on the eastern sides of the laid and unmanaged EHH. The highest value was located on the western side of Hedge 8 (Figure A5.7h). The comparison of the mean values of individuals in the second size class suggest that survival of *Rosa canina* is most successful on the western side of Hedges 1 and 4. The mean values of individuals within the third size class were similar in each of the EHH, but the lowest value was found on the eastern side of Hedge 4.

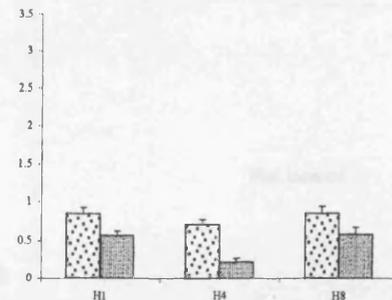
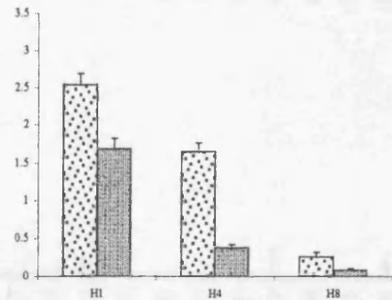
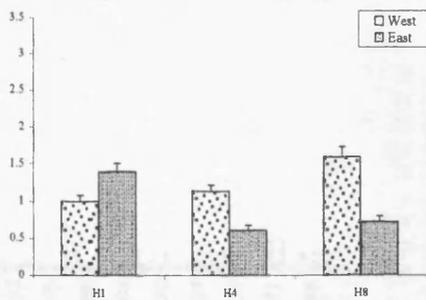
The mean values of individuals in the colonization phase of *Rubus* agg. was found to be lowest on the western side of Hedge 1 (Figure A5.7i). Values of individuals in the survivorship and establishment phase were lowest in Hedge 8. Fewer individuals were located in the survivorship phase, the lowest mean value being found on each side of the unmanaged hedgerow.

g) *Quercus robur*

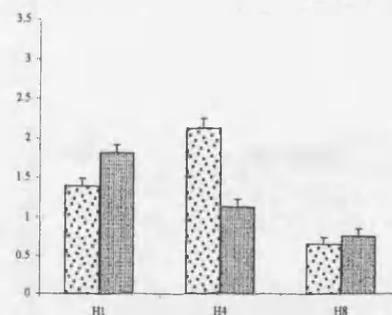
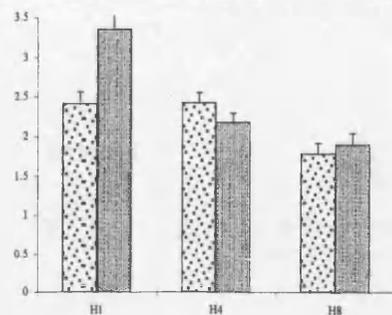
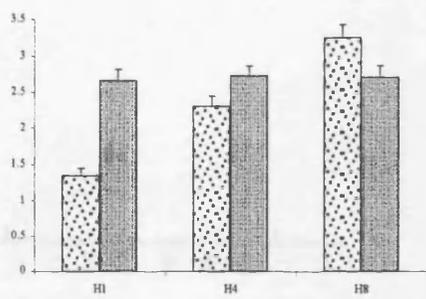


