The long-term relationship between plant diversity and total plant biomass depends on the mechanism maintaining diversity

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The relationship between plant diversity and total plant biomass is of great current interest in ecology. Niche differences among plants are widely thought to promote both plant coexistence, and higher biomass in more diverse polycultures. Using simple mechanistic models, I demonstrate that not all niche differences among plants are equally likely to promote high total biomass in polyculture. In particular, transgressive overyielding (when a polyculture of plants outperforms any monoculture) occurs for a wide range of parameter values when plants coexist in polyculture due to differences in resource use. Transgressive overyielding occurs only for a limited set of parameter values when specialist herbivores mediate plant coexistence, and is impossible when generalist herbivores mediate coexistence. Niche differences among plants promote high biomass in polyculture only when plants coexist in polyculture at the expense of other trophic levels – that is, by converting into biomass resources that would otherwise be bound in herbivores, or exist in a free state. A major challenge for future work will be to identify the joint consequences of different coexistence mechanisms for plant diversity and ecosystem performance.

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The relationship between the diversity of an ecosystem and the way in which it functions has emerged as a central issue in ecology (reviewed by Loreau et al. 2001). Besides being of fundamental interest, this issue is of great practical relevance because human activities are causing historically high extinction rates (Pimm et al. 1995). Depauperate ecosystems might not be able to perform all the functions on which humans depend (Loreau et al. 2001).

Current debate about the relationship between biodiversity and ecosystem function focuses on how the number of locally coexisting plant species affects standing plant biomass, primary productivity, and nutrient retention (Loreau et al. 2001). This focus is a natural starting point because plants are a dominant component of most ecosystems and because plant biomass, primary productivity and nutrient retention are under direct plant control. Laboratory experiments with algae as well as greenhouse and field experiments with grasses often find that increasing producer diversity increases producer biomass and productivity (Bell 1991, Naeem et al. 1996, Hector et al. 1999, Tilman et al. 2001, Fridley 2002, but see Bell 1990, Hooper and Vitousek 1997), although the reality and interpretation of these increases has been hotly debated (Huston 1997, Loreau et al. 2001, Huston and McBride 2002).

Current theory largely attributes the increased performance of more diverse ecosystems to differences in resource use among plants (Tilman et al. 1997a, Loreau 1998a). Differences in resource use are thought not only to maintain diversity (Tilman 1982, McKane et al. 2002), but also to allow more diverse plant communities to make more complete use of available resources, thereby producing higher total biomass (Tilman et al. 1997a, Loreau 1998a). The current focus on resource use raises the question of whether other niche differences among plants also promote increasing total biomass with increasing diversity. Intuition, heuristic
arguments, and some phenomenological models suggest that any niche difference among plants should promote more complete use of the available “niche space,” thereby increasing total biomass and productivity (Tilman et al. 1997a, Cardinale et al. 2000, Chesson et al. 2002, Mouquet et al. 2002). Loreau and Hector (2001) proposed a method for quantifying the contribution of niche differences to total biomass, independent of knowledge of which niche differences maintain diversity.

However, whether increasing plant diversity increases total plant biomass depends on the species involved and the environmental conditions (Bell 1990, Hector et al. 1999, Fridley 2002). Further, other species can alter the relationship between producer diversity and ecosystem function (van der Heijden et al. 1998, Mülder et al. 1999, Naeem et al. 2000). Changes in diversity on all trophic levels can alter ecosystem performance (Naeem et al. 1994, McGrady-Steed et al. 1997, Naeem and Li 1997, Downing and Leibold 2002). These empirical results highlight the importance of understanding the mechanisms by which plants interact within food webs in order to understand the effects of plant diversity on total plant biomass.

Here I use three simple mechanistic food web models, focusing on differential resource use and herbivory, to examine how the effect of plant diversity on total plant biomass depends on the mechanism of coexistence among plants. I first briefly consider a model of differential use of essential resources (e.g. nitrogen and phosphorus, León and Tumpson 1975, Tilman 1982). Tilman et al. (1997a) also predicted total plant biomass from a model of differential resource use. However, their model contained spatial heterogeneity, making its behavior difficult to compare to that of the other models I consider (see below). I focus on a somewhat simpler version in order to isolate the effects of differences in resource use.

I then consider two models of herbivore-mediated coexistence. One model incorporates specialist herbivores (Grover 1994), the other generalist herbivores (Leibold 1996). Consideration of herbivory is important because both specialist and generalist herbivores can strongly affect plant diversity and composition (Proulx and Mazumder 1998, Carson and Root 2000, Chase et al. 2000a). In particular, herbivory typically increases plant diversity in moderately- to highly-enriched habitats (Proulx and Mazumder 1998). Previous analyses of these herbivory models have focused on how plant traits and environmental conditions interact to determine plant diversity and composition (Grover 1994, Leibold 1996). Here I focus on the consequences of plant diversity and composition for total plant biomass.

