Plant Water Use Affects Competition for Nitrogen: Why Drought Favors Invasive Species in California

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ABSTRACT: Classic resource competition theory typically treats resource supply rates as independent; however, nutrient supplies can be affected by plants indirectly, with important consequences for model predictions. We demonstrate this general phenomenon by using a model in which competition for nitrogen is mediated by soil moisture, with competitive outcomes including coexistence and multiple stable states as well as competitive exclusion. In the model, soil moisture regulates nitrogen availability through soil moisture dependence of microbial processes, leaching, and plant uptake. By affecting water availability, plants also indirectly affect nitrogen availability and may therefore alter the competitive outcome. Exotic annual species from the Mediterranean have displaced much of the native perennial grasses in California. Nitrogen and water have been shown to be potentially limiting in this system. We parameterize the model for a Californian grassland and show that soil moisture–mediated competition for nitrogen can explain the annual species' dominance in drier areas, with coexistence expected in wetter regions. These results are concordant with larger biogeographic patterns of grassland invasion in the Pacific states of the United States, in which annual grasses have invaded most of the hot, dry grasslands in California but perennial grasses dominate the moister prairies of northern California, Oregon, and Washington.

Keywords: competition, competitive exclusion, grassland, invasion, multiple stable states, coexistence.

Introduction

By altering their environments, organisms modify their resource supplies and competitive arenas (Jones et al. 1997; Kieft et al. 1998; Eviner and Chapin 2003; Eviner 2004). While classic resource competition theory treats resource supplies as independent (Tilman 1982), resources strongly covary in natural systems (Seabloom et al. 2003*a*, 2009).

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Many studies and models have focused on nutrient interactions in plants—for example, uptake ratios of nutrients and plant litter chemistry (Tilman 1982; Gusewell 2004)—and have looked at the consequential effects of these on competition, but very few have looked at the interactions of nutrients in the soil and how plants themselves may be able to alter the availability of a limiting resource through differential use of a second resource (but see Clark et al. 2005 and Daufresne and Hedin 2005). In this article, we model the interaction between two major plant resources, water and nitrogen, to show how plant water use affects the nitrogen cycle and plant competition for nitrogen.

Plant competition for one resource has been well documented: simple mechanistic models have led to the principle of competitive exclusion embodied by the R^* rule (Tilman 1982), whereby, with only one limiting resource, at equilibrium only the species that can reduce the limiting resource to the lowest level will survive. Therefore, in a well-mixed, temporally invariant environment, no more species than limiting resources can coexist. In natural ecosystems, we often see many more species than known limiting resources, and many hypotheses have been put forward to explain this apparent discrepancy. For example, both the unified neutral theory of biodiversity and intransitive competitive interactions can promote more diversity of species than of limiting resources in temporally invariant, well-mixed environments (Sinervo and Lively 1996; Hubbell 2001; Nowark and Sigmund 2004). And when the assumption of a homogeneous environment is relaxed, through spatial or temporal heterogeneity, a higher number of competitors than of limiting resources can be demonstrated (Chesson and Warner 1981; Tilman 1982; Comins and Noble 1985; Pacala and Crawley 1992; Pacala and Tilman 1994; Huisman and Weissing 1999; Amaresekare 2003).

Most terrestrial ecosystems are limited by water (Huxman et al. 2004), by nitrogen (Vitousek and Howarth

1991), or, more typically, by both (Kirchner 1977; Lauenroth and Dodd 1978; Hooper and Johnson 1999). Each plant species affects nitrogen availability in a unique way through many processes, including litter production and chemistry, specific plant-mycorrhizal mutualisms, and modification of the soil microclimate (Knops et al. 2002; Clark et al. 2005). Nitrogen availability is also regulated by soil moisture, through a variety of mechanisms. Microbial processes in the soil, such as decomposition of plant litter and soil organic matter into plant-available nitrogen, denitrification, and immobilization, are strongly regulated by soil moisture (Brady and Weil 2002). Leaching and plant uptake are dependent on soil moisture as the transport medium for nitrogen. Plant species can affect soil moisture by means of mechanisms such as reduction of evaporation from the soil surface through shading, water uptake, and effects on the soil's structure that affect its water-holding capacity (Angers and Caron 1998). By affecting water availability, plants also indirectly affect nitrogen availability as well as their ability to deplete this resource (Hooper and Johnson 1999; Craine et al. 2005). Changes in the supply of each can also affect the availability of the other, with consequences for plant phenology and ecosystem gas exchange (Harpole et al. 2007). This creates complex feedbacks between plant strategy, ecosystem processes, and interspecific competition.

Annual and perennial grass species show differing requirements for soil moisture in California (Seabloom et al. 2003*b*). It has been suggested that invasive species in California may change the water regime in a way that prevents the reestablishment of native species (Holmes and Rice 1996; Dyer and Rice 1999; Norton et al. 2004). Both nitrogen and water have been shown to be potentially limiting in this system. Given the importance of nitrogen and water in this system, the effect of soil moisture on the nitrogen cycle is likely to be particularly important in the Californian system.

Here we present a simple model of the nitrogen and water cycles that incorporates their interactions. We consider the case in which plant growth is solely nitrogen limited and examine the effects of differing water usage and input on competition between two species. We then parameterize the model, using data from a California grassland, and show that at low soil moisture, the annual species should competitively exclude the perennial species because of the effect on nitrogen competition. There are other examples of interactions between resources that create conditions for coexistence, but the effect of water on the nitrogen cycle has, to our knowledge, never been investigated. These two resources are acknowledged to be two of the most important ones driving terrestrial systems, and their interaction is well established. Therefore, we believe that what we investigate here is new and potentially important in terrestrial systems.

