Caroline E. Farrior, David Tilman, Ray Dybzinski, Peter B. Reich, Simon A. Levin, and Stephen W. Pacala. 2013. Resource limitation in a competitive context determines complex plant responses to experimental resource additions

Appendix B. Relaxation of territoriality and well-mixed assumptions

In the main text, we assume that aboveground plants are strictly territorial and do not share space. We assume the opposite belowground; that plants are not at all territorial and fine roots share space equally. In reality, however, there is some shading among leaves aboveground and some degree of spatial segregation of fine roots belowground. Here we show that deviations from these strict assumptions of the main text do not change the qualitative predictions of our model.

As in the main text, we assume that plant communities are approximately composed of only mature individuals, that individuals each occupy the same amount of ground area, and individuals arrange their leaves to maintain constant leaf area per unit ground area within individual plants. Let T_a, represent the territoriality of plants aboveground, specifically the fraction of a plant's total area that is free of shading from leaves of other individuals. Let T_b represent the territoriality of root biomass belowground, specifically the fraction of a plant's root biomass that is free of competition with other roots. The portion of a plant's area that is shared with other individuals is then $(1 - T_a)$ aboveground and $(1 - T_b)$ belowground. With these definitions, the case presented in the main text is the specific case where $T_a = 1$ and $T_b = 0$.

Where plants are territorial aboveground, they only shade themselves. Where they share space, they are shaded by both their own leaves and those of one neighbor (Figure B1). We assume each individuals' biomass does not depend on T_a and thus, as T_a decreases from 1, the density of individuals in the community increases, and thus the total area occupied by s individuals decreases. We make the simplifying assumption here that all neighbors of the target strategy have the same

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Strict territoriality (T_a=1)
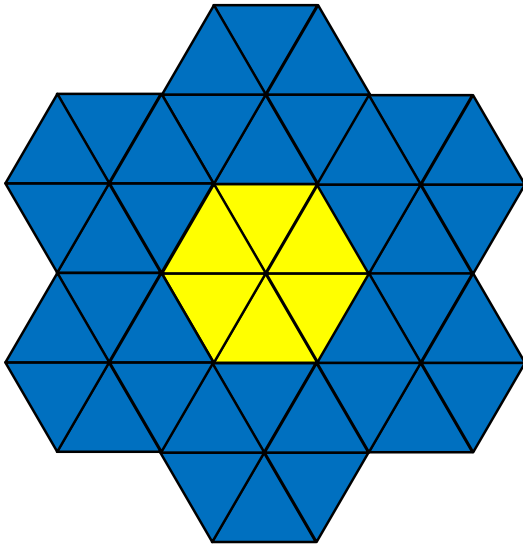
Overlapping Individuals (T_a<1)

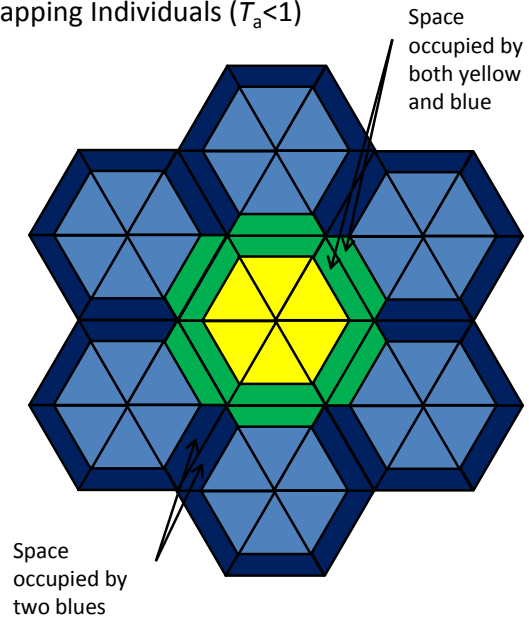Space occupied by both yellow and blue

Space occupied by two blues

Figure B1: A depiction of plants aboveground. A single individual (yellow hexagon) and its neighbors (blue hexagons) do not share any space (left, $T_a = 1$) and share a portion of their space with their neighbors (right, $T_a < 1$). The green and dark blue portions are occupied by the leaves of the two adjacent individuals. As T_a decreases the light blue and yellow triangles decrease in size while green and dark blue (the shared portions) increase in size.