In analyzing each model I pay particular attention to the consequences of resource enrichment. The supply of limiting resources ultimately constrains the total amount of biomass an ecosystem can support. Changes in diversity will affect what fraction of the available resource supply is converted into biomass, and how that biomass is partitioned among species. The effects of enrichment on various aspects of community structure, including food chain length (Lindeman 1942, Oksanen et al. 1981), stability (Rosenzweig 1971), and diversity (Grime 1973, Tilman 1982), have long been of fundamental interest in community ecology. These effects of enrichment are also of great practical interest because human activities have increased the input rates of several limiting resources (particularly nitrogen) into the environment (Vitousek et al. 1997). Theoretical and empirical studies of the relationship between plant diversity and ecosystem performance have rarely considered the effects of resource enrichment (but see Fridley 2002), or how those effects might depend on the mechanism(s) of plant coexistence.

While the models I consider are obviously too simple to be quantitatively correct descriptions of any particular system, simple models are analytically tractable and can help sharpen our intuitions and focus our questions. Further, each of the models examined here is sufficiently complex to predict various experimental outcomes, depending on parameter values. More complex models would only broaden the range of possible outcomes. A simple model can serve as a base upon which more elaborate models can be built, and can help us understand the behavior of more elaborate models (Schwinning and Parsons 1996).

I use each model to predict the long-term (equilibrial) outcome of a standard experiment manipulating the initial diversity (species richness) of plants in a community and examining the effect on total plant biomass (Bell 1990, 1991, Naeem et al. 1996, Hector et al. 1999, Tilman et al. 2001). Experimental units receive an inoculum of species chosen at random from a larger pool of species, with the number of species varying among units. Each level of plant diversity (initial species richness) comprises a number of different, randomly selected plant compositions, so that any effect of plant diversity is not confounded with plant composition. The lowest diversity level comprises monocultures of every species in the pool. I consider models with two plant species, and so the standard experimental design requires three treatments: plant species 1 and 2 alone (monocultures), and both species together (polyculture). I consider only equilibrial biomasses because the effect of biodiversity on ecosystem function in a variable environment is a large problem that the models presented here are not designed to address (Norberg et al. 2001).

Real experiments typically involve more than two species, but the two-species case of each model is a useful starting point for several reasons. First, many current ideas about the relationship between plant diversity and total plant biomass are based on consideration of only a few species (Loreau 1998b, Cardinale et
Second, the two-species case of each model is analytically tractable, and acts as a limiting case for the behavior of more speciose models. Third, the two-species version of each model might be expected to capture many (though by no means all) aspects of the dynamics of more speciose models. For instance, Leibold (1996) and Tilman et al. (1997a) incorporated spatial heterogeneity into two of the models analyzed here, thereby allowing an unlimited number of plant species to coexist. Both Leibold (1996) and Tilman et al. (1997a) found that addition of spatial heterogeneity did not reveal any qualitatively new behavior not displayed by two-species models. Fourth, the fact that two-species models can predict the qualitative behavior of more speciose models suggests that two-species models might also predict the qualitative outcomes of more speciose experiments. Indeed, the two-species models analyzed here are capable of reproducing a number of qualitative trends in plant diversity and composition along natural enrichment gradients. For instance, simple models of generalist herbivory (Leibold 1996) predict (a) maximal plant diversity at intermediate enrichment levels, (b) correlated increases in biomass on all trophic levels with increasing enrichment, and (c) that herbivory will shift plant composition towards herbivore-resistant species, particularly in highly-enriched systems. Many comparative and experimental studies support one or more of these predictions (Grime 1973, Tilman 1982, Leibold et al. 1997, Proulx and Mazumder 1998, Leibold 1999, Carson and Root 2000, Chase et al. 2000a, Dodson et al. 2000). However, the ability of two-species models to predict the qualitative outcomes of plant diversity manipulations may well be limited for several reasons. In particular, a two-species model cannot generate a non-monotonic relationship between plant diversity and total plant biomass, as observed by Hooper and Vitousek (1997) and at some sites by Hector et al. (1999).

All three models can predict a variety of relationships between initial plant diversity and total plant biomass depending on parameter values, but not all parameter values are equally realistic. For each model I focus only on those parameter values that permit stable coexistence of both plants in polyculture. I focus on parameters permitting coexistence because experimental polycultures rarely collapse to a single species (Bell 1990, 1991, Hector et al. 1999, Tilman et al. 2001). Future work examining parameters for which diversity is not maintained would provide an informative contrast to the cases examined here.