Model Description

We set up a simple mechanistic model of the nitrogen and water cycles, as shown in figure 1. All the parameters and variables of the model are defined in table 1. The system
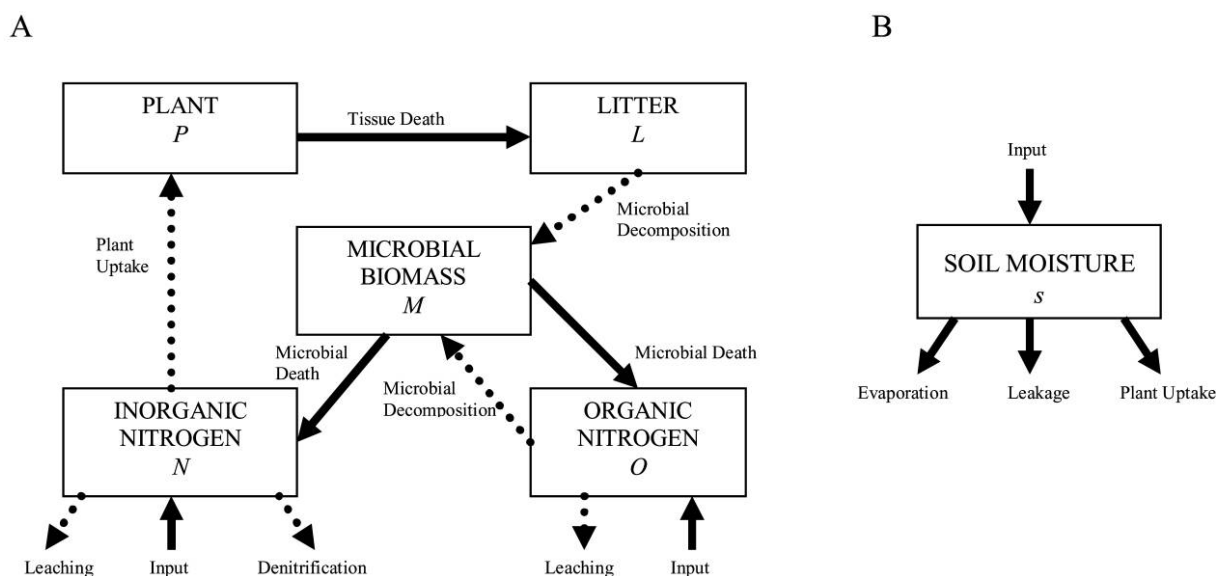

Figure 1: Diagrams of the model. *A*, Nitrogen cycle model. *B*, Water model. The arrows represent fluxes between the pools and into and out of the system. Dotted arrows represent processes that are considered to be water dependent and solid arrows those that are independent of soil moisture.

Table 1: Model parameter and variable definition and units

Parameter/ variable[a]	Dimension/ units	Definition	California estimates Annual	Perennial
N	mg m^{-2}	Inorganic N in the soil		
P	g m^{-2}	Plant biomass in terms of N	26.7	14.9
L	g m^{-2}	Litter biomass in terms of N		
M	mg m^{-2}	Microbial biomass in terms of N		
O	mg m^{-2}	Organic nitrogen in the soil		
N_{conc}	mg m^{-3}	N concentration in the soil moisture	4,515	4,141
I_O	mg m^{-2}	Input of organic N to the ecosystem		
I_N	mg m^{-2}	Input of inorganic N to the ecosystem		
α_O	Dimensionless	Fraction organic N dissolved		
α_N	Dimensionless	Fraction inorganic N dissolved	1	1
s	Dimensionless	Soil moisture	.344	.333
n	Dimensionless	Soil porosity	.66	.66
Z_r	mm	Rooting depth	600	1,500
m_P	day^{-1}	Plant tissue death rate	.016	.005
m_O	day^{-1}	Organic N decomposition rate		
m_M	day^{-1}	Death rate of microbial biomass		
m_L	day^{-1}	Decomposition rate of litter		
a_1	mm day^{-1}	Active uptake efficiency	.0024	37.75
a_2	Dimensionless	Nonlinearity of active uptake with respect to soil moisture	-9.980	.686
a_3	day^{-1}	Plant N demand rate		
γ	Dimensionless	Proportion of microbial death going to organic pool		
K_s	mm day^{-1}	Saturated hydraulic conductivity		
s_h	Dimensionless	Hygroscopic point	.19	.19
s_w	Dimensionless	Wilting point	.27	.27
s_{fc}	Dimensionless	Field capacity	.7	.7
s_{ws}	Dimensionless	Onset of plant water stress	.5	.31
T_{max}	mm day^{-1}	Maximum rate of transpiration	2.6	.81
h	mm day^{-1}	Rainfall	.543	.543
E_w	mm day^{-1}	Maximum rate of evaporation	.27	2.31
d	day^{-1}	Denitrification rate		
W	mm/m^2	Total water in the soil (snZ_r)		
$L(s)$	mm day^{-1}	Leaching rate (eq. [4])		
$T(s)$	mm day^{-1}	Transpiration rate (eq. [3])	.84	.81
$I(s, t)$	mm day^{-1}	Water input rate (eq. [2])	.543	.543

[a] When used with subscripts or superscripts "inv" or "res," the parameter or variable is specifically associated with the invasive or resident species, respectively.

is assumed to be directly limited by a single nutrient resource, nitrogen, while water may indirectly limit plant growth by altering the supply of this limiting nutrient.

First, we consider a monoculture of a plant species. This model is solved to obtain equilibrium values for each of the pools for an individual plant species, and the invasibility of the system is then considered by looking at the growth rate of an invasive plant species under the equilibrium conditions maintained by the resident.