allocation strategy and have the same amount of leaf area. Thus the leaf area within these mixed regions is equal to the leaf area of the target plant ($\frac{l(r',r)}{\eta}$) plus the leaf area of the neighboring individuals ($\frac{l(r,r)}{\eta}$). If an individual has more leaves than another, in the shared space the additional leaves are placed above those of the neighbors.

We model belowground territoriality in a slightly different way. Instead of adding overlap, here we add territoriality to the assumption of well-mixed roots. As plants gain territoriality, as T_b increases from zero, plants gain a portion of space that they have sole access to. The density of roots in this patch is equal to the root density of the target individual (r'). In non-territorial patches, individuals completely share resources as they do in the main text. Here the density of roots is approximately equal to the density of the resident strategy (r).

With these new descriptions of plant territoriality, the leaf biomass of a nitrogen-limited individual with fine-root biomass r' in an environment of individuals with fine-root biomass r depends on the territoriality belowground:

$$l(r', r) = T_\mathrm{b} \, \frac{N_0}{\rho} + (1 - T_\mathrm{b})\frac{N_0}{\rho} \frac{r'}{r}. \tag{B.1}$$

The yearly carbon assimilation rate is still the sum of light limited and water limited rates:

$$A = q \, A_\mathrm{L} + (1 - q) \, A_\mathrm{W}, \tag{B.2}$$

where now light limited photosynthesis is moderated by the increased shading in shared portions:

$$A_\mathrm{L}(r', r) = T_\mathrm{a} \, \frac{V}{k} \left(1 + \ln\left(\frac{\alpha_\mathrm{f} \, L_0}{V} \right) - \frac{\alpha_\mathrm{f} \, L_0}{V} \, e^{-k \, \frac{l(r',r)}{\eta}} \right)$$

$$+ (1 - T_\mathrm{a}) \, \frac{V}{2 \, k} \left(1 + \ln\left(\frac{\alpha_\mathrm{f} \, L_0}{V} \right) - \frac{\alpha_\mathrm{f} \, L_0}{V} \, e^{-k \, \frac{(l(r',r)+l(r,r))}{\eta}} \right)$$

$$+k\ \frac{(l(r',r) - l(r,r))}{\eta}\Bigg)\,. \tag{B.3}$$

For a detailed derivation of A_{L} see Section B2.

Water limited photosynthesis is proportional to water uptake, which also now depends on territoriality belowground:

$$A_{\mathrm{W}}(r',r) = T_{\mathrm{b}}\ W_0\ \omega + (1 - T_{\mathrm{b}})\ W_0\ \omega\ \frac{r'}{r}\,. \tag{B.4}$$

Fitness remains the same:

$$F(r',r) = \frac{f(r',r)}{f(r,r)}, \tag{B.5}$$

where

$$f(r',r) = \frac{1}{c_{\mathrm{f}}}\left(q\ A_{\mathrm{L}}(r',r) + (1 - q)\ A_{\mathrm{W}}(r',r) - c_{\mathrm{l}}\ l(r',r) - c_{\mathrm{r}}\ r'\right). \tag{B.6}$$

And again r^* is the competitive-dominant strategy (evolutionarily stable strategy, ESS) if it satisfies the following conditions:

$$\forall\, r' \neq r^* : F(r',r^*) < F(r^*,r^*)\ \text{or}\ F(r',r^*) = F(r^*,r^*)\ \text{and}\ F(r^*,r') > F(r',r'). \tag{B.7}$$