Within the region of parameter space permitting coexistence, I ask two questions for each model. First, under what conditions does total plant biomass in polyculture exceed that expected based on a weighted average of monoculture biomasses (non-transgressive overyielding, Trenbath 1974)? If we denote the biomass of species i in monoculture by $M_i$ and its biomass in polyculture by $P_i$, then the relative yield (RY) of species i is $R_Y = P_i/M_i$. The relative yield total (RYT) of the polyculture is given by $RYT = \sum_i R_Y_i$, where summation is over all i species. Non-transgressive overyielding is defined by $RYT > 1$, indicating that any proportional decline(s) in the yield(s) of one (or more) species in polyculture compared to monoculture is more than compensated by proportional increase(s) in the yield(s) of other species. Non-transgressive overyielding indicates that interspecific interactions have a role in determining the total performance of a polyculture, but does not imply that high performance requires high biodiversity (Loreau 1998b).

Second, I ask under what conditions does total plant biomass in polyculture exceed that of the best monoculture (transgressive overyielding, Trenbath 1974)? Transgressive overyielding is thought to require strong niche differentiation, so that maximizing ecosystem performance would require maintenance of high diversity (Tilman et al. 2001).

Coexistence due to differential resource use

I consider the dynamics of two plant species, $N_i$ ($i = 1, 2$) competing for two essential resources, $R_j$ ($j = 1, 2$) (León and Tumpson 1975, Tilman 1982). Examples of essential resources include nitrogen and phosphorus, both of which are required for plant growth. The model neglects complexities such as spatial structure to focus on the consequences of a trade-off between the resource competitive abilities of the two plants, so that each is the superior competitor for a different resource. The model is defined by

$$\frac{dR_j}{dt} = D(S_j - R_j) - \sum_i u_{ij}N_iR_j$$  \hspace{1cm} (1a)

$$\frac{dN_i}{dt} = N_i \left[ \min \left( \frac{u_{ij}R_j}{c_{ij}} \right) - m_i \right]$$  \hspace{1cm} (1b)

where $u_{ij}$ is the per-unit uptake rate of resource j by plant species i, $c_{ij}$ is a conversion factor of units of resource j into units of plant i, and $m_i$ is the per-unit mortality rate of plant species i. Resource j is supplied from an external source at incoming concentration $S_j$ and dilution rate D, and leaves the system at the same rate. Inflow concentration $S_j$ can be viewed as a measure of enrichment of resource j (Tilman 1982). Note that the assumed form of resource supply may be more appropriate for mineral nutrients than for light, since the supply of light has an inherent directionality (but see Stevens and Carson 2002). The assumption of spatial homogeneity may be more appropriate for aquatic algae than terrestrial plants, but the model is neverthe-
less adequate for illustrating some of the possible effects of herbivores and enrichment in both aquatic and terrestrial systems. The minimum function in (1b) arises because, when a plant consumes two essential resources, its growth rate will be a function of the availability of the resource that most constrains growth (León and Tatum 1975). Stable coexistence of both plants in polyculture requires that each be limited by a different resource (León and Tatum 1975), which in turn requires that neither resource be supplied at a much lower concentration than the other (Tilman 1982).

The behavior of (1) near equilibrium is well-approximated by the Lotka-Volterra competition equations (Tilman 1982), allowing analyses of overyielding in Lotka-Volterra competition communities (Hughes and Roughgarden 2000, Pacala and Tilman 2002) to be reinterpreted in mechanistic terms. I assume without loss of generality that plant species i is limited by resource j = i in both monoculture and polyculture, and that resource dynamics are fast relative to plant dynamics. We can now rewrite (1b) in the usual Lotka-Volterra form, with equilibrial polyculture biomasses given by

\[ N_{1(12)} = \frac{K_i - \alpha_{i2}K_2}{1 - \alpha_{i2}\alpha_{21}} \]  
\[ N_{2(12)} = \frac{K_j - \alpha_{j2}K_1}{1 - \alpha_{j2}\alpha_{21}} \]  

where \( N_{i(12)} \) is the equilibrial biomass of plant species i in a polyculture containing both species 1 and 2, \( K_i \) is the carrying capacity (= equilibrial monoculture biomass) of plant i, and \( \alpha_{ij} \) is the competition coefficient of plant j on plant i (Tilman 1982). The carrying capacities and competition coefficients are related to the parameters of (1) as

\[ \alpha_{12} = \frac{u_{21}}{u_{11}} \]  
\[ \alpha_{21} = \frac{u_{12}}{u_{22}} \]  
\[ K_i = \frac{D}{u_{i0}} \left( \frac{S_i}{R_i} - 1 \right) \]  

where \( R_i = \frac{m_i}{u_{i0}} \) is the amount of resource j required by plant i to maintain a population in monoculture (Tilman 1982).