Size Class 3
None found

h) *Rosa canina*

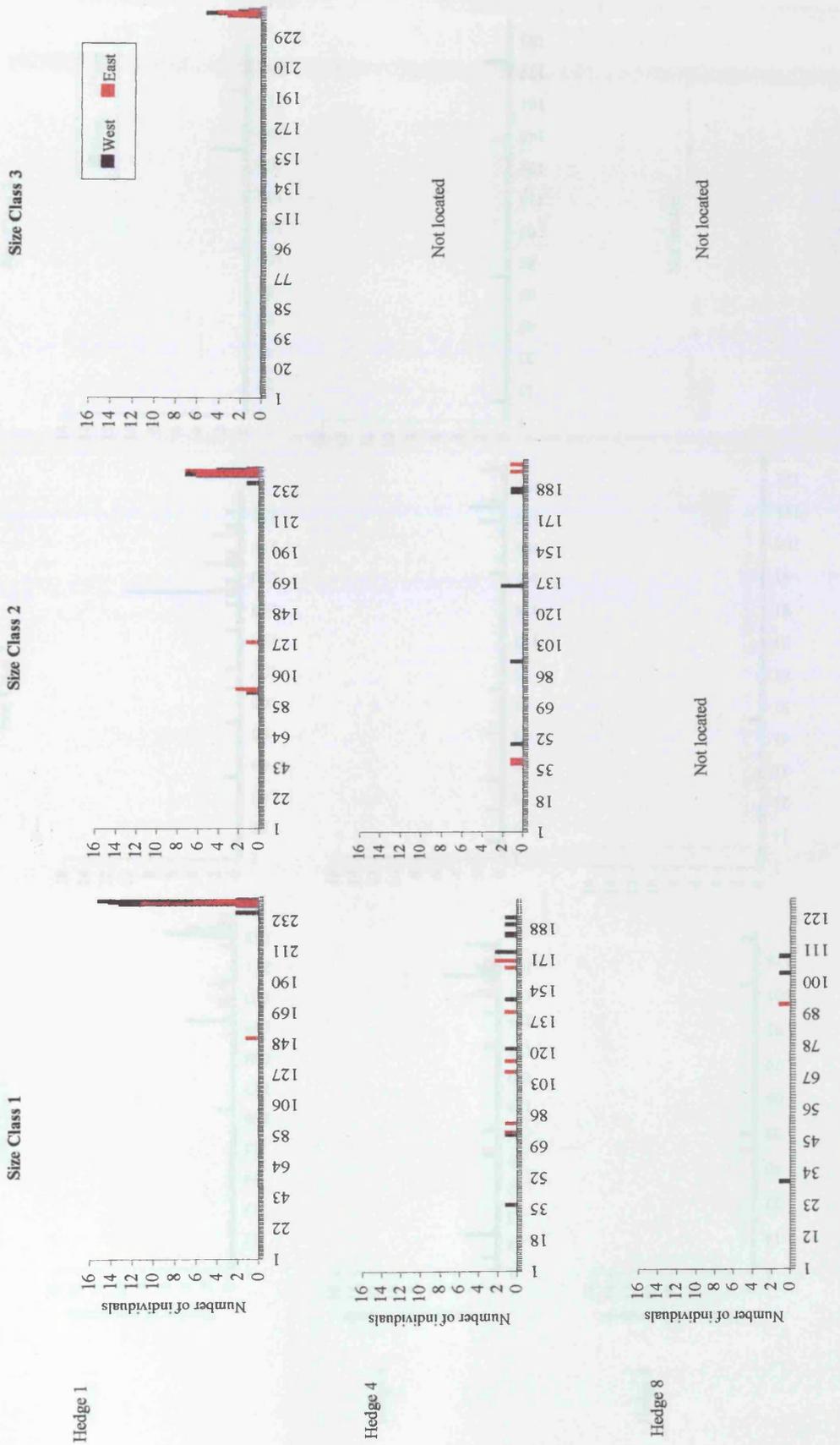


i) *Rubus agg.*

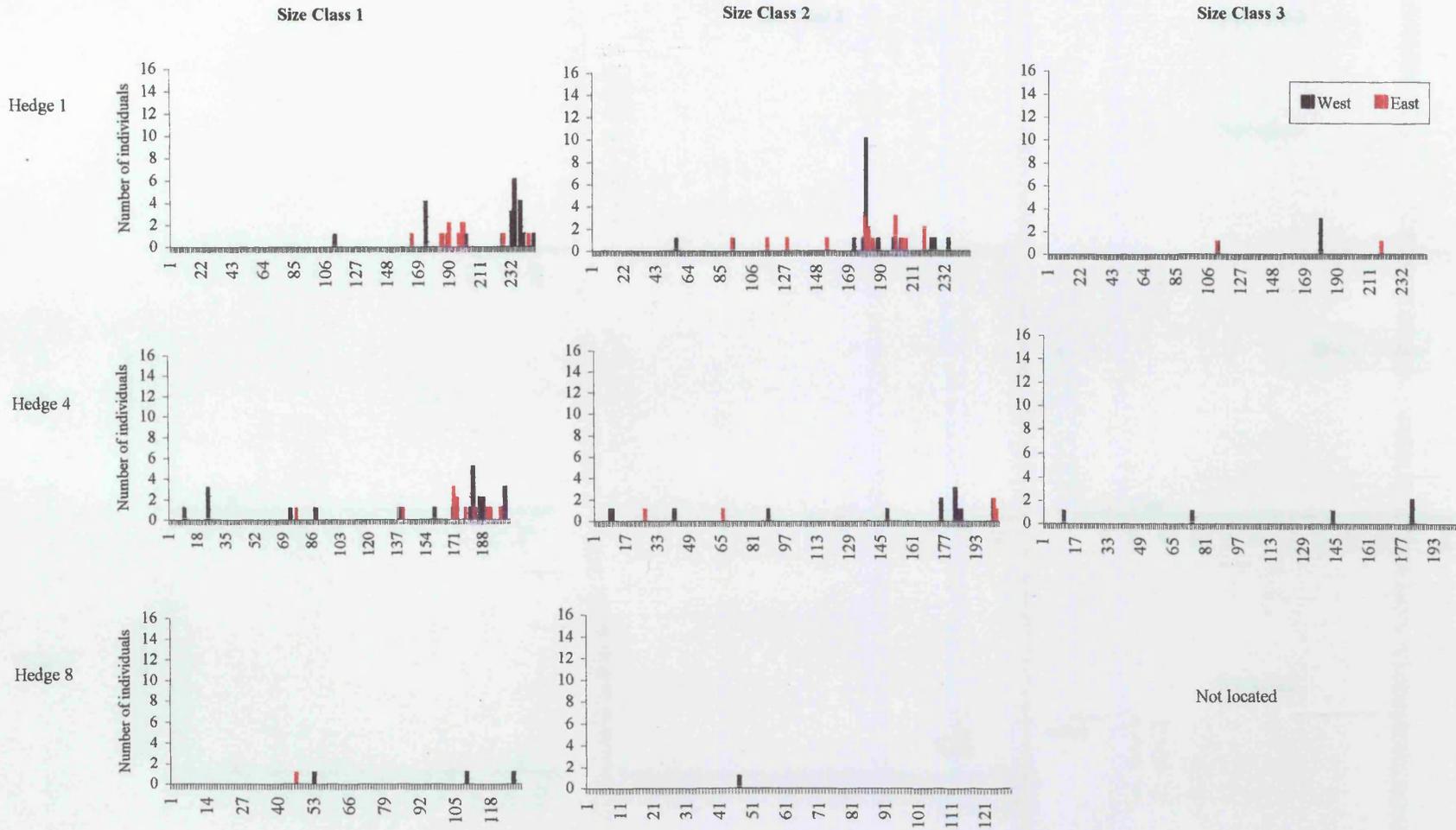


5.8 The spatial distribution of individual woody plant species in each EHH by aspect.

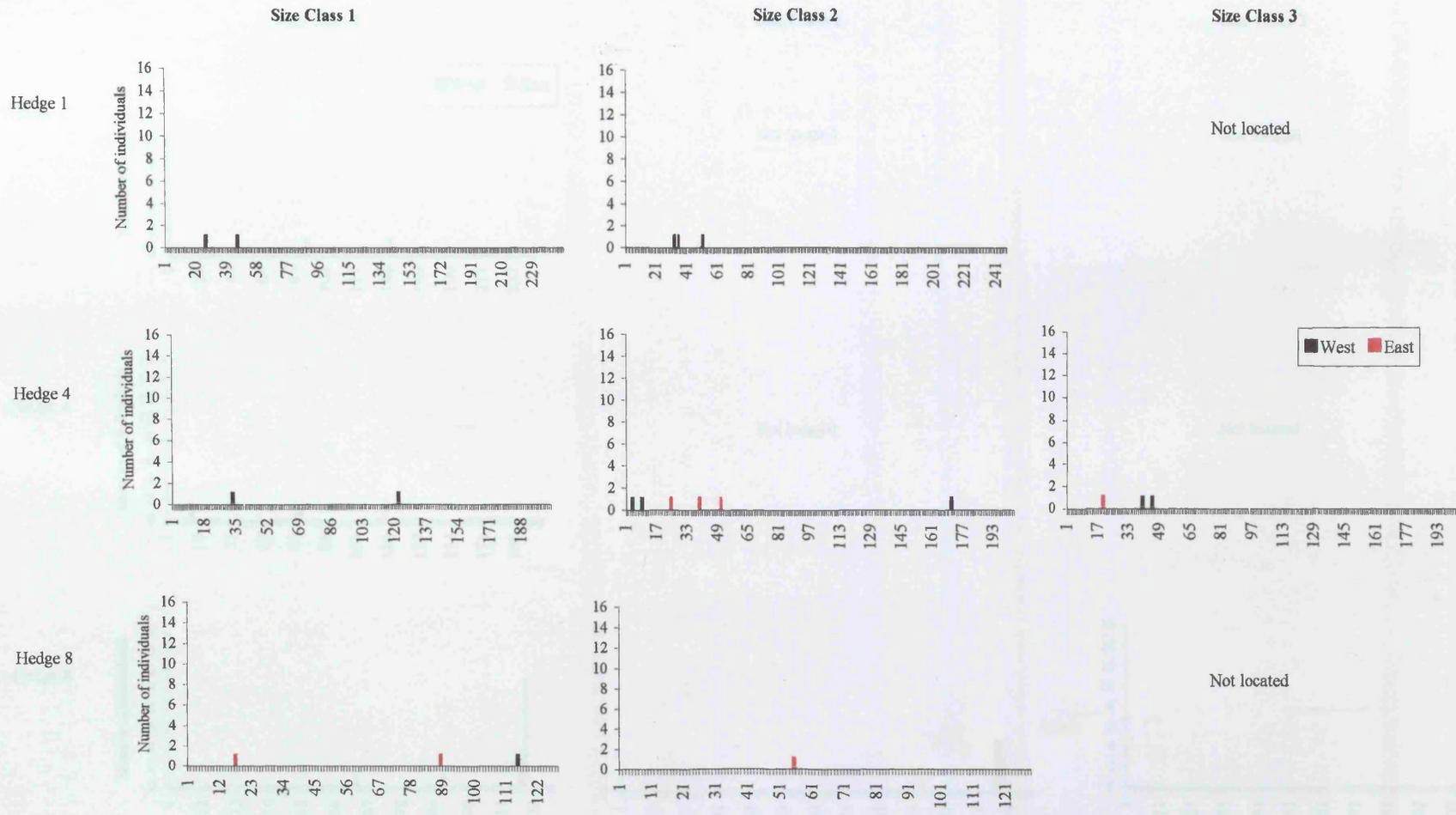
Spatial distribution of *Cornus sanguinea*