Section B1: Results

Given that plants are nitrogen, water, and light limited, the ESS fine-root biomass is the following:

$$r^* = \frac{(1 - T_{\mathrm{b}})}{c_{\mathrm{r}}}\left[q\ \frac{l^*}{\eta}\left(T_{\mathrm{a}}\ \alpha_{\mathrm{f}}\ L_0\ e^{-k\ \frac{l^*}{\eta}} + (1 - T_{\mathrm{a}})\frac{\alpha_{\mathrm{f}}\ L_0}{2}\ e^{-2\,k\ \frac{l^*}{\eta}} + (1 - T_{\mathrm{a}})\ \frac{V}{2}\right)\right.$$

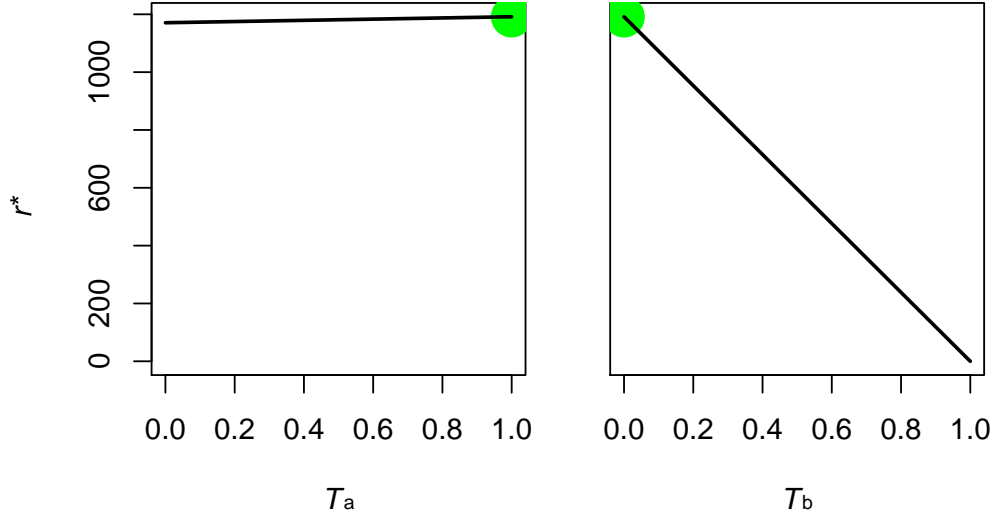$$\left. + (1 - q)\ W_0\ \omega - c_{\mathrm{l}}\ l^*\right], \tag{B.8}$$

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Figure B2: The effect of relaxing territoriality assumptions on competitive fine-root investment (assuming nitrogen limitation). Left: strict territoriality of leaves aboveground is relaxed while roots completely overlap belowground ($T_b = 0$). Right: effect territoriality belowground is relaxed while leaves are completely non-overlapping aboveground ($T_a = 1$). The green dot marks the r^* for the strict assumptions that $T_a = 1$ (left) and $T_b = 0$ (right). Parameter values used in this demonstration can be found in Table B1.

where

$$l^* = \frac{N_0}{\rho}. \tag{B.9}$$

If T_b does not equal zero and T_a does not equal one, predictions of ESS allocation to fine roots is less than that of the model in the main text. However, as T_b approaches zero and T_a approaches one r^* and l^* converge on the r^* and l^* of the strict territoriality assumptions (Figures B2 and B4). Additionally, the dependence of r^* on N_0, W_0 and q also converge on the case of $T_a = 1$ and $T_b = 0$ (Figure B3), making the qualitative predictions of the paper robust to small deviations from the strict territoriality assumptions.