The water dynamics are described on a daily timescale by the following equation, which is based on a model developed by Rodriguez-Iturbe et al. (1999):

$$nZ_r\frac{ds}{dt} = I(s, t) - E_w - T(s) - L(s), \qquad (1)$$

where n is soil porosity, Z_r is rooting depth, s is soil moisture, $I(s, t)$ is the input (the part of rainfall that enters the soil), E_w is the evaporation, $T(s)$ is transpiration, and $L(s)$ is leakage. Soil moisture, s, varies between 0 and 1 and is the proportion of the maximum available space in the soil that is taken up by water. Water is assumed to be spread evenly through the soil (Guswa et al. 2002). We assume and hence investigate competition between species with relatively similar rooting depths. When rooting depths differ widely, as between grasses and trees, other processes, such as hydraulic lift (Caldwell et al. 1998) or water preemption (Weiner and Thomas 1986), would potentially have to be considered. Water input is equal to the daily rainfall, h, if there is enough "space" in the soil to accommodate it; otherwise, it is equal to the available space,

$nZ_r(1 - s)$, and the remainder of the rainfall is lost as runoff:

$$I(s, t) = \min (h, nZ_r(1 - s)). \qquad (2)$$

Transpiration has a maximum rate, T_{max}, when the soil moisture is above the onset of plant water stress, s_{ws}, which is typically around a soil matric potential of -0.03 MPa (Laio et al. 2001). There is no transpiration when soil moisture is below the permanent wilting point, s_w, which is typically assumed to be at a soil matric potential of -1.5 MPa for temperate crops, although it can be as low as -3 or -5 MPa for plants in semiarid environments (Laio et al. 2001). Between the onset of plant water stress and the wilting point, transpiration decreases linearly to 0:

$$T(s) = \begin{cases} T_{max}\dfrac{s - s_w}{s_{ws} - s_w} & s_w \leq s < s_{ws} \\ T_{max} & s_{ws} < s < 1 \end{cases}. \qquad (3)$$

Biomass-dependent transpiration in this model led to unstable dynamics, because of the added interactions between nitrogen concentration in the soil and changes in transpiration rate and the increased number of equilibrium solutions. Therefore, transpiration is assumed to be independent of plant biomass for a given soil area, as in other models (Rodriguez-Iturbe et al. 1999; Porporato et al. 2003; Botter et al. 2008). This assumption is reasonable, because we consider mature stands at equilibrium. A study by Gordon and Rice (1993) on four California annual grassland species showed that species identity is a more important driver of water depletion than is shoot biomass.

Leakage is assumed to have a maximum rate, the saturated hydraulic conductivity, at $s = 1$. It then decreases linearly to 0 as the soil moisture decreases to the field capacity, s_{fc}, remaining at 0 as soil moisture decreases to 0 (Laio et al. 2001):

$$L(s) = \begin{cases} 0 & s_w \leq s \leq s_{fc} \\ \dfrac{K_s(s - s_{fc})}{(1 - s_{fc})} & s_{fc} \leq s \leq 1 \end{cases}. \qquad (4)$$

The nitrogen cycle has been split into five pools—plant P, litter L, soil organic nitrogen O, soil inorganic nitrogen N, and the microbial pool M—to ensure that the effect of soil moisture on the processes occurring in the soil was captured. A rate-of-change equation is associated with each of the pools and is equal to fluxes in minus fluxes out. Change in plant biomass equals plant uptake of N (passive uptake plus active uptake) minus plant tissue death:

$$\frac{dP}{dt} = \frac{\alpha_N N}{W}(T(s) + a_1 s^{a_2}) - m_P P. \qquad (5)$$

Change in litter equals input from plant tissue death minus loss from decomposition of litter:

$$\frac{dL}{dt} = m_P P - m_L L f(s). \qquad (6)$$

Change in organic N equals external N input plus portion of microbial death/decomposition minus uptake of organic N by the microbial biomass minus leached organic N:

$$\frac{dO}{dt} = m_M M \gamma - m_O O f(s) + I_O - \frac{\alpha_O L(s)O}{W}. \qquad (7)$$

Change in microbial pool equals microbial uptake of litter and organic N minus microbial death:

$$\frac{dM}{dt} = m_L L f(s) - m_M M + m_O O f(s). \qquad (8)$$

Change in inorganic N equals external N input plus portion of microbial death/decomposition minus leached inorganic N minus plant uptake of inorganic N minus denitrification:

$$\frac{dN}{dt} = (1 - \gamma)m_M M - \frac{\alpha_N L(s)N}{W}$$
$$+ I_N - \frac{\alpha_N N}{W}(T(s) + a_1 s^{a_2}) - dN. \qquad (9)$$

The plant is considered to be nitrogen limited, and uptake occurs via two pathways: passive and active uptake. Passive uptake (mass flow) is the amount of inorganic nitrogen dissolved in the soil water taken up for transpiration. Active uptake (diffusion) occurs when the nitrogen demand exceeds that supplied by passive uptake, and a local concentration gradient is created that causes diffusion of nitrogen toward the roots (Porporato et al. 2003). Plant uptake is proportional to the concentration of inorganic nitrogen dissolved in the soil water, $\alpha_N N/W$, where W is the amount of water in the active soil depth: $W = snZ_r$. Plant tissue death, at rate m_P, is assumed to be proportional to plant biomass.