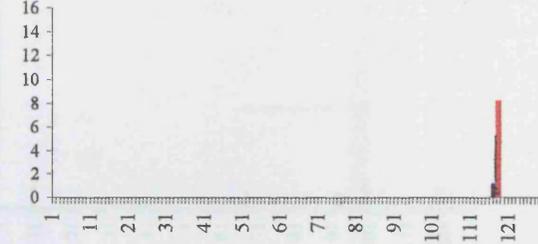
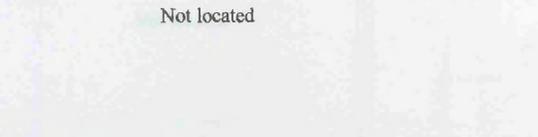
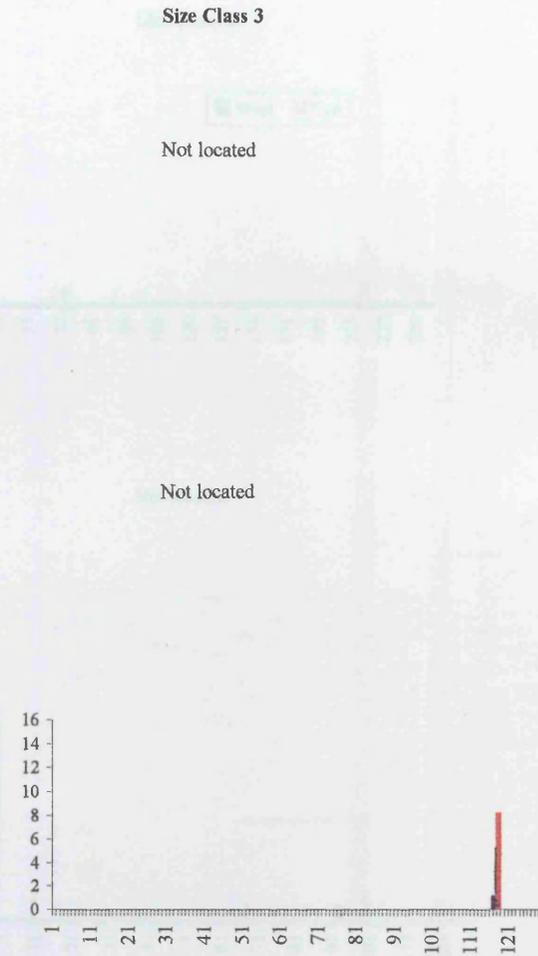
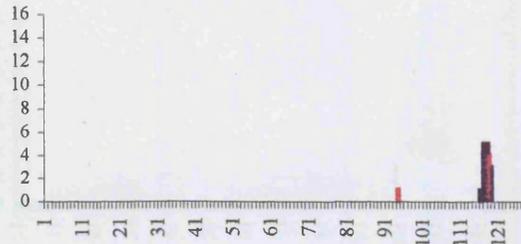
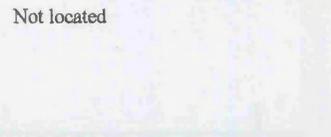
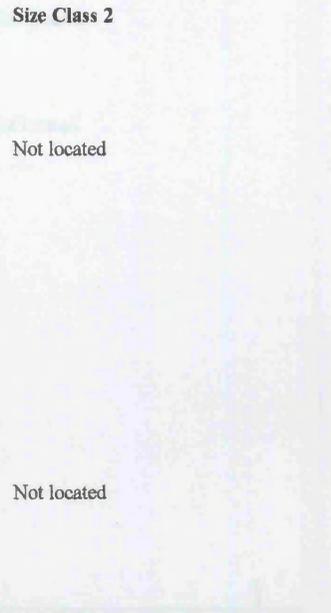
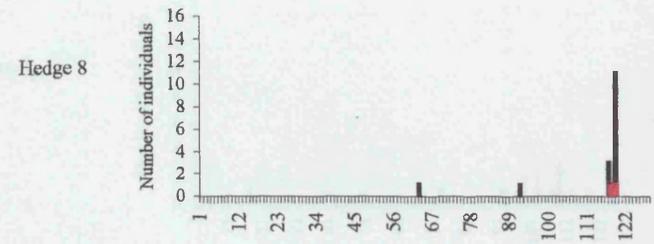
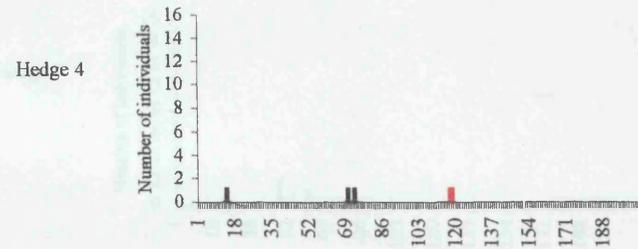
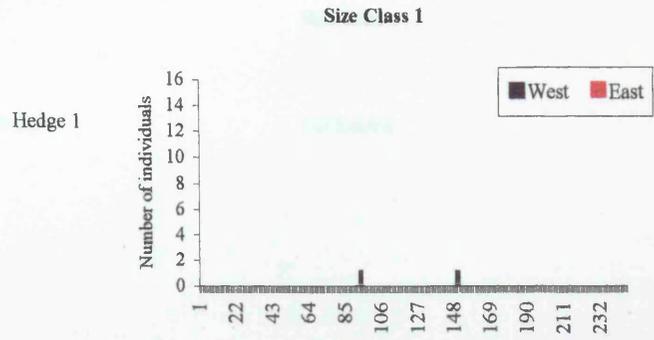
Spatial distribution of *Euonymus europaeus*