Unless belowground is entirely territorial ($T_b = 1$), deviations of T_b from zero, and T_a from 1 only modify the strength of the responses to water and nitrogen and not the direction of the

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response (Figure B3). Notably, the closer leaves are to being completely well-mixed (T_a closer to 0), the weaker the negative effect of nitrogen on fine-roots becomes. Additionally, if fine roots are completely territorial ($T_b = 1$) this model predicts there would be no response of fine roots to environmental variables.

$$\frac{\partial r^*}{\partial W_0} = (1 - T_b)\frac{(1 - q)\,\omega}{c_r} \tag{B.10}$$

$$\frac{\partial r^*}{\partial q} = \frac{(1 - T_b)}{c_r}\left[\frac{N_0}{\rho\,\eta}\left(T_a\,\alpha_f\,L_0\,e^{-k\,\frac{N_0}{\rho\,\eta}} + \frac{(1 - T_a)}{2}\left(\alpha_f\,L_0\,e^{-2\,k\,\frac{N_0}{\rho\,\eta}} + V\right)\right) - W_0\,\omega\right] \tag{B.11}$$

$$\frac{\partial r^*}{\partial N_0} = \frac{(1 - T_b)}{c_r}\left[\frac{q}{\rho\,\eta}\left(T_a\,\alpha_f\,L_0\,e^{-k\frac{N_0}{\rho\,\eta}} + (1 - T_a)\frac{\alpha_f\,L_0}{2}e^{-2k\frac{N_0}{\rho\,\eta}} + (1 - T_a)\frac{V}{2}\right)\right.$$
$$\left. - \frac{q\,N_0\,\alpha_f\,L_0\,k}{\rho^2\,\eta^2}\left(T_a e^{-k\,\frac{N_0}{\rho\,\eta}} + (1 - T_a)e^{-2\,k\,\frac{N_0}{\rho\,\eta}}\right) - \frac{c_l}{\rho}\right] \tag{B.12}$$

$$\frac{\partial^2 r^*}{\partial q\,\partial W_0} = -(1 - T_b)\frac{q\,W_0}{c_r} \tag{B.13}$$