Microbial activity is maximized at intermediate soil moisture. Decomposition occurs at a reduced rate when the soil moisture is low, because water is necessary as a transport medium and a resource to the microbes, and when the soil moisture is high and the conditions become anoxic. Decomposition of plant litter, as well as of organic

nitrogen, is decreased from its maximum by a soil moisture–dependent function, $f(s) = 4s(1 - s)$. This function approximates the soil moisture effect on microbial activity, both decomposition and nitrification, as described in Brady and Weil (2002).

Decomposition of the litter and organic nitrogen pools is proportional to the size of the pool, with the rates of decomposition, m_L and m_O, respectively, limited by the soil moisture–dependent function. Microbial death is proportional to the size of the microbial pool, with a proportion γ of the nitrogen going to the organic pool and the remainder $(1 - \gamma)$ going to the inorganic pool. Note that immobilization is included implicitly in the model; movement between the microbial pool and the inorganic pool is modeled as a one-way flow because this is the net movement between the two pools.

Leaching is the amount of organic or inorganic nitrogen dissolved in the water that leaks from the system, that is, the concentration of organic, $\alpha_O O/W$, or inorganic, $\alpha_N N/W$, nitrogen multiplied by the amount of water leaked from the system, $L(s)$. External inputs to the system are assumed to be constant for both the organic, I_O, and inorganic, I_N, nitrogen pools. For simplicity, we ignore N fixation in the system. Denitrification is assumed to occur at a very low rate, independent of soil moisture, and is equal to dN, where d is the denitrification rate. The results remained unchanged when denitrification was dependent on soil moisture.

Competition and Invasion

The equilibrium pool sizes are combined with an invasion criterion to evaluate whether a stand of one species at equilibrium is susceptible to invasion by a second species. The standard invasion criterion is used: if the growth rate of the competitor is positive under the equilibrium conditions of the resident, then the competitor is assumed to be able to invade (e.g., Gurney and Nisbet 1998; Otto and Day 2007). Coexistence occurs if both species can invade the other, multiple stable states if neither can invade the other, and competitive exclusion if only one can invade the other. The growth rate of the invasive species is defined as

$$\frac{dP_{inv}}{dt} = \qquad (10)$$

$$\frac{\alpha_N N^*_{res}}{W^*_{res}}\left(T_{inv}(s^*_{res}) + a^{inv}_1(s^*_{res})^{a^{inv}_2}\right)\frac{P_{inv}}{P^*_{res}} - m^{inv}_P P_{inv},$$

where "inv" refers to the invasive species, "res" to the resident, and i^* to the equilibrium size of pool i. This comes from the growth rate equation for this model (eq. [5]), where environmental conditions (i.e., soil moisture

and nitrogen) are set by the resident ("res") and plant traits (i.e., transpiration, active uptake, and plant death rate) are set by the invasive ("inv"), a standard practice in invasion analysis (Gurney and Nisbet 1998; Otto and Day 2007). We introduced a scaling modification to the N uptake term; it is multiplied by the proportion of biomass that the invasive makes up (P_{inv}/P^*_{res}) to reflect the effect of plant size on uptake.

Model Results

Equilibrium pool sizes were derived by setting the derivatives in equations (5)–(9) to 0 and solving. The resulting equations are shown in appendix A in the online edition of the *American Naturalist*, and simulations indicated that the equilibrium was stable.

In order to survive, each species requires rainfall to be within a certain range. This is dependent on individual effects on the soil moisture, so species with differing maximum transpiration rates will be able to survive for differing rainfall ranges. If these ranges overlap, then the species involved could be in competition with each other.

The model predicts that for a given soil moisture, the species with the higher value of the "competitive index,"

$$C_i = \frac{a_1 s^{a_2} + T(s)}{m_P}, \qquad (11)$$

will outcompete the other species (see derivation in app. A). This is equivalent to

$$C_i = \frac{\text{N in biomass}}{\text{N concentration in the soil}}. \qquad (12)$$

From the first formulation of the competitive index, it is clear that competitive index is strongly dependent on soil moisture. Plant competitive index increases with the species' ability to take up nitrogen passively (transpiration rate $T(s)$ increases) or actively ($a_1 s^{a_2}$ increases) and its ability to retain nitrogen (plant tissue death rate m_P decreases). The identity of the superior competitor can change with soil moisture, because the competitive index is dependent on s. Therefore, the effect of each species on soil moisture constrains the outcome of competition for nitrogen.

Each species has an effect on the soil moisture through its water uptake (transpiration rate $T(s)$), which is seen in the soil moisture equilibrium equation,

Table 2: Competitive outcomes for two species when $T_{max1} > T_{max2}$, so that $s_1^* < s_2^*$

Competitive index at s_1^*	Competitive index at s_2^*	Competitive outcome
SPECIES 1 > species 2	SPECIES 1 > species 2	Competitive exclusion by species 1
species 1 < SPECIES 2	species 1 < SPECIES 2	Competitive exclusion by species 2
SPECIES 1 > species 2	species 1 < SPECIES 2	Multiple stable states
species 1 < SPECIES 2	SPECIES 1 > species 2	Coexistence

Note: Capital letters indicate the species with the higher competitive index.

$$s^* = \begin{cases} (h - E_w)\dfrac{(s_{ws} - s_w)}{T_{max}} + s_w & E_w < h \leq E_w + T_{max} \\[2ex] (h - E_w - T_{max})\dfrac{(1 - s_{fc})}{K_s} & E_w + T_{max} \leq h \end{cases} \quad .$$

(13)

We assume that all soil moisture parameters except maximum transpiration rate T_{max} remain the same between the species. If both species have the same maximum transpiration rate T_{max}, then their soil moisture equilibria will be equal, and the only possible outcome is competitive exclusion. The competitive hierarchy can switch, but there is almost always a clear winner for any rainfall rate. We consider what happens when the species differ in their water use. The outcome is dependent on the competitive index at both the soil moisture equilibrium of species 1, s_1^*, and that of species 2, s_2^*. Without loss of generality, we assume that $s_1^* < s_2^*$, that is, that species 1 has a higher maximum transpiration rate T_{max} than species 2. The outcome for each combination of competitive indices is seen in table 2.