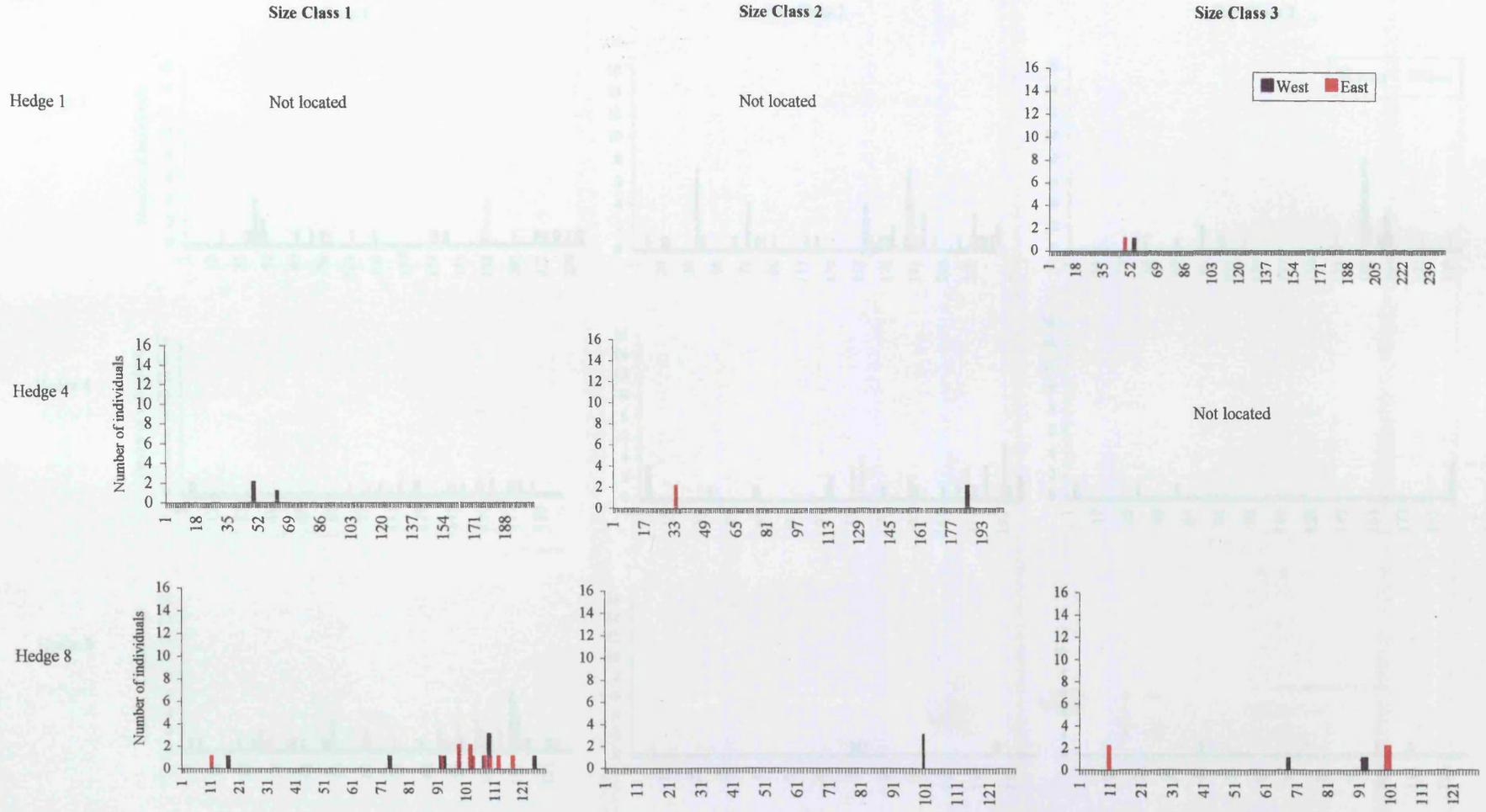
Spatial distribution of *Fraxinus excelsior*



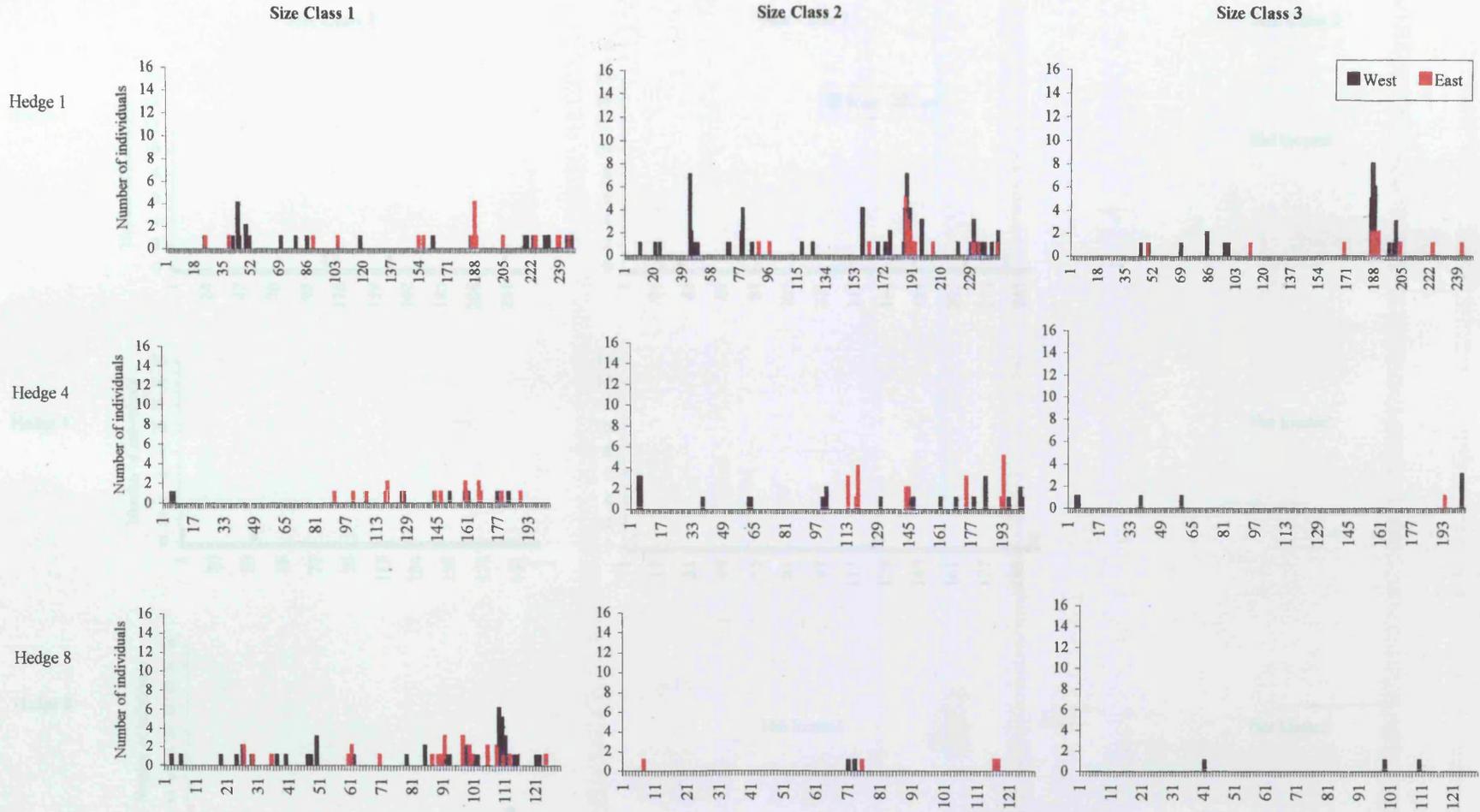
Spatial distribution of *Ligustrum vulgare*