$$\frac{\partial^2 r^*}{\partial W_0\,\partial N_0} = 0 \tag{B.14}$$

$$\frac{\partial^2 r^*}{\partial q\,\partial N_0} = \frac{(1 - T_b)}{c_r}\left[\frac{1}{\rho\,\eta}\left(T_a\,\alpha_f\,L_0\,e^{-k\,\frac{N_0}{\rho\,\eta}} + \frac{(1 - T_a)}{2}\left(\alpha_f\,L_0\,e^{-2\,k\,\frac{N_0}{\rho\,\eta}} + V\right)\right)\right.$$
$$\left. - \frac{N_0\,k\,\alpha_f\,L_0}{\rho^2\,\eta^2}\left(T_a\,e^{-k\,\frac{N_0}{\rho\,\eta}} + (1 - T_a)\,e^{-2\,k\,\frac{N_0}{\rho\,\eta}}\right)\right] \tag{B.15}$$
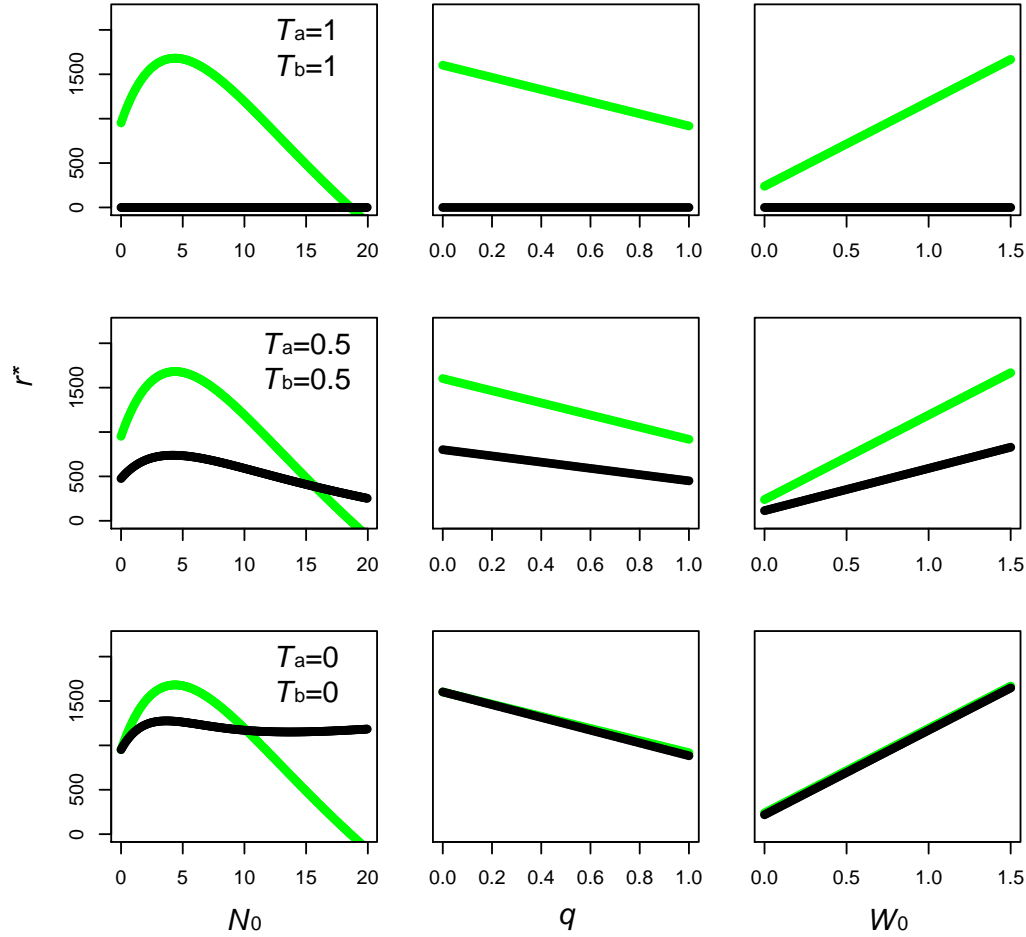
Figure B3: Dependent of r^* on the nitrogen mineralization rate (N_0, left panels), fraction of the growing season in water saturation (q, middle panels) and water input rate during water limitation (W_0, right panels). Green lines show the strict assumptions of the main text: territoriality aboveground and complete space sharing belowground ($T_a=1, T_b=0$). Deviations from these conditions (black lines, legends in the first figure of each row) only result in qualitative differences of predictions of the dependence of ESS r^* in extreme cases ($T_b=1$, top panels and $T_a=0$, bottom panels). Where only half of the aboveground and belowground plant areas are territorial (middle panels), r^* follows the same form of dependence as in the strict case of the main text. Parameter values used in this demonstration can be found in Table B1. Where they are not varying, $N_0 = 10$ gN m^{-2} yr^{-1}, q = 0.6, and $W_0 = 1$ m yr^{-1}.

Section B2: Derivation of light-limited photosynthesis, $A_{\rm L}$

By approximating leaf layers as a continuum we can find the photosynthetic rate of the whole plant by integrating through the leaf layers. Recall, we assume the leaf-level photosynthetic rate increases proportionally with light level (by $\alpha_{\rm f}$ gC (MJ PAR)$^{-1}$) up to a maximum V (V, gC m^{-2} yr^{-1})) and that light level decays exponentially at a rate, k through the leaf layers ($\frac{l}{\eta}$, m^2 m^{-2}).

Whole plant water-saturated photosynthetic rate is then the integral of the photosynthesis of leaf layers operating at the maximum rate (V) plus the photosynthesis of the leaves operating in proportion to their light level:

$$A_{\rm L}(l') = \int_0^{\frac{l^\sim}{\eta}} V \ {\rm d}x + \int_{\frac{l^\sim}{\eta}}^{\frac{l'}{\eta}} \alpha_{\rm f} \ L(x) \ {\rm d}x, \tag{B.16}$$

where $L(x)$ is the light level below $\frac{x}{\eta}$ leaf layers:

$$L(x) = L_0 \ e^{-k \ \frac{x}{\eta}}, \tag{B.17}$$

and $\frac{l^\sim}{\eta}$ is the leaf layer at which light first becomes limiting in the plant (photosynthesis $< V$):

$$V = \alpha_{\rm f} \ L_0 e^{-k \ \frac{l^\sim}{\eta}}. \tag{B.18}$$

By rearranging, we find:

$$\frac{l^\sim}{\eta} = \frac{1}{k} \ln\left(\frac{\alpha_{\rm f} \ L_0}{V}\right). \tag{B.19}$$