When the species with the higher competitive index differs between s_1^* and s_2^*, the outcome is either multiple stable states or coexistence and is determined by whether each species maintains the soil moisture at a level at which it is more competitive or at a level at which its competitor is more competitive. As the soil moisture level for each species is dependent on rainfall, it is possible to see varying outcomes along a rainfall gradient (fig. 2).

Multiple stable states or coexistence are possible only when one of the following trade-offs holds: (1) one species is better at one method of nitrogen uptake, either passive (higher transpiration rate) or active, and worse at the other; (2) one species is better at overall nitrogen uptake but is worse at maintaining the nitrogen it has (higher tissue death rate). Where passive uptake, active uptake, and nitrogen maintenance differ between the species, then the relative strength of these differences comes into play.

If we consider the graphs of the competitive index (fig. 2 and eq. [11]), we see that the shape is predominantly determined by the active-uptake term and the start and end points by the passive-uptake term and the tissue death rate. With the functions used in this model, it is possible to have no, one, or two points at which two graphs cross. These crossing points indicate the soil moisture levels at which we see multiple stable states or coexistence. If different functions are used, then there may be a different number of switching points; for example, if the active-uptake rate is a linear function of soil moisture, then there would be one or no crossing points.

Comparison with the R^* Competition Rule

The R^* competition rule for one limiting nutrient states that the species that can deplete the limiting nutrient to the lowest availability should exclude the other species (Tilman 1982). In our model, this will be the species with the lowest value of $\alpha_N N^*/W$, the inorganic nitrogen concentration in the soil moisture. While the competitive index increases as $\alpha_N N^*/W$ decreases (eq. [12]), the weaker competitor may not be excluded, because equilibrium plant biomass also affects the competitive index. This model shows that competitive ability is a function of both the ability to deplete a limiting nutrient and total biomass. A resident species with high biomass will suppress the growth of an invasive species and limit the invader's access to a small fraction of the limiting resource. When the same

Figure 2: Competitive dominance as a function of soil moisture (*A–D*), and resulting competitive outcomes along a rainfall gradient (*E–H*). Species S (*solid lines*) has a higher value of maximum transpiration rate T_{max} and so maintains the soil moisture at a lower level than species D (*dashed lines*). *A–D,* Competitive index of each species against soil moisture. The species with the higher competitive index excludes the other species for that soil moisture. *E–H,* Corresponding growth rate of each species when it is an invasive in a stand of the other species, against rainfall. This includes species effects on the soil moisture. Species invade when their growth rate is positive, that is, is above the gray line. The actual competitive outcomes for the system as a whole are indicated by the letters at the top of each plot, delimited by dashed lines. When the growth rates of both species are positive, there is coexistence (*Co*); where both growth rates are negative, there are multiple stable states (*MSS*); and where one is positive and the other negative, there is competitive exclusion by either the species represented by the solid line (*S*) or the species represented by the dashed line (*D*).
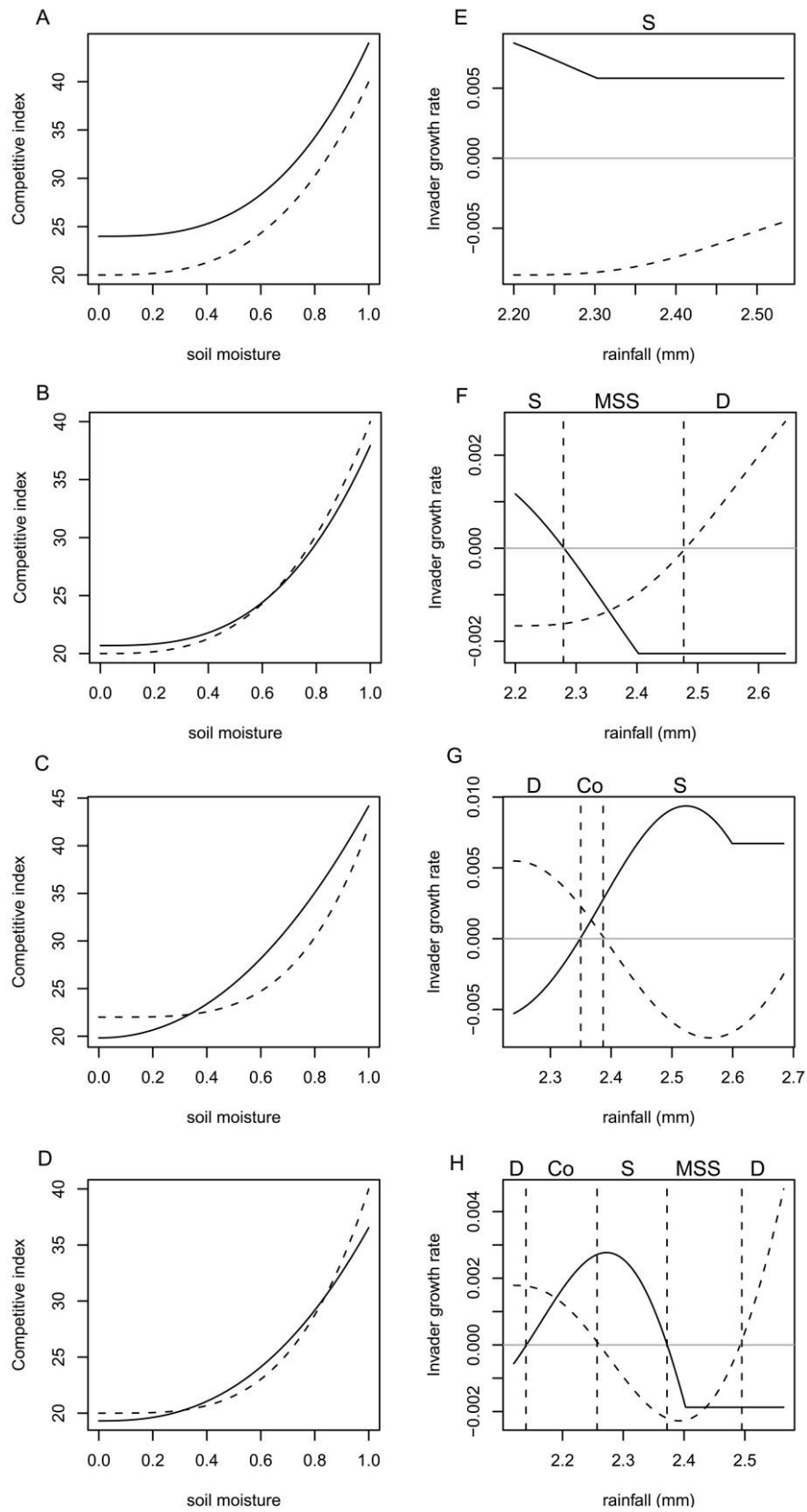
species is invasive, it is increasing the proportion of total biomass that it makes up, compared to the resident, and so decreases the ability of the resident to suppress its growth.