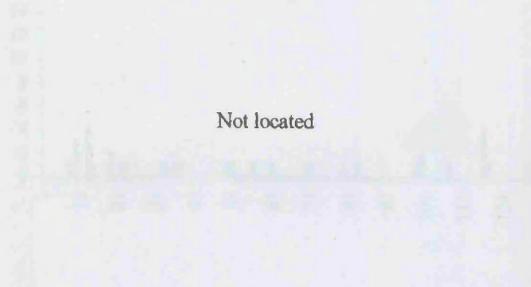
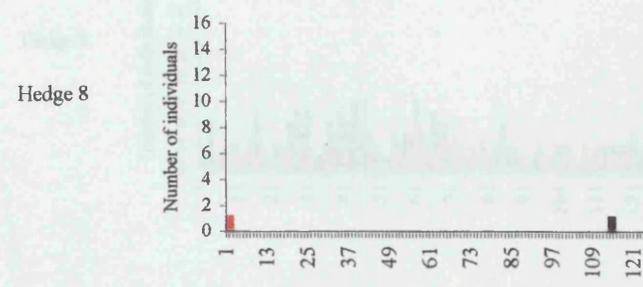
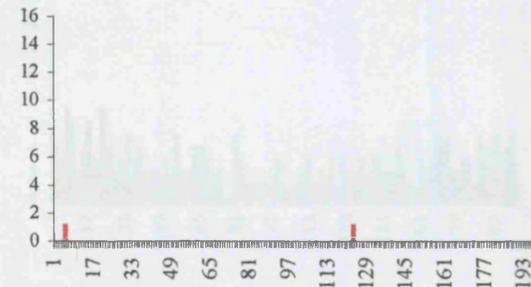
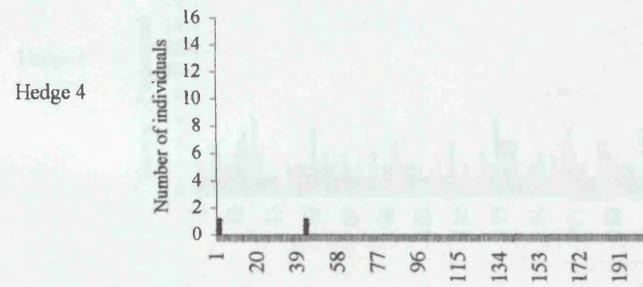
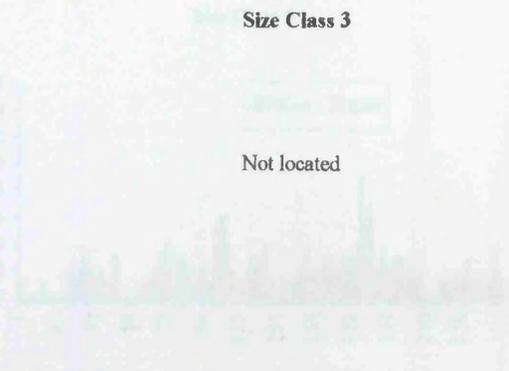
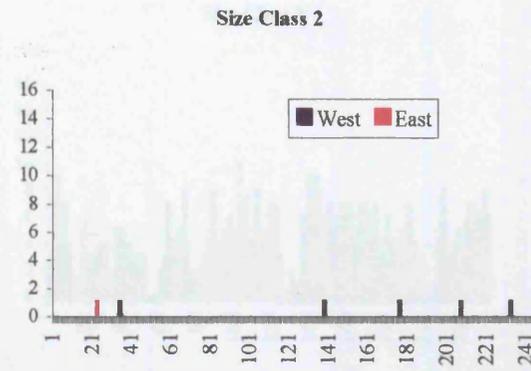
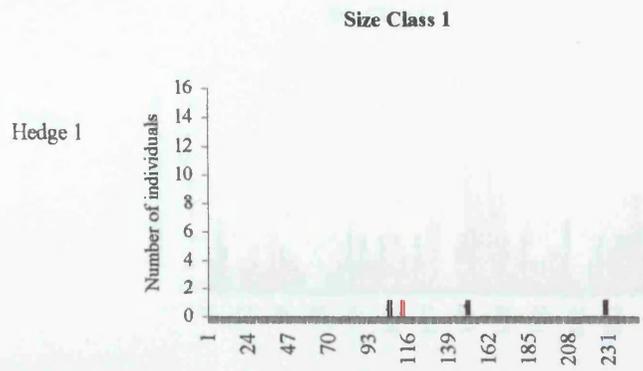
Spatial distribution of *Lonicera periclymenum*



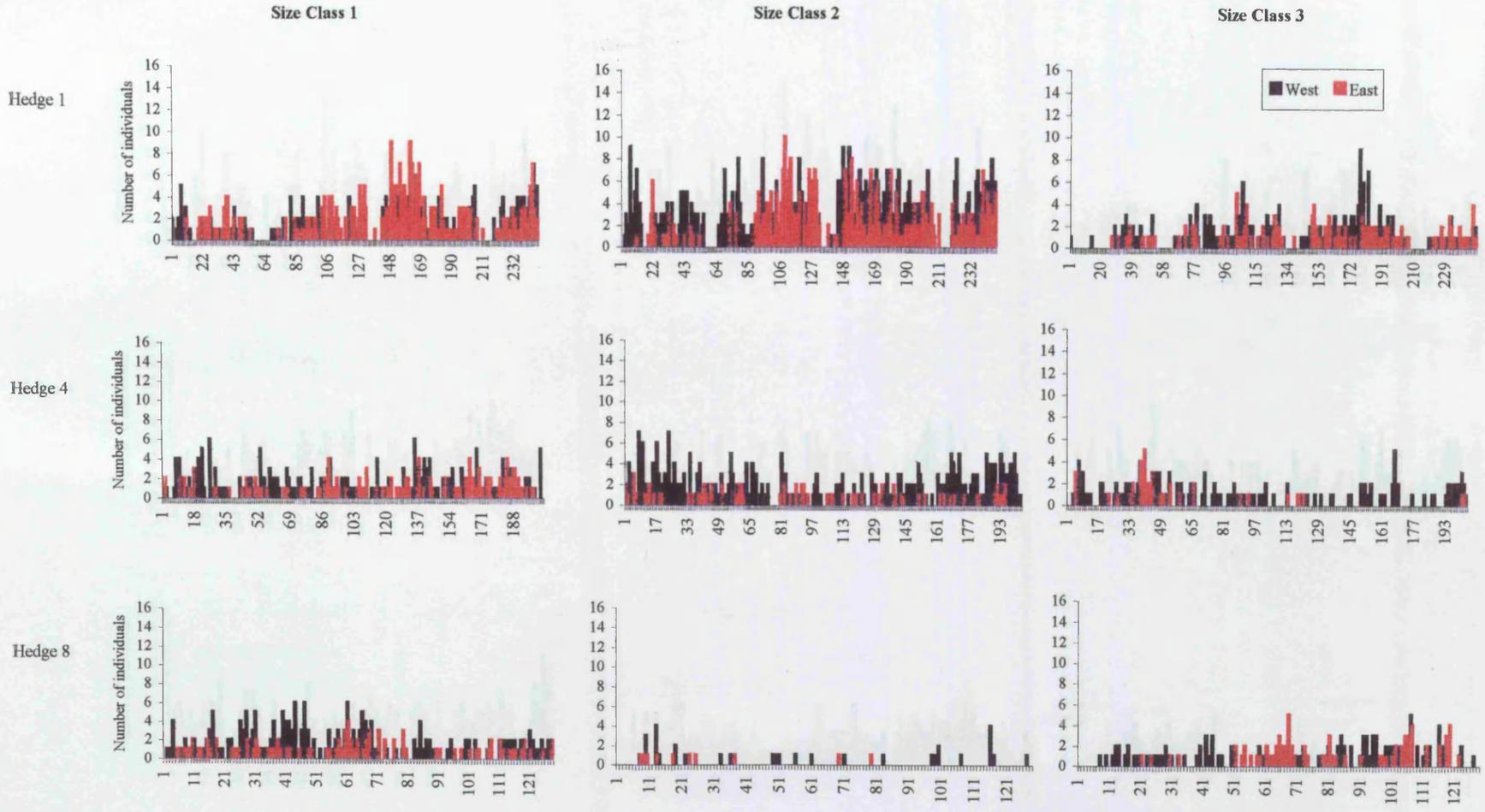
Spatial distribution of *Prunus spinosa*