Assuming that the plant has enough leaf layers such that not all of its leaf layers are light saturated ($l' > l^\sim$), we find:

$$A_{\rm L}(l') = \frac{V}{k}\left(1 + \ln\left(\frac{\alpha_{\rm f} \ L_0}{V}\right) - \frac{\alpha_{\rm f} \ L_0}{V} e^{-k \ \frac{l'}{\eta}}\right). \tag{B.20}$$

This is Eq 1 of the main text.

Now, in a similar derivation, we find the total plant water-saturated rate of photosynthesis if the plant is not entirely territorial, $T_a \neq 1$. The plant will have T_a proportion operating at Eq 1 (same as Eq B.20) and $1 - T_a$ operating at a rate dependent on the number of leaf layers of neighboring plants ($\frac{l}{\eta}$).

If $l' > l$, then in the area of overlap the target plant has a few leaf layers that are free of shade from neighbors. We assume that l' is close enough to l such that $l^\sim$ is greater than $l' - l$. The total plant photosynthesis is then:

$$A_{\mathrm{L}}(l', l) = T_a \text{ Eq } 1 + (1 - T_a) \left(\int_0^{\frac{l^\sim}{\eta}} V \, \mathrm{d}x + \int_{\frac{l^\sim}{\eta}}^{\frac{l'}{\eta}} \alpha_{\mathrm{f}} \, L(x, l) \, \mathrm{d}x \right), \tag{B.21}$$

where for $x > l' - l$

$$L(x, l) = L_0 \, e^{-2k\frac{x}{\eta} + k\frac{(l'-l)}{\eta}}, \tag{B.22}$$

and thus:

$$\frac{l^\sim}{\eta} = \frac{\ln\left(\frac{\alpha_{\mathrm{f}} \, L_0}{V}\right) + k\frac{(l'-l)}{\eta}}{2 \, k}. \tag{B.23}$$

This makes:

$$A_{\mathrm{L}}(l', l) = T_a \text{ Eq } 1 + (1 - T_a) \left(\frac{V}{2 \, k} \left(1 + \ln\left(\frac{\alpha_{\mathrm{f}} \, L_0}{V}\right) - \frac{\alpha_{\mathrm{f}} \, L_0}{V} e^{-k\frac{(l'+l)}{\eta}} + k\frac{(l' - l)}{\eta} \right) \right). \tag{B.24}$$

If the target strategy has fewer leaves than its neighbor ($l' < l$):

$$L(x, l) = L_0 \, e^{-2k\frac{x}{\eta} - k\frac{(l-l')}{\eta}}, \tag{B.25}$$

which is equal to Eq B.22, making $l^\sim$ and $A_{\mathrm{L}}(l', l)$ the same whether $l' > l$ or $l > l'$.

Section B3: Nitrogen limitation condition without strict territoriality aboveground

The maximum nitrogen input rate N_0 for nitrogen limitation increases rapidly with relaxation of T_a from 1 (Figure B4) and likewise the ESS leaf investment (l^*) for a nitrogen-saturated plant increases rapidly with relaxation of T_a from 1.