Stable coexistence guarantees non-transgressive overyielding. Non-transgressive overyielding is defined by

\[ RY_1 + RY_2 = \frac{K_1 - \alpha_{12}K_2}{(1 - \alpha_{12}\alpha_{21})K_1} + \frac{K_2 - \alpha_{21}K_1}{(1 - \alpha_{12}\alpha_{21})K_2} > 1 \]  

which after some tedious algebra reduces to the requirement for stable coexistence. Stable coexistence does not guarantee transgressive overyielding. Transgressive overyielding is defined by

\[ N_{1(12)} + N_{2(12)} = \frac{K_1 - \alpha_{12}K_2 + K_2 - \alpha_{21}K_1}{1 - \alpha_{12}\alpha_{21}} > \max(K_i) \]  

Assume without loss of generality that \( K_1 \geq K_2 \). Then (5) reduces to

\[ \alpha_{21}(\alpha_{12} - 1) + \frac{K_j}{K_i}(1 - \alpha_{12}) \geq 0 \]  

which holds if and only if \( \alpha_{12} < 1 \), since \( \alpha_{21} < K_2/K_1 \) is required for stable coexistence. Inequality (6) essentially requires that each species take up the resource that limits the other species’ growth at a sufficiently low rate for transgressive overyielding to occur. This requirement is more stringent, the greater the difference between species’ carrying capacities. Carrying capacities reflect rates of resource supply (as well as other parameters; see Eq. 3c), and generally approach equality at a resource supply ratio \( S_1/S_2 \) near the midpoint of the range of ratios allowing coexistence (Tilman 1982). Fig. 1 illustrates the behavior of (1) along a resource supply ratio gradient. This is the most useful way of illustrating the behavior of (1), since the resource supply ratio determines the species’ carrying capacities, and therefore the potential for coexistence and transgressive overyielding.

While the resource supply ratio determines the potential for transgressive overyielding, the absolute rates of

![Fig. 1. Equilibrial monoculture biomass of each plant species (\( N_1 \) and \( N_2 \)), and total polyculture biomass, in the differential resource use model along a resource ratio (\( S_1/S_2 \)) gradient produced by varying \( S_1 \) while \( S_2 = 18 \) was held constant. In the hatched regions stable coexistence in polyculture is impossible. Parameter values are \( D = m_1 = m_2 = 0.05 \), \( u_{i0} = u_{21} = 1.5 \), \( u_{12} = u_{21} = 0.5 \), \( c_1 = c_2 = 10 \), \( c_{12} = c_{21} = 5 \). Parameter values are arbitrary and intended for illustration only. Results are from analytical model solutions.](image)
resource supply determines the absolute magnitude of overyielding. Both the monoculture and polyculture biomasses of species i are directly proportional to $S_i$, and polyculture biomass of species i is inversely proportional to the inflow concentration of the resource that limits its competitor’s growth (2–3). For a given resource supply ratio $S_1/S_2$, the absolute value of the difference between polyculture biomass and the biomass of the best monoculture will increase with the absolute magnitudes of $S_1$ and $S_2$ (2–3). The ratio of polyculture biomass to that of the best monoculture depends on the ratio of $S_1$ to $S_2$, rather than their absolute magnitudes.

Coexistence due to specialist herbivory

Grover (1994) modelled the dynamics of primary producers competing for a shared limiting nutrient resource $R$ and consumed by an herbivore $H$. I consider a special case with just two plant species, $N_1$ and $N_2$, and linear functional responses. Non-linear functional responses would not qualitatively alter the results presented here, unless the non-linearity led to non-equilibrial dynamics at high enrichment levels (Grover 1994). The model focuses on the consequences of a trade-off between competitive ability and herbivore resistance. Plant species 1 is consumed by the (specialist) herbivore, while species 2 is not. The invulnerability of species 2 comes at the cost of being an inferior competitor for the limiting resource. Many examples of such trade-offs are known in plants (Chase et al. 2000b). The model is defined by

$$\frac{dR}{dt} = D(S - R) - u_1RN_1 - u_2RN_2 \quad (7a)$$

$$\frac{dN_1}{dt} = N_1(u_1c_1R - m_1 - fH) \quad (7b)$$

$$\frac{dN_2}{dt} = N_2(u_2c_2R - m_2) \quad (7c)$$

$$\frac{dH}{dt} = H(feN_1 - m_H), \quad (7d)$$

where $u_i$ is the per-capita resource uptake rate of plant species i ($i = 1, 2$), $c_i$ is the conversion efficiency of plant species i, $m_i$ is the per-capita mortality rate of plant species i, $f$ is the per-capita feeding rate of the herbivore on plant species 1, and $e$ is the conversion efficiency of the herbivore, and $m_H$ is the per-capita mortality rate of the herbivore. The resource is supplied from an external source at incoming concentration $S$ and dilution rate $D$, and leaves the system at the same rate.

