

LETTER

Competition on productivity gradients – what do we expect?

Mark Rees*

Department of Animal and Plant
Sciences, University of Sheffield,
Sheffield S10 2, Tennessee, UK

*Correspondence:

E-mail: m.rees@sheffield.ac.uk

Abstract

Many experimental studies have quantified how the effects of competition vary with habitat productivity, with the results often interpreted in terms of the ideas of Grime and Tilman. Unfortunately, these ideas are not relevant to many experiments, and so we develop an appropriate resource competition model and use this to explore the effects of habitat productivity on the intensity of competition. Several mechanisms influencing the productivity–competition intensity relationship are identified, and these mechanisms explored using two classic data sets. In both cases, there is good agreement between the model predictions and empirical patterns. Quantification of the mechanisms identified by the models will allow the development of a simple predictive theory linking measures of the intensity of competition with ecosystem-level properties.

Keywords

Competition intensity, productivity, Grime–Tilman debate, resource competition.

Ecology Letters (2013) 16: 291–298

INTRODUCTION

A large number of experimental studies have explored how plant competition varies on productivity gradients, with many studies suggesting that the intensity of competition either increases with productivity (Gurevitch 1986; Wilson & Keddy 1986; Campbell & Grime 1992; Turkington *et al.* 1993; Kadmon 1995; Twolan-Strutt & Keddy 1996; Sammul *et al.* 2000, 2006; Carlyle *et al.* 2010), or is independent of productivity (Fowler 1982; Gibson 1988; Wilson & Shay 1990; Wilson & Tilman 1991; Campbell & Grime 1992; Turkington *et al.* 1993; Belcher *et al.* 1995; Carlyle *et al.* 2010), whereas a small number of studies have demonstrated a decline (Di-Tommaso & Aarssen 1991; Turkington *et al.* 1993). These differences are thought to reflect (1) different measures of the intensity of competition, in particular whether the authors use absolute or relative measures of competition intensity (Grace 1993; Oksanen *et al.* 2006), (2) whether the productivity gradient is natural or experimental, with increases in the intensity of competition occurring more often on natural gradients (Goldberg & Novoplansky 1997; Goldberg *et al.* 1999), (3) the range of productivity (Belcher *et al.* 1995), (4) the type of resources (water vs. nutrients) that plants compete for (Goldberg & Novoplansky 1997), (5) the response variable (e.g. plant biomass, survival) and species used to assess this (Belcher *et al.* 1995; Goldberg *et al.* 1999) and (6) statistical power (Belcher *et al.* 1995; Goldberg *et al.* 1999).

Typically, the experiments are interpreted in terms of the theories of Grime and Tilman (Tilman 1988b; Grime 2002), which deal primarily with large-scale, between-habitat patterns of community structure. Therefore, there is a serious mismatch between what the experiments measure (short-term growth responses of individual plants) and the theoretical predictions (Grace 1991, 1993; Freckleton *et al.* 2009). However, the experiments are of general interest for several reasons:

(1) Numerous authors have speculated how resource availability affects the intensity of competition, with arguments for increasing, decreasing and no effect all being presented: Keddy (1991) described this as the paradox of resource limitation (Newman 1973; Grime 1977, 2002; Grubb 1985; Tilman 1987, 1988a,b; Taylor *et al.* 1990; Keddy 1991; Reader *et al.* 1994);

(2) The experiments document how an ecosystem-level property (i.e. productivity) influences the intensity of competition experienced by individuals, so quantifying fundamental links between different levels of organisation;

(3) The within-habitat covariance between the intensity of competition and the quality of the environment quantifies the role of spatial environmental niches in allowing coexistence – the spatial storage effect (Sears & Chesson 2007; Chesson 2008);

(4) Quantifying the covariance between competition and the quality of the environment is critical for identifying environmental controls on plant distributions using observational data (Dahlgren & Ehrlén 2011). If the intensity of competition is greater in favourable environments, then ignoring the effects of competition will result in the impact of the environment being severely underestimated.