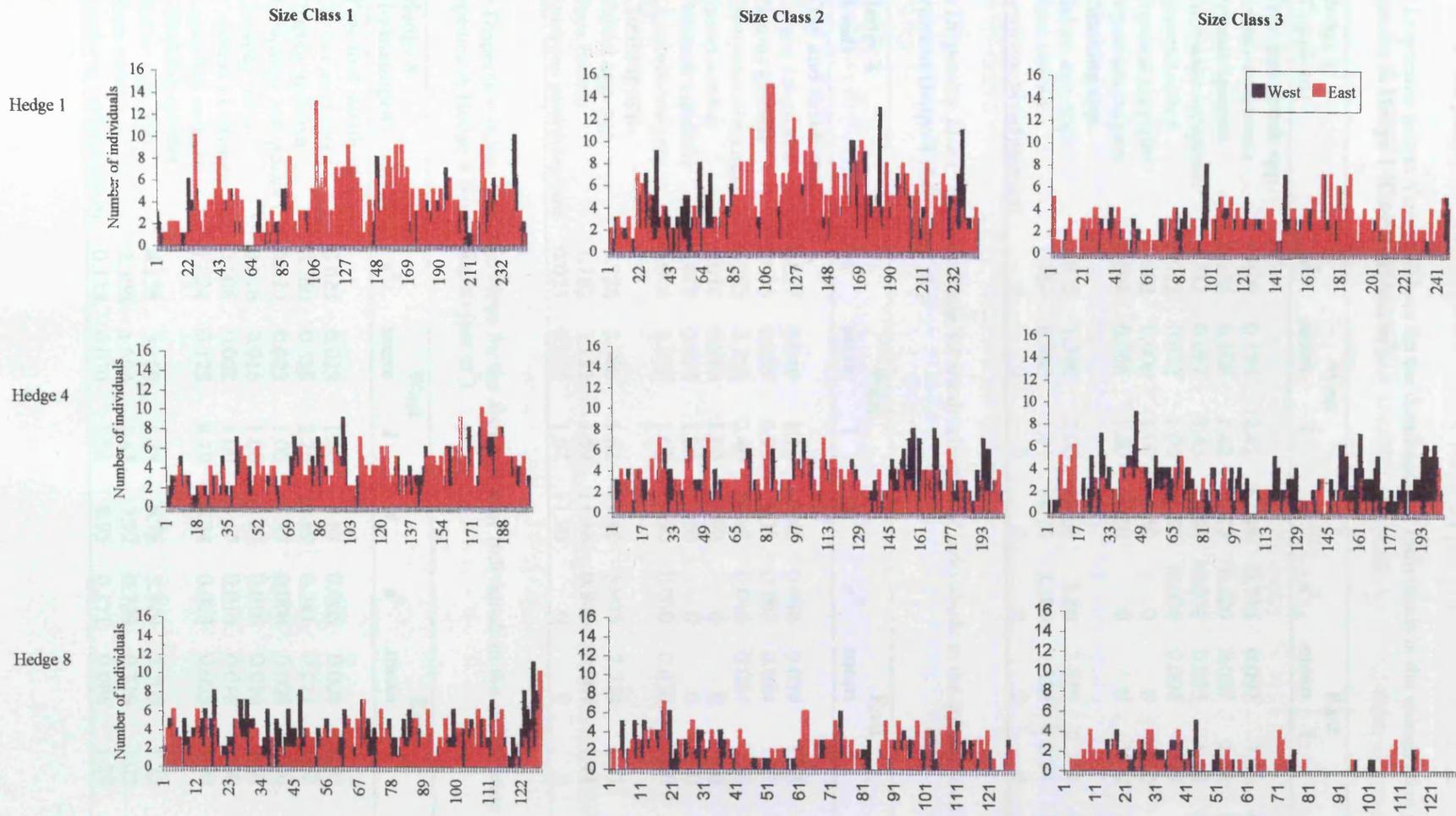
Spatial distribution of *Quercus robur*



Spatial distribution of *Rosa canina*



Spatial distribution of *Rubus* agg.



5.9 Dispersion values for woody plant species

5.9.1 Colonization phase

Table a Dispersion index: Variance/Mean for the distribution of Individuals in the colonization phase: for each species in Hedge 1 (Coppiced) (per m³).

Hedge 1 (Coppiced)	West				East			
	s ²	mean	I	d	s ²	mean	I	d
Tree and shrub spp.								
<i>Cornus sanguinea</i>	2.409	0.194	12.42	62.49	0.714	0.097	7.36	44.50
Prunus spinosa	0.155	0.109	1.42	10.75	0.120	0.077	1.56	12.02
<i>Euonymus europaeus</i>	0.333	0.097	3.43	25.40	0.074	0.053	1.40	10.57
<i>Quercus robur</i>	0.012	0.012	1.00	6.50	0.004	0.004	1.00	6.50
<i>Fraxinus excelsior</i>	0.008	0.008	1.00	6.50	0	0	0	0
<i>Ligustrum vulgare</i>	0.008	0.008	1.00	6.50	0	0	0	0
Climbing spp.								
<i>Rubus</i> agg. spp.	2.673	1.340	2.00	15.68	5.80	2.656	2.184	17.10
<i>Rosa canina</i>	1.784	0.988	1.81	14.16	3.109	1.389	2.24	17.52
<i>Lonicera periclymenum</i>	0	0	0	0	0	0	0	0

Table b Dispersion index: Variance/Mean for the distribution of Individuals in the colonization phase: for each species in Hedge 4 (Laid) (per m³).

Hedge 4 (Laid)	West				East			
	s ²	mean	I	d	s ²	mean	I	d
Tree and shrub spp.								
<i>Cornus sanguinea</i>	0.057	0.049	1.16	7.45	0.048	0.039	1.23	8.10
Prunus spinosa	0.056	0.059	0.95	5.39	0.107	0.084	1.27	8.46
<i>Euonymus europaeus</i>	0.283	0.118	2.40	16.97	0.010	0.064	0.16	-6.19
<i>Quercus robur</i>	0.010	0.010	1.00	5.90	0	0	0	0
<i>Fraxinus excelsior</i>	0.010	0.010	1.00	5.90	0	0	0	0
<i>Ligustrum vulgare</i>	0.016	0.016	1.00	5.90	0.010	0.010	1.00	5.90
Climbing spp.								
<i>Rubus</i> agg. spp.	3.728	2.306	1.62	11.40	3.993	2.724	1.47	10.18
<i>Rosa canina</i>	1.782	1.123	1.59	11.16	0.845	0.601	1.41	9.68
<i>Lonicera periclymenum</i>	0.025	0.015	1.67	11.79	0	0	0	0

Table c Dispersion index: Variance/Mean for the distribution of Individuals in the colonization phase: for each species in Hedge 8 (Unmanaged) (per m³).