Equilibrial biomass of plant species 1 in monoculture is found by setting $N_2 = 0$, and then setting (7a, b, d) equal to zero and solving for $N_1$. This procedure yields

$$N_{1*}^* = \frac{m_H}{fe} \quad (8)$$

where $N_{1*}^*$ denotes the equilibrial biomass of plant species i in a monoculture of species i. Note that a monoculture of plant species 1 will also contain herbivores. Equilibrial biomass of plant species 2 in monoculture is found by setting $N_1 = 0$, and then setting (7a, c, d) equal to zero and solving for $N_2$, giving

$$N_{2*}^* = \frac{D(u_2c_2S - m_2)}{u_2m_2} \quad (9)$$

Note that monocultures of (inedible) species 2 do not support herbivores. The equilibrial biomasses of species 1 and 2 in polyculture are found by setting (7a–d) equal to zero and solving for $N_1$ and $N_2$. Species 1 attains the same biomass in monoculture and polyculture (i.e. $N_{1*}^* = N_{1*}^{1*}$). The equilibrial biomass of species 2 in polyculture, $N_{2*}^{12}$, is

$$N_{2*}^{12} = \frac{D(u_2c_2S - m_2)}{u_2m_2} - \frac{u_1m_H}{u_2fe} = N_{2*}^* - \frac{u_1N_{1*}^*}{u_2} \quad (10)$$

The derivations of (8–10) all assume a sufficiently high enrichment ($S$) level. This enrichment level can be found by solving (10) for the value of $S$ just sufficient for $N_{2*}^{12} > 0$ (Grover 1994). The derivations of (8–10) also assume that species 1 outcompetes species 2 in the absence of herbivores, which requires

$$\frac{m_1}{u_1c_1} < \frac{m_2}{u_2c_2} \quad (11)$$

Equation (11) defines an $R^*$ rule (Tilman 1982). In the absence of herbivores, plant species 1 reduces the resource to a lower level than can species 2, thereby competitively excluding species 2.

Stable coexistence guarantees non-transgressive overyielding, since species 1 attains the same biomass in monoculture and polyculture (i.e. $RY_1 = 1$) and $RY_2 > 0$. In the specialist herbivore model, increases in enrichment beyond threshold for coexistence of both plants in polyculture simply increase the biomass of species 2. Species 2 is an invulnerable competitor which “siphons off” surplus resources that would otherwise accumulate in herbivores, or exist in a free state (Grover 1994).

Transgressive overyielding is defined by

$$N_{1*}^{12} + N_{2*}^{12} > \max(N_{1*}^*, N_{2*}^*) \quad (12)$$

Inequality (12) simplifies to the requirement that
Inequality (13) states that species 2 takes up resources at a higher per-unit rate than species 1. The ratio \( \frac{u_2}{u_1} \) acts as a competition coefficient (see Eq. 10), and transgressive overyielding occurs when this coefficient is < 1.

Note that satisfaction of (13) implies that species 1 would attain a higher monoculture biomass than species 2 if herbivores were removed from the system, since satisfaction of (11) is required for coexistence (Tilman et al. 1997a). Tilman et al. (1997a) provide a thorough analysis of the outcome of herbivore-free biodiversity experiments in the case when the plant that attains the highest biomass in monoculture also excludes all other species from polyculture (as species 1 would in the absence of herbivores). In the absence of herbivores the performance of polycultures relative to monocultures would be determined simply by a "sampling" or "selection" effect for species 1: all polycultures, but only some of the monocultures, contain this dominant species (Tilman et al. 1997a, Loreau and Hector 2001).

Transgressive overyielding with specialist herbivores occurs when a selection effect that would operate in the absence of herbivores combines with niche differences that operate in the presence of herbivores. Niche differences can permit species 2 to coexist with species 1 at sufficiently high biomass to generate transgressive overyielding. However, even in the absence of transgressive overyielding, stable coexistence of both plants at equilibrium implies that they have different niches (Levin 1970, Leibold 1995, Chesson 2000), so that niche differentiation contributes to the relationship between plant diversity and total biomass.

Fig. 2 illustrates the behavior of (7) along an enrichment gradient, for parameters permitting transgressive overyielding (Fig. 2A), and for parameters that do not permit transgressive overyielding (Fig. 2B).