Model Parameterization with Californian Grassland Data

The model was parameterized with data collected from the Sedgwick Reserve in the Santa Ynez Valley, California (34°42′30″N, 120°02′30″W). The climate is Mediterranean, with hot, dry summers and cool, wet winters (Nahal 1981). The annual mean rainfall is 506 mm; however, this is highly variable, as elsewhere in California (Michaelsen et al. 1987). In our study areas, all the native grass species were perennial and all the exotic species were annual (Seabloom et al. 2003*b*), a bias typical of the California grass flora as a whole (Seabloom et al. 2006). The soil is a sandy clay loam. Previous experiments have shown nitrogen and water to be potentially limiting at this site (Seabloom et al. 2003*a*, 2005; Harpole and Tilman 2007).

The data used are from part of a larger mutual invasibility experiment, the full details of which can be found in Seabloom et al. (2003*b*). The goal of this experiment is to empirically mimic the invasibility analysis, as described above (Gurney and Nisbet 1998). Plots were established in the summer of 2000, when native perennial species dominated the 2.5-ha experimental field. Each plot had an experimentally determined initial composition as either exotic annual or native perennial. Species included in the native perennial plots were *Nassella pulchra*, *Elymus glaucus*, and *Poa secunda*. In the case of the exotic annual plots, a short-lived herbicide (Roundup) was applied 1 year before establishment (Seabloom et al. 2003*b*). To ensure the establishment of a dense stand of exotic species, all the seeds of a nearby stand of equal area were added to each of these plots. The three most common species in the annual plots were *Bromus hordeaceus*, *Bromus diandrus*, and *Brassica nigra*.

Half of the initial composition treatments received a supplemental weekly watering to match the 50-year mean rainfall plus 2 SD, which was 854 mm year^{-1}. There were eight replicates for both annuals and perennials, giving a total of 32 5 × 5-m plots. Further experimental details and methods of parameter estimation are in appendix B in the online edition of the *American Naturalist*.

Results from California

Table 1 shows the values of the variables and parameters that have been calculated from the data. We found that the perennial species depleted the soil moisture more than the annuals; by the end of the growing season, this dif-

ference was equal to 0.034 (percent saturation), although it was only marginally significant ($P = .056$). In areas of low or no leaching, the model predicts that the environmental conditions should predominantly determine the level of inorganic nitrogen in the soil, which is what we found in these plots, because the difference between the species in the depletion of nitrate of 0.382 mg kg^{-1} soil (used to calculate the inorganic nitrogen concentration) was not significant ($P = .547$).

While the difference in maximum rates of transpiration between the species is large, the actual transpiration rates at the mean soil moisture are similar, 0.837 and 0.81 mm day^{-1} for the annual and perennial species, respectively. This shows that the annual species have a higher rate of passive nitrogen uptake through higher transpiration. However, the main difference in nitrogen uptake is in active uptake, in which the annual species take up 460 mg m^{-2} day^{-1}, compared to the perennials' 74 mg m^{-2} day^{-1}. This difference is necessary because of the annuals' greater tissue death rate (three times that of the perennials) and higher concentration of nitrogen in their biomass (nearly twice that in the perennial biomass, 26.7 vs. 14.9 g m^{-2}).

Figure 3 shows the competitive indices for each species for a range of soil moisture; the dashed lines show the maxima and minima of the competitive index for each species when the parameter values are varied by ±10%. This demonstrates the robustness of the competitive order—the annual species have a higher competitive index at low soil moisture and the perennials a higher one at high soil moisture—and shows the uncertainty of the switching point of this competitive hierarchy.

Three years after the start of the experimental invasion trials (2003), perennial residents had a significantly higher shoot biomass (+182 g m^{-2} dry weight) in the water addition than the control plots (paired *t*-test, $P = .003$), and the annual invaders had correspondingly lower shoot biomass in the watered plots (−208 g m^{-2} dry weight) but not significantly so (paired *t*-test, $P = .099$). In the plots in which the annuals were the residents, there were no statistical differences due to water addition ($P = .249$ and .427 for perennials and annuals, respectively).