Hedge 8 (Unmanaged)	West				East			
	s ²	mean	I	d	s ²	mean	I	d
Tree and shrub spp.								
<i>Cornus sanguinea</i>	0.023	0.023	1.00	4.67	0.008	0.008	1.00	4.67
Prunus spinosa	0.760	0.336	2.26	12.69	0.341	0.211	1.62	9.02
<i>Euonymus europaeus</i>	0.023	0.023	1.00	4.67	0.008	0.008	1.00	4.67
<i>Quercus robur</i>	0.016	0.016	1.00	4.67	0.016	0.016	1.00	4.67
<i>Fraxinus excelsior</i>	0.008	0.008	1.00	4.67	0.016	0.016	1.00	4.67
<i>Ligustrum vulgare</i>	1.024	0.125	8.19	34.34	0.023	0.023	1.00	4.67
Climbing species								
<i>Rubus</i> agg. spp.	4.158	3.250	1.28	6.76	3.329	2.703	1.23	6.41
<i>Rosa canina</i>	2.306	1.594	1.45	7.92	0.739	0.719	1.03	4.91
<i>Lonicera periclymenum</i>	0.113	0.070	1.61	8.95	0.111	0.086	1.29	6.83

5.9.2 Survivorship phase

Table a Dispersion index: Variance/Mean for the distribution of Individuals in the survivorship phase: for each species in Hedge 1 (Coppiced) (per m³).

Hedge 1 (Coppiced)	West				East			
	s ²	mean	I	d	s ²	mean	I	d
Tree and shrub spp.								
<i>Cornus sanguinea</i>	0.655	0.126	5.20	34.90	0.508	0.117	4.34	30.53
Prunus spinosa	0.871	0.283	7.44	44.82	0.223	0.093	3.78	27.44
<i>Euonymus europaeus</i>	0.441	0.081	5.31	35.43	0.129	0.069	2.87	21.90
<i>Quercus robur</i>	0.020	0.020	1.00	6.50	0.004	0.004	1.00	6.50
<i>Fraxinus excelsior</i>	0.012	0.012	1.00	6.50	0.012	0.012	1.00	6.50
<i>Ligustrum vulgare</i>	0	0	0	0	0	0	0	0
Climbing spp.								
<i>Rubus</i> agg. spp.	5.138	2.417	2.13	16.69	8.546	3.352	2.55	19.74
<i>Rosa canina</i>	5.299	2.530	2.10	16.46	4.337	1.688	2.57	19.88
<i>Lonicera periclymenum</i>	0	0	0	0	0	0	0	0

Table b Dispersion index: Variance/Mean for the distribution of Individuals in the survivorship phase: for each species in Hedge 4 (Laid) (per m³).

Hedge 4 (Laid)	West				East			
	s ²	mean	I	d	s ²	mean	I	d
Tree and shrub spp.								
<i>Cornus sanguinea</i>	0.039	0.030	1.30	8.72	0.019	0.020	0.95	5.39
Prunus spinosa	0.217	0.123	1.76	12.48	0.331	0.103	3.21	21.85
<i>Euonymus europaeus</i>	0.114	0.069	1.65	11.68	0.034	0.025	1.36	9.25
<i>Quercus robur</i>	0	0	0	0	0.019	0.020	0.95	5.39
<i>Fraxinus excelsior</i>	0.015	0.015	1.00	5.90	0.015	0.015	1.00	5.90
<i>Ligustrum vulgare</i>	0	0	0	0	0	0	0	0
Climbing spp.								
<i>Rubus</i> agg. spp.	3.552	2.419	1.47	10.18	2.731	2.177	1.26	8.37
<i>Rosa canina</i>	2.516	1.650	1.53	10.67	0.414	0.374	1.11	6.98
<i>Lonicera periclymenum</i>	0.020	0.010	2.00	14.25	0.020	0.010	2.00	14.25

Table c Dispersion index: Variance/Mean for the distribution of Individuals in the survivorship phase: for each species in Hedge 8 (Unmanaged) (per m³).

Hedge 8 (Unmanaged)	West				East			
	s ²	mean	I	d	s ²	mean	I	d
Tree and shrub spp.								
<i>Cornus sanguinea</i>	0	0	0	0	0	0	0	0
Prunus spinosa	0.016	0.016	1.00	4.67	0.031	0.031	1.00	4.67
<i>Euonymus europaeus</i>	0.008	0.008	1.00	4.67	0	0	0	0
<i>Quercus robur</i>	0	0	0	0	0	0	0	0
<i>Fraxinus excelsior</i>	0	0	0	0	0.008	0.008	1.00	4.67
<i>Ligustrum vulgare</i>	0.460	0.109	4.22	21.47	0.132	0.039	3.39	18.07
Climbing species								
<i>Rubus</i> agg. spp.	2.235	1.781	1.26	6.62	2.738	1.898	1.44	7.86
<i>Rosa canina</i>	0.461	0.258	1.79	10.05	0.073	0.078	0.94	4.18
<i>Lonicera periclymenum</i>	0	0	0	0	0.070	0.023	3.04	16.52

5.9.3 Establishment phase

Table a Dispersion index: Variance/Mean for the distribution of Individuals in the establishment phase: for each species in Hedge 1 (Coppiced) (per m³).

Hedge 1 (Coppiced)	West				East			
	s ²	mean	I	d	s ²	mean	I	d
Tree and shrub spp.								
<i>Cornus sanguinea</i>	0.160	0.049	3.27	24.43	0.108	0.036	3.00	22.74
Prunus spinosa	0.577	0.130	4.44	31.06	0.090	0.061	1.48	11.30
<i>Euonymus europaeus</i>	0.041	0.016	2.56	19.81	0.008	0.008	1.00	6.50
<i>Quercus robur</i>	0	0	0	0	0	0	0	0
<i>Fraxinus excelsior</i>	0	0	0	0	0	0	0	0
<i>Ligustrum vulgare</i>	0	0	0	0	0	0	0	0
Climbing spp.								
<i>Rubus</i> agg. spp.	2.188	1.381	1.584	12.20	2.293	1.809	1.27	9.32
<i>Rosa canina</i>	1.612	0.838	1.924	15.60	0.816	0.563	1.45	11.03
<i>Lonicera periclymenum</i>	0.004	0.004	1.000	6.50	0.004	0.004	1.00	6.50

Table b Dispersion index: Variance/Mean for the distribution of Individuals in the establishment phase: for each species in Hedge 4 (Laid) (per m³).