**Coexistence due to generalist herbivory**

I again consider the dynamics of two plant species, \( N_i \) (\( i = 1,2 \)) competing for a single abiotic resource \( R \), but now both plants experience herbivory from a generalist herbivore \( H \). Plants still vary in vulnerability to herbivores, but neither is invulnerable (Leibold 1996). The model is defined by

\[
\begin{align*}
\frac{dR}{dt} &= D(S - R) - \sum_i u_i R N_i \\
\frac{dN_i}{dt} &= N_i(u_i c_i R - m_i - f_i H) \\
\frac{dH}{dt} &= H \left( \sum_i f_i e_i N_i \right) - m_H
\end{align*}
\]

where the resource is supplied in chemostat fashion at dilution rate \( D \) and inflow concentration \( S \), \( u_i \) is the per-unit resource uptake rate of plant species \( i \), \( c_i \) is the efficiency with which plant species \( i \) converts resource into biomass, and \( m_i \) is the per-unit density-independent mortality rate of plant species \( i \). Parameters \( f_i \) and \( e_i \) respectively define the per-capita feeding rate and conversion efficiency of the herbivore on plant species \( i \), and \( m_H \) is the density-independent mortality rate of the herbivore. Equation (14) reduces to Eq. (7) when \( f_i = 0 \).

As our concern is with the effects of herbivory on coexistence and total plant biomass, I restrict attention to cases where the herbivore can persist at equilibrium on either plant species alone, or both together. This requires a trade-off among plants between resource competitive ability and ability to sustain or withstand herbivory, and an intermediate enrichment level (Leibold 1996). At low enrichment levels, herbivores are rare or absent and the more competitive plant (assumed without loss of generality to be species 1) excludes the less competitive plant, as in the specialist herbivore model. However, at high enrichment levels abundant generalist herbivores generate strong apparent competi-
tion between the two plants (Leibold 1996). The species better able to resist or tolerate herbivory (assumed to be species 2) excludes the other species.

Equilibrial biomass of plant species i in monoculture is determined by setting the biomass of the other species equal to zero, setting (14) equal to zero, and solving for \( N_{i0}^* \). This procedure yields

\[
N_{i0}^* = \frac{m_i}{f_i e_i}
\]  

(15)

Setting (14) equal to zero and solving provides the equilibrial biomass of each plant in polyculture, given by

\[
N_{i(12)}^* = \frac{f_i e_i D \left( \frac{S}{R_{i(12)}^*} - 1 \right) - u_i m_i}{f_i e_i u_i - f_i e_i u_2}
\]  

(16a)

\[
N_{2(12)}^* = \frac{u_1 m_i - f_1 e_1 D \left( \frac{S}{R_{1(12)}^*} - 1 \right)}{f_2 e_2 u_1 - f_1 e_1 u_2}
\]  

(16b)

where \( R_{i(2)}^* \) is the equilibrial resource level in polyculture, given by

\[
R_{i(12)}^* = \frac{m_i f_2 - m_2 f_i}{u_i c_1 f_2 - u_2 c_2 f_1}
\]  

(17)

Note that the assumptions that plant species 1 is the superior resource competitor in the absence of herbivores, and that coexistence in polyculture is stable, imply that both the numerators and denominators in (16a–b) are < 0 (Leibold 1996).

Inspection of (16) indicates that the polyculture biomasses of species 1 and 2 are negatively related over the range of enrichment (S) levels permitting coexistence (i.e. \( R_Y < 1 \) for all i) (Leibold 1996). However, this fact alone does not rule out non-transgressive overyielding, defined by

\[
R_Y = \frac{N_{1(2)}^* + N_{2(12)}^*}{N_{1(1)}^*} > 1
\]  

(18)

Since we assume that \( f_i e_i u_i < f_i e_i u_2 \), as required for stable coexistence, (18) reduces to the requirement that \( 0 < 0 \), which is impossible. Coexistence under generalist herbivory implies \( R_Y = 1 \), ruling out both non-transgressive and transgressive overyielding. Fig. 3 illustrates the behavior of (14) along an enrichment gradient.

**Discussion**

**Niche differentiation and overyielding**

Current models of niche differentiation and total plant biomass fall into two broad classes. Phenomenological models based on a Hutchinsonian concept of the niche as a “hypervolume” predict that a greater diversity of species tends to “fill” a greater fraction of the total “niche space” (Hutchinson 1957, Tilman et al. 1997a). Models of spatial environmental variability fall into this category, and typically predict that increased plant diversity increases total biomass by increasing the proportion of habitat occupied by species well-adapted to the local conditions (Cardinale et al. 2000, Chesson et al. 2002, Mouquet et al. 2002). Similarly, increasing diversity can increase long-term average biomass in temporally variable environments by increasing the proportion of time that the ecosystem is dominated by a species well-adapted to the current conditions (Norberg et al. 2001).