This suggests that if plants are completely overlapping aboveground nitrogen saturation is impossible.
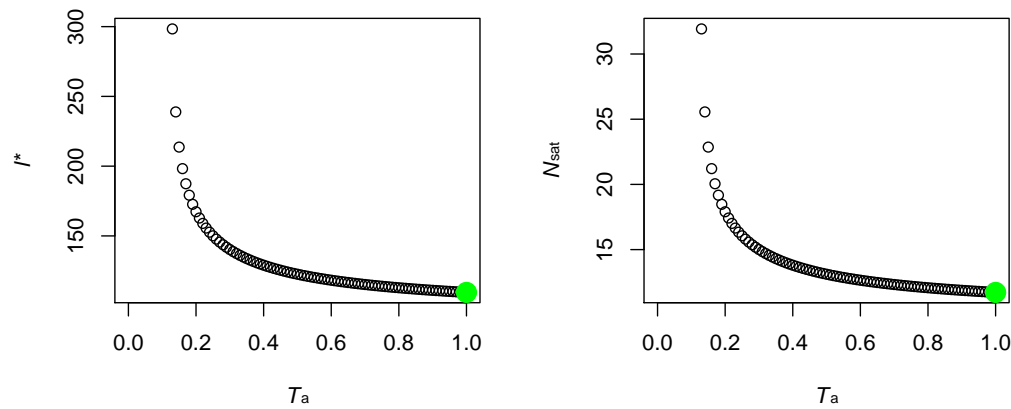
Figure B4: Responses to territoriality aboveground if nitrogen is saturating. Left: Changing competitive leaf investment with differing degrees of overlap aboveground, where T_a ranges from 0 - all overlapping and 1 no overlap. Right: The nitrogen mineralization rate required for nitrogen saturation dependence on aboveground overlap, T_a. Green indicates the solution given the strict assumption that leaves are completely non-overlapping aboveground.

Table B1: Model parameters with default values used in demonstrations. Constants whose value does not affect the predictions are not given a value.

Variable	Definition	Units	Value
s	size of the community	m^2	
r	fine-root biomass	gC m^{-2}	
$l(r',r)$	leaf biomass of individuals with strategy, r', in an environment set by individuals with strategy r	gC m^{-2}	
$f(r',r)$	rate of seed production of strategy r' in an environment set by individuals of strategy r	$\text{seeds m}^{-2} \text{ yr}^{-1}$	
η	leaf mass per unit area	gC m^{-2}	30
N_0	nitrogen mineralization rate	$\text{gN yr}^{-1} \text{ m}^{-2}$	10
N	nitrogen availability	gN m^{-2}	
u_{N}	conductance of nitrogen from root to leaf	$\text{m}^2 \text{ gC}^{-1} \text{ yr}^{-1}$	
L_0	photosynthetically active radiation	$\text{MJ PAR m}^{-2} \text{ yr}^{-1}$	1200
α_{f}	leaf-level photosynthetic dependence on light level	gC MJ PAR^{-1}	1.81
V	maximum photosynthetic rate	$\text{gC m}^{-2} \text{ yr}^{-1}$	800
q	fraction of the growing season spent in water saturation	yr yr^{-1}	0.6
W_0	precipitation during water limitation	m yr^{-1}	1
W	water availability	m	
u_{W}	conductance of water from root to leaf	$\text{m}^2 \text{ gC}^{-1} \text{ yr}^{-1}$	
ω	intrinsic water-use efficiency	gC m^{-1}	2000
A	rate of carbon assimilation	$\text{gC m}^{-2} \text{ yr}^{-1}$	
A_{L}	light-limited carbon assimilation	$\text{gC m}^{-2} \text{ yr}^{-1}$	
A_{W}	water-limited carbon assimilation	$\text{gC m}^{-2} \text{ yr}^{-1}$	
c_{l}	carbon cost of leaf respiration and maintenance	$\text{gC gC}^{-1} \text{ yr}^{-1}$	7
c_{r}	carbon cost of fine-root respiration and maintenance	$\text{gC gC}^{-1} \text{ yr}^{-1}$	0.84
c_{f}	carbon cost of seed production	gC seed^{-1}	1
ρ	plant nitrogen required per year per leaf biomass	$\text{gN gC}^{-1} \text{ yr}^{-1}$	0.107
$F(r',r)$	fitness of strategy r' in the environment set by a monoculture of individuals of strategy r		