However, despite the clear importance of understanding the relationship between the quality of the environment and intensity of competition, there is currently no theory that predicts when particular patterns will be observed, or guides the interpretation of the experimental studies. For example, what mechanisms drive, the often observed, increase in the intensity of competition with productivity? In what follows, we first develop a model for resource competition, appropriate for short-term field experiments, and then use this to calculate how the intensity of competition, as measured in the field experiments, should vary along a productivity gradient. Throughout, we will measure the intensity of competition using $C = B_{NC}/B_C$, where B_{NC} is biomass in no competition, and B_C is biomass in competition. Note, in some experiments, B_{NC} should be more precisely defined as performance in the absence of interspecific competition (Mahmoud & Grime 1976; Campbell & Grime 1992; Turkington *et al.* 1993). However, for ease of presentation, we will use B_{NC} to cover cases where individual plants are weeded around and so experience little or no competition, and also where species are sown in single-species plots and so experience intraspecific but not interspecific competition.

Resource dynamics and competition

Most experimental studies in this area are of short duration, for example in Goldberg *et al.*'s (1999) review, 62% were less than a

year in duration, and so focus on transient dynamics rather than the long-term outcome of competition. As a consequence of the short duration of the experiments, there is no reproduction or recruitment, and mortality will be negligible (Goldberg *et al.* 1999). To model this, we will assume there is some resource level available at the beginning of the experiment and this is depleted as a result of resource uptake. The dynamics of the resource, R , and biomass of competitors, B_i , we will assume, can be described by the following system of equations

$$\begin{aligned}\frac{dR}{dt} &= - \sum_j \beta_j B_j(t) R(t), \\ \frac{dB_i}{dt} &= \gamma_i \beta_i B_i(t) R(t). \quad i = 1..N\end{aligned}\quad (1)$$

So, each species is characterised by a resource uptake rate, β_i , and a rate of conversion of resources to biomass, γ_i . The rate of resource uptake is proportional to resource availability and plant mass, and so plants grow faster when there are more resources and large plants capture resources more rapidly than small ones. However, on a per unit mass basis, the rate of uptake is independent of plant size ($\beta R(t)$), and so competition is perfectly symmetrical (Weiner 1990; Schwinning & Weiner 1998). The assumption of symmetrical competition is realistic for soil resources, and also light in low-density or biomass populations (Schwinning & Weiner 1998) as in many experiments. In the model, each species has a maximum relative growth rate (RGR, dB/Bdt) of $\gamma_i \beta_i R(0)$, where $R(0)$ is the initial resource level. As we assume that $\gamma_i \beta_i$ does not vary across the gradient, this means that a species' ability to capture resources and convert them to biomass does not vary across the gradient, which is in agreement with several experiments (Mahmoud & Grime 1976; Campbell & Grime 1992; Grime 2002).

The dynamics of eqn 1 for a fast (large $\gamma\beta$) and slow (small $\gamma\beta$) -growing species in competition are illustrated in Fig. 1a. As expected, the fast-growing species dominates, and the intensity of competition experienced increases during the experiment, Fig. 1b. The reason for this increase is that initially the biomasses in the competition and control treatments are equal, and so $C = 1$, then as the plants compete, so the intensity of competition increases. The fast-growing species is the competitive dominant in this situation, as it can more rapidly capture resources and convert these to biomass, and as a consequence, it experiences less intense competition.

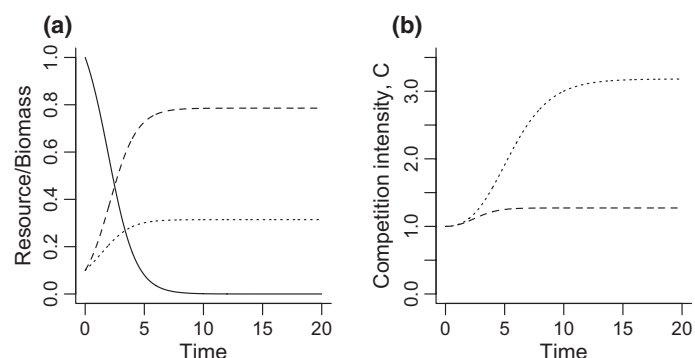


Figure 1 (a) Resource (solid) and biomass dynamics for a fast-growing (dashes) and slow-growing species (dots) competing according to eqn 1. (b) Dynamics of the intensity of competition, $C_x(t)$ for the fast- (dash) and slow- (dot)-growing species in (a).