A second class of models is based on mechanistic descriptions of trophic interactions (Tilman et al. 1997a, Holt and Loreau 2002). The models analyzed here fall into this class. Stable coexistence in these models also requires niche differentiation, but not in a way that Hutchinson recognized (Leibold 1995). Leibold (1995) and Chesson (2000) argue persuasively that mechanistic models of trophic interactions cannot be interpreted in a Hutchinsonian fashion. Stable coexistence of species demands not only that species differ in their requirements (i.e. that their niches do not “overlap” too much), but also that species differ in their impacts on the environment, where “environment” is interpreted broadly to include other species (Leibold 1995). For instance, stable coexistence in the differential resource use model requires not just that plants be limited by different resources (= different requirements), but also that plants exhibit an appropriate trade-off in the rates at which they take up different resources (= different impacts, Leibold 1995). Mechanistic models predict that there is no simple relationship between the amount of variation in species’ requirements and the total biomass produced by all species.

Previous mechanistic models of plant diversity and total biomass emphasize interactions between plants...
and their resources, often in spatially heterogeneous environments (Tilman et al. 1997a). The three models analyzed here build on previous work by incorporating another trophic level, and by analyzing the effects of differential resource use in the absence of spatial heterogeneity. Comparison of the three models analyzed here makes it clear that not all niche differences among plants are equally likely to cause polycultures to outperform monocultures. Transgressive overyielding can occur only when the addition of more plant species to the most productive monoculture reduces the amount of resources bound in some other trophic group(s). It is widely recognized that increased plant diversity can reduce the total amount of inorganic nutrients, thereby increasing total plant biomass (this paper, Tilman et al. 1997a, b). It is less-widely recognized that increased plant diversity can reduce, e.g. herbivore density, thereby increasing total plant biomass.

However, of the types of niche differentiation examined here, only differential resource use appears likely to produce transgressive overyielding. Specialist herbivores promote transgressive overyielding only in limited circumstances. Transgressive overyielding with specialist herbivores requires that the inferior competitor take up resources at a higher per-unit rate than the superior competitor. In this case the superior competitor owes its superiority to a relatively low density-independent mortality rate, and a relatively high conversion efficiency. Superior competitors generally are characterized by both higher conversion efficiencies and lower loss rates than inferior competitors (Chapin 1980, Craine et al. 2002). Superior and inferior competitors often have similar resource uptake rates, although in some systems superior competitors exhibit higher uptake rates over at least some range of resource availabilities (Chapin 1980, Tilman 1982, Craine et al. 2002). Transgressive overyielding also requires a strictly specialized herbivore. Even a small rate of herbivory on the less competitive plant prevents transgressive overyielding by preventing the inedible plant from “siphoning off” resources from the rest of the food web. No plant in nature is entirely inedible, suggesting that the generalist herbivore model may better-approximate the total effect of the herbivore guild in many natural communities.

Both the differential resource use model and the specialist herbivore model predict that stable coexistence in polyculture guarantees non-transgressive overyielding. The observed degree of non-transgressive overyielding in these cases reflects both a sampling effect (more diverse plots are more likely to contain any given species) and niche differentiation. If the plants did not have different niches, they could not coexist. However, niche differentiation does not imply non-transgressive overyielding, as indicated by the lack of non-transgressive overyielding under generalist herbivory. Loreau (1998b) emphasizes that there is no simple relationship between niche differentiation and non-transgressive overyielding.

Comparison with empirical studies

All three models emphasize that the availability of limiting resources ultimately limits the total biomass an ecosystem can support. Increasing plant diversity increases total plant biomass only when increasing diversity causes resources to be redistributed from other “compartments” of the food web into plant biomass. The extent to which increasing total plant biomass with increasing plant diversity comes at the expense of compartments other than inorganic nutrient pools has received little empirical attention. Studies of plant diversity and herbivory typically treat plant diversity as a response variable, rather than manipulating plant diversity (Proulx and Mazumder 1998). Nor do studies manipulating plant diversity often consider enrichment.

Fridley (2002) grew monocultures of nine grass species, several two-species polycultures of varying composition, and a nine-species polyculture, at three enrichment levels. Enrichment was manipulated via addition of N-P-K fertilizer (to produce the highest enrichment level) and a sawdust-sugar mixture (carbon supplementation to produce the lowest enrichment level). The difference between mean biomass in the nine-species polyculture and the biomass of the average monoculture increased with enrichment, while the ratio remained relatively unchanged (Fridley 2002). Results were similar when comparing two-species polycultures and monocultures (Fridley 2002). These results are consistent with the predictions of the differential resource use model, assuming that the enrichment treatments did not dramatically alter nutrient supply ratios, and that the short-term outcome of the experiment (which lasted <3 months) reflects the long-term outcome.

Long-term experiments with algae find that changing the nutrient supply ratio changes the ratio of polyculture biomass to mean monoculture biomass, consistent with the differential resource use model (Bell 1990, 1991). However, Bell (1990, 1991) also found evidence for interference competition among algae, the intensity of which may have varied with the resource supply ratio. The differential resource use model (1) does not consider interference competition.