Discussion

By taking into account the well-demonstrated interaction between nitrogen and water cycling, we have shown that it is possible to see coexistence and multiple stable states, as well as competitive exclusion, for two species competing for a single resource, nitrogen, in a temporally invariant, well-mixed environment. The mechanism that generates coexistence is a soil moisture dependence of competitive hierarchy and a plant species-specific effect on soil moisture. Water thus indirectly acts as a limiting factor in the
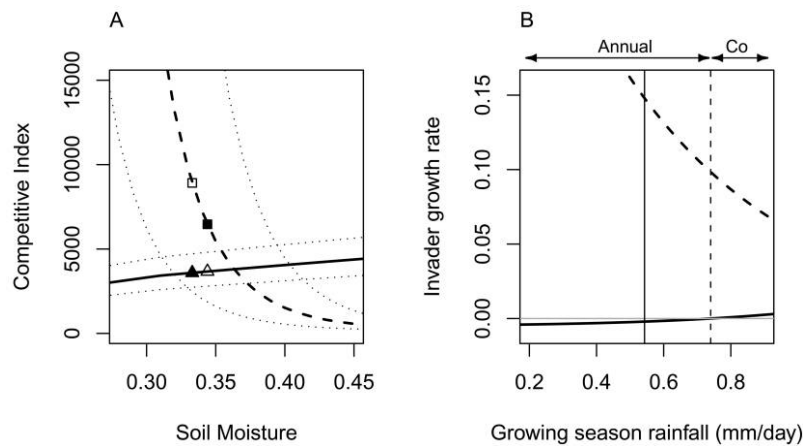
Figure 3: *A*, Competitive indices for the annual (*dashed line*) and perennial (*solid line*) species, with the dotted lines representing the maximum and minimum values of the competitive index when the parameters are varied by $\pm 10\%$. The square points represent the competitive index for the annual and the triangular points represent that for the perennial, as a resident (*filled symbols*) and as an invasive (*open symbols*), at the soil moistures seen at Sedgwick. *B*, Growth rates of the annual (*dashed line*) and perennial (*solid line*) as an invasive for a rainfall gradient through the growing season (see app. B in the online edition of the *American Naturalist* for details on the calculation). The solid vertical line represents the 2001 rainfall at Sedgwick (0.543 mm day^{-1}) and the dashed vertical line the switching point from competitive exclusion by the annual to coexistence (0.74 mm day^{-1}). *Annual* indicates the region in which the annual is expected to be dominant and *Co* the region of coexistence.

sense of Levin (1970) and Armstrong and McGehee (1980), because it indirectly affects growth through its effect on the uptake of the limiting resource, nitrogen. Water addition would thus affect growth because of its effect on nitrogen uptake; although water per se would not be limiting, the results of a water addition experiment could conclude that water is limiting.

It is likely that competitive hierarchies are mediated by soil moisture in many systems. Using a very different model, Craine et al. (2005) showed that R^* was indeed dependent on soil moisture. In the field, different plant species are found along soil moisture gradients (Pickett and Bazzaz 1976; Adams and Anderson 1980; Cabido et al. 1993; Richards et al. 1995). Plant species are also known to differ in their water use, with water use efficiency varying between co-occurring species (Field et al. 1983; Ehleringer and Cooper 1988). Some species use available shallow water conservatively, while others exploit deeper water sources (Fitter and Hay 2002). Consequently, species effects on soil moisture also vary (Gordon and Rice 1993), with differences between annual and perennial grass species seen in deep-soil moisture depletion (Seabloom et al. 2003*b*) and uptake after a rain event (Gebauer and Ehleringer 2000). A limitation of this model is that it does not include differences in rooting depth, and therefore the influence of spatial differences in water use are not seen.

Multiple stable states or coexistence arises when the competitive hierarchy changes along a soil moisture gradient. Transpiration must differ between the species so that

each has a different soil moisture equilibrium. The existence of a trade-off either between the two nitrogen uptake rates or between nitrogen uptake and maintenance in the plant ensures that the competitive hierarchy changes along the moisture gradient. Whether the trade-off results in coexistence or multiple stable states depends on whether species' effects on soil moisture favor themselves (multiple stable states) or their competitors (coexistence).

Differing mineralization rates between species and changes in nitrogen deposition would alter the equilibrium pool sizes in the model; however, there would be no change in the competitive outcomes, assuming that the system remains N limited. This is because the inorganic nitrogen level and plant biomass respond in the same way; an increase in the available nitrogen increases the plant biomass, and hence the nitrogen available to the invasive species remains relatively the same.

The results from the model using the parameters derived from the Sedgwick experiments show that the annual species should competitively exclude the perennial species at the mean soil moistures seen during the 2001 growing season (fig. 3). The model predicts that annuals should dominate at low soil moisture and that perennials should dominate at high soil moisture (fig. 3). As each species harbors soil moisture conditions more favorable to its competitor, the competitive outcome is restricted to either competitive exclusion or coexistence and depends on the rainfall level. This contrasts with the competitive output expected if only competition for water or nitrogen were

considered; the conclusion then would be that the perennial species should dominate because it can reduce these two resources to a lower level than can the annual, highlighting the potential importance of this mechanism in this system.