Hedge 4 (Laid)	West				East			
	s ²	mean	I	d	s ²	mean	I	d
Tree and shrub spp.								
<i>Cornus sanguinea</i>	0	0	0	0	0	0	0	0
Prunus spinosa	0.063	0.035	1.80	12.78	0.005	0.005	1.00	6.50
<i>Euonymus europaeus</i>	0.034	0.025	1.36	9.25	0	0	0	0
<i>Quercus robur</i>	0	0	0	0	0	0	0	0
<i>Fraxinus excelsior</i>	0.010	0.010	1.00	6.50	0.005	0.005	1.00	6.50
<i>Ligustrum vulgare</i>	0	0	0	0	0	0	0	0
Climbing spp.								
<i>Rubus</i> agg. spp.	3.168	2.123	1.49	10.35	1.768	1.118	1.58	11.08
<i>Rosa canina</i>	0.912	0.704	1.30	8.72	0.468	0.217	2.16	15.36
<i>Lonicera periclymenum</i>	0	0	0	0	0	0	0	0

Table c Dispersion index: Variance/Mean for the distribution of Individuals in the establishment phase: for each species in Hedge 8 (Unmanaged) (per m³).

Hedge 8 (Unmanaged)	West				East			
	s ²	mean	I	d	s ²	mean	I	d
Tree and shrub spp.								
<i>Cornus sanguinea</i>	0	0	0	0	0	0	0	0
Prunus spinosa	0.023	0.023	1.00	4.67	0	0	0	0
<i>Euonymus europaeus</i>	0	0	0	0	0	0	0	0
<i>Quercus robur</i>	0	0	0	0	0	0	0	0
<i>Fraxinus excelsior</i>	0	0	0	0	0	0	0	0
<i>Ligustrum vulgare</i>	0.203	0.047	4.32	21.86	0.500	0.063	7.94	33.64
Climbing species								
<i>Rubus</i> agg. spp.	1.019	0.641	1.59	8.83	1.102	0.750	1.47	8.05
<i>Rosa canina</i>	1.098	0.859	1.28	6.76	1.016	0.586	1.73	9.69
<i>Lonicera periclymenum</i>	0.023	0.023	1.00	4.67	0.092	0.047	1.60	8.90

5.10 Temporal data for woody plant species in three Experimental Hawthorn Hedgerows: mean number of individuals

Temporal data for *Cornus sanguinea* : mean number of individuals

Year	Hedge 1		Hedge 4		Hedge 8	
	West	East	West	East	West	East
Size Class 1						
1970	0	0.004	0	0	0	0
1971	0	0.004	0	0	0	0
1972	0	0.004	0	0	0	0
1997	0.194	0.097	0.049	0.039	0.023	0.008
Size Class 2						
1970	0	0	0	0	0	0
1971	0	0	0	0	0	0
1972	0	0	0	0	0	0
1997	0.126	0.117	0.029	0.02	0	0
Size Class 3						
1970	0	0	0	0	0	0
1971	0	0	0	0	0	0
1972	0	0	0	0	0	0
1997	0.049	0.036	0	0	0	0

Temporal data for *Euonymus europaeus* : mean number of individuals

Year	Hedge 1		Hedge 4		Hedge 8	
	West	East	West	East	West	East
Size Class 1						
1970	0	0	0	0	0	0
1973	0	0	0	0.005	0	0
1975	0	0	0.005	0	0	0
1997	0.097	0.053	0.118	0.064	0.023	0.008
Size Class 2						
1970	0	0	0	0	0	0
1973	0.004	0	0	0	0	0
1975	0.008	0	0	0	0	0
1997	0.081	0.069	0.069	0.025	0.008	0
Size Class 3						
1970	0	0	0	0	0	0
1973	0	0	0	0	0	0
1975	0	0	0	0	0	0
1997	0.016	0.008	0.025	0	0	0

Temporal data for *Fraxinus excelsior* : mean number of individuals

Year	Hedge 1		Hedge 4		Hedge 8	
	West	East	West	East	West	East
Size Class 1						
1970	0.036	0.012	0.020	0.025	0.008	0.008
1971	0.020	0.012	0.025	0.005	0.008	0
1972	0.036	0.020	0.039	0.020	0.008	0.008
1997	0.008	0	0.010	0	0.008	0.016
Size Class 2						
1970	0.049	0.016	0.020	0.015	0.008	0
1971	0.024	0.008	0.010	0.010	0.016	0
1972	0.016	0.012	0.010	0	0	0.008
1997	0.012	0.012	0.015	0.015	0	0.008
Size Class 3						
1970	0.008	0	0.010	0	0	0
1971	0.016	0	0.029	0.005	0	0
1972	0.016	0	0.025	0.010	0	0.008
1997	0	0	0.010	0.005	0	0

Temporal data for *Ligustrum vulgare* : mean number of individuals

Year	Hedge 1		Hedge 4		Hedge 8	
	West	East	West	East	West	East
Size Class 1						
1970	0	0	0	0.010	0	0
1971	0	0	0	0.005	0.008	0
1972	0	0	0	0.005	0.008	0
1973	0	0	0.005	0.010	0	0
1997	0.008	0	0.015	0.010	0.125	0.023
Size Class 2						
1970	0	0	0	0.010	0	0
1971	0	0	0	0.010	0	0
1972	0	0	0	0.005	0	0
1973	0	0	0	0.005	0	0
1997	0	0	0	0	0.109	0.039
Size Class 3						
1970	0	0	0	0	0	0
1971	0	0	0	0	0.008	0
1972	0	0	0	0	0.008	0
1973	0	0	0	0	0.008	0
1997	0	0	0	0	0.047	0.063

Temporal data for *Prunus spinosa* : number of individuals

Year	Hedge 1		Hedge 4		Hedge 8	
	West	East	West	East	West	East
Size Class 1						
1970	0.073	0.061	0.02	0.02	0	0
1971	0.061	0.061	0.015	0.029	0	0
1972	0.069	0.077	0.005	0.02	0.016	0
1997	0.109	0.077	0.059	0.083	0.336	0.211
Size Class 2						
1970	0.028	0.028	0	0	0	0
1971	0.045	0.032	0	0.02	0.008	0.023
1972	0.057	0.032	0.005	0.005	0.031	0
1997	0.283	0.093	0.123	0.103	0.016	0.031
Size Class 3						
1970	0.008	0.004	0	0	0	0
1971	0.032	0.008	0	0	0	0
1972	0.028	0.008	0.01	0	0	0
1997	0.13	0.061	0.034	0.005	0.023	0

Temporal data for *Rosa canina* : number of individuals

Year	Hedge 1		Hedge 4		Hedge 8	
	West	East	West	East	West	East
Size Class 1						
1970	0.267	0.482	0.069	0.113	0	0
1971	1.109	0.745	0.127	0.255	0.133	0.203
1972	1.032	0.846	0.118	0.265	0.055	0.094
1997	0.988	1.389	1.123	0.598	1.594	0.719
Size Class 2						
1970	0.032	0.073	0	0.005	0	0
1971	0.13	0.117	0.034	0.025	0	0.016
1972	0.409	0.17	0.034	0.054	0.023	0.031
1997	2.53	1.668	1.642	0.373	0.258	0.078
Size Class 3						
1970	0.012	0.024	0.005	0	0	0
1971	0.02	0.061	0.01	0.01	0.016	0.016
1972	0.036	0.085	0.015	0.015	0.008	0.016
1997	0.838	0.563	0.701	0.216	0.859	0.586