Clear support for the herbivory models comes from recent laboratory experiments with algae and zooplankton (Steiner 2001). These experiments find that competition from inedible algae reduces the productivity of edible algae, thereby reducing herbivore density in algal polycultures (Steiner 2001). Increased algal biomass in polycultures comes at least partially at the expense of herbivores, although the experimental design employed by Steiner (2001) does not allow a test for transgressive overyielding.
Haddad et al. (2001) examined insect abundances along an experimental gradient of plant species and functional group richness. They found that insect abundances declined with increasing plant functional group richness because more functionally diverse plots were more likely to contain a low-quality functional group, C₄ grasses. However, the consequences of changes in insect abundance for total plant biomass are unclear. Plant biomass increased with increasing plant species and functional group richness, probably due to complementary patterns of nitrogen use in more diverse plots, rather than reduced insect abundances (Tilman et al. 1997b).

Mülder et al. (1999) assembled an experimental plant diversity gradient, and sprayed some polycultures to remove insect herbivores. They found that plants with high monoculture biomass tended to dominate polycultures, that total plant biomass increased more rapidly with increasing plant diversity in sprayed plots, and that herbivory led to a more even distribution of biomass among plants. All of these effects are consistent with the herbivory models over a wide range of parameter values (J. W. Fox, unpubl.). Unfortunately, the data of Mülder et al. (1999) do not allow a test for the effect of herbivores on overyielding, since monocultures were not sprayed.

Plant diversity and total community biomass

The fact that increasing producer diversity can reduce total herbivore abundance or biomass (Haddad et al. 2001, Steiner 2001) raises the question of whether overyielding on one trophic level necessarily implies overyielding for the entire community. Numerical results indicate that there is no 1:1 correspondence between transgressive overyielding at the plant- and whole-community levels. For instance, numerical results for the specialist herbivore model (not shown) indicate that total community biomass (plants + herbivores) in a plant polyculture may or may not exceed that in either plant monoculture (“transgressive community overyielding”). Transgressive community overyielding in the specialist herbivore model can occur in cases where total plant biomass does not exhibit transgressive overyielding.

Unfortunately, an analytical comparison of total biomass of plants + herbivores in either herbivory model yields extremely complex expressions that defy easy interpretation. One way to simplify the problem is to measure both herbivore and plant biomass in resource units, thereby eliminating the conversion efficiency parameters c and e. If we further simplify the problem by assuming a universal per-unit density-independent loss rate (i.e. \(m_1 = m_2 = m_4 = D\)), then at equilibrium the total amount of resource in the system is fixed at S, independent of species composition (Grover 1997). The total amount of resource bound in herbivores and plants equals S-R*, where R* is the equilibrial resource level. Comparing total community biomass (measured in resource equivalents) among communities with different species compositions thus amounts to comparing R* among communities.

In the specialist herbivore model, R* is determined by a selection effect (Loreau and Hector 2001). The two treatments containing plant species 1 have the same R*, and thus the same total community biomass (measured in resource equivalents). Monocultures of plant species 2 have a higher R* than the other two treatments, and thus lower total community biomass (Grover 1994). In the generalist herbivore model, R* in a polyculture of both plants is always intermediate between the R* values of the two plant monocultures, and so total community biomass in polyculture is also intermediate (Leibold 1996).

However, this analysis is not directly comparable to that presented above for total plant biomass, since the analysis of total plant biomass does not measure total plant biomass in resource equivalents. Measuring total community biomass in resource equivalents simplifies the algebra, but effectively changes the question by eliminating one biological aspect of the original question (interspecific variation in conversion efficiency). A more thorough analysis of the effect of within-trophic-level diversity on total community biomass would be a challenging but interesting topic for future research.

Future directions

Most published models relating biodiversity and ecosystem properties, like most analytical models in community ecology, either model species coexistence in a phenomenological fashion, or assume a single mechanism of coexistence (this study, Tilman et al. 1997a, b, Loreau 1998a, Cardinale et al. 2000, Hughes and Roughgarden 2000, Chesson et al. 2002, Mouquet et al. 2002). In nature multiple mechanisms of coexistence likely operate simultaneously. A major challenge for future theoretical and empirical work will be to identify the joint consequences of multiple mechanisms of coexistence.

A second major challenge will be to model the consequences of simultaneous changes in diversity on multiple trophic levels. Current, historically-high extinction rates are not restricted to plants (Pimm et al. 1995). Several recent experiments manipulated diversity on several trophic levels (Naeem et al. 1994, McGrady-Steed et al. 1997, Naeem and Li 1997, Downing and Leibold 2002), but ecologists currently lack a theoretical framework in which to interpret these experiments. Complete removal of higher trophic levels frequently has strong indirect effects on biomass and composition on lower trophic levels (Terborgh et al. 2001), and it
would be surprising if changes in diversity and composition within higher trophic levels did not also have substantial effects.

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References


References