The annual species has a higher plant biomass and a higher inorganic nitrogen concentration in the soil (table 1). It is the difference in plant biomass that dominates the outcome at the observed soil moisture levels and lower. The annual species are better than the perennial species at active uptake and hence have a higher plant biomass and can therefore successfully suppress the growth of the perennial species. The annual species' active-uptake rate decreases as the soil moisture increases, while the perennial species have an increasing active-uptake rate. This behavior is a result of the opposite signs for a_2, the exponent of soil moisture in the active-uptake term (table 1). At higher soil moisture, the perennial has a higher competitive index than the annual. The perennial can obtain enough nitrogen, even in the presence of the annual, to invade or to resist the invasion of the annual. If the outcome of competition is still determined by nitrogen at this point, then the perennial will become competitively dominant and should exclude the annual.

The outcome of the field trials partially matched model predictions but were inconclusive as to the competitive hierarchy of species. Watering increased the biomass of perennial residents and decreased the success of annual invaders; however, we did not observe complementary effects when perennials were invading resident stands of annuals. In addition, we did not observe the competitive exclusion predicted by the model, either because species can actually coexist or because the time frame of the experiment was not long enough to see the long-term competitive outcome. In our model, there is uncertainty surrounding the actual soil moisture range that promotes coexistence. The model predicts that the transient dynamics are likely to be complicated, with competitive dominance switching between the species in the growing season and interannually with rainfall variations.

Rout and Callaway (2009) put forward two mechanisms through which nonleguminous invasive species may increase soil nitrogen and primary productivity: (1) rapid natural selection in the invaded range for key leaf traits that affect the N cycle and (2) the microbial communities interact in a different way with the invasive species than with the native species and so cause changes in the N cycle. Our model highlights a different mechanism through which invasive species may increase soil nitrogen, namely, by affecting the soil moisture.

Other mechanisms can favor invasive species, such as the enemy release hypothesis (Keane and Crawley 2002), feedbacks with microbial communities (Rout and Callaway 2009), hydraulic redistribution (Caldwell et al. 1998), and resource preemption (Weiner and Thomas 1986). Recent work also suggests that generalist viral pathogens may broaden the region of coexistence between annual and perennial grasses through apparent competition (Borer et al. 2007), a mechanism not included in our model. Species parameters that we estimate (e.g., plant tissue death and litter decomposition rate) should be affected by factors such as the level of herbivory that a species experiences in the field. Thus, facilitation through enemy release is not incompatible with the mechanism we highlight and might actually play a role in the higher competitive ability of the exotic species.

Our model results are concordant with larger biogeographic patterns of invasion in the Pacific states of the United States. Most of the hot and dry interior-valley grasslands in California have been heavily invaded by exotic annual grasses (Heady 1977; Sawyer and Keeler-Wolf 1995; Keeler-Wolf et al. 2007). In contrast, the cooler and moister coastal prairies in northern California are dominated by perennial grasses (Sawyer and Keeler-Wolf 1995; Keeler-Wolf et al. 2007), as are the wet interior-valley grasslands of Oregon and Washington (Franklin and Dyrness 1973). Our results are also consistent with the suggestion that drought was a contributor to the initiation of the invasion of the Californian grasslands by these annual species (Jackson 1985; D'Antonio and Vitousek 1992).

Our conclusions suggest that an attempt to restore native perennial grasses to this system is likely to result in an exotic-dominated or mixed community if the rainfall and soil moisture regime remains at its current level. The projections of precipitation and soil moisture due to climate change in this area are uncertain. Variability in rainfall is predicted to increase, but the direction of change of mean amount depends on the global climate model and emissions scenario used (Li et al. 2007; Maurer 2007). We expect that if the conditions become wetter, perennials will become more competitive, and if they become drier, the annuals should become more competitive.

The mechanisms highlighted in this model are likely to be applicable to any nitrogen-limited system in which species differ in their water use. This mechanism is likely to be important in the competition between annual and perennial grasses, as in California. Another possible candidate system where this mechanism is likely to be important is savannas. Explaining tree-grass coexistence in savannas is an unsolved problem in ecology (Scholes and Archer 1997; Sankaran et al. 2004). Nitrogen cycling and nitrogen limitation have been shown to be important in savanna systems (Scholes and Archer 1997; Bustamante et al. 2006). Trees and grasses differ in their effects on soil moisture through transpiration, effects on evaporation of shading, and hydraulic redistribution. Thus, the essential ingredi-

ents for this mechanism, namely, nitrogen limitation and species-specific effects on soil moisture, occur in savanna systems and could play a role, along with other mechanisms usually considered, such as differential response to fire and grazing.

This simple model, by its nature, ignores many important features of the real world in order to remain analytically tractable and interpretable. This allows us to show that the interaction of nitrogen and water in the soil can be very important in determining the outcome of competition. These results show that even simple interactions in the soil that are influenced by plants can play an important role in determining species composition and should not be ignored in designing and interpreting experimental studies. They particularly highlight the importance of water availability in transporting nutrients for species competition, and they are consistent with general patterns of N and water colimitation across large biogeographic gradients of precipitation (Kirchner 1977; Lauenroth and Dodd 1978; Hooper and Johnson 1999). The main mechanisms that produce the results highlighted in this article, namely, soil moisture dependence of competitive hierarchy and a plant species-specific effect on soil moisture, are likely to be extremely general and robust to the model's formulation. Therefore, we expect soil moisture–mediated coexistence or competitive exclusion to be likely in nature.

More generally, we have shown that linkages between potentially limiting resources can dramatically alter the predictions of resource competition theory. In natural systems, many important nutrients covary because their supply rates are directly linked (as is the case between nitrogen and water) or are driven by a common external driver (e.g., pH). Exploring the effects of the mechanistic links between limiting resources will likely broaden the applicability of resource competition theory to real ecosystems.

Acknowledgments

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Field experiments at Sedgwick Reserve, California (photograph by Eric Seabloom).