The equations for the change in biomass can be integrated, and so $B_i(t) = B_i(0) \exp(\gamma_i \beta_i \int_0^t R(t) dt)$. In the two-species case, we can calculate the ratio of biomasses for species growing together

$$\frac{B_1(t)}{B_2(t)} = \frac{B_1(0)}{B_2(0)} \exp((\gamma_1 \beta_1 - \gamma_2 \beta_2) \int_0^t R(t) dt) \quad (2)$$

and so whether the initial ratio of biomasses changes when competing depends on the between-species difference in the parameter combination $\gamma\beta$, and the magnitude of this is mediated by the integrated resource availability, $\int R(t) dt$. This means that within a species, an individual captures resources in proportion to its initial biomass. For example, if $B_1(0)$ is the biomass of a seedling, and $B_2(0)$ the biomass of other plants of the same species, then the seedling will capture $B_1(0)/(B_1(0) + B_2(0))$ of the resources captured by that species. This is a consequence of the assumption of perfectly symmetrical competition.

We will use this framework to explore how the intensity of competition is expected to vary along a productivity gradient. To specify the resource gradient, we will assume that at each point, x , on the gradient there is some initial resource level, $R_x(0)$, and that competition occurs within sites of constant size. If these sites are of unit area, then $R_x(0)$ is the resource density per site. The assumption that plants compete within sites of constant size along the gradients is clearly not a terribly realistic assumption for studies using natural productivity gradients, and so will be relaxed later. However, in studies using pots of constant size, this assumption is more reasonable (Mahmoud & Grime 1976; Campbell & Grime 1992; Carlyle *et al.* 2010).

Using the equation for the dynamics of biomass, we find the intensity of competition is given by

$$\begin{aligned}C(t) &= \frac{B(0) \exp(\gamma\beta \int_0^t R_{NC}(t) dt)}{B(0) \exp(\gamma\beta \int_0^t R_C(t) dt)} \\ &= \exp\left(\gamma\beta \left[\int_0^t R_{NC}(t) dt - \int_0^t R_C(t) dt\right]\right),\end{aligned}$$

where the subscripts refer to the no competition (NC) and competition treatments (C). As this is not terribly transparent, we will initially assume the duration of the experiment is sufficient for all the available resources to be consumed, and so the value of C is no longer a function of time, Fig. 1b. We first consider the single-species case before moving onto the more complex dynamics of multi-species competition.

Single-species dynamics

For a species growing in isolation, eqn 1 has the following solution

$$\begin{aligned}B(t) &= \frac{\psi B(0) \exp(\beta\psi t)}{\gamma R(0) + B(0) \exp(\beta\psi t)} \\ R(t) &= \frac{\psi R(0)}{\gamma R(0) + B(0) \exp(\beta\psi t)}\end{aligned}\quad (3)$$

where $\psi = \gamma R(0) + B(0)$, which is the total mass produced as $t \rightarrow \infty$, made up of the initial mass, $B(0)$, and the new mass produced as a result of resource consumption and growth, $\gamma R(0)$. Assuming all the resources are consumed, so ψ is the biomass at the end of the experiment and there are n_x individuals, which compete for resources within a site allows the derivation of the competitive intensity C_x at any point on the gradient. First, consider a thinning experiment where the no-competition treatment plots are thinned to a single individual, and so the mass at the end of the

experiment is $B_{NC} = \gamma R_x(0) + B_s$, where B_s is initial seedling mass. In the competition treatment, the *per capita* biomass is

$$B_C = \frac{\gamma R_x(0) + n_x B_s}{n_x}, \quad (4)$$

and so C_x is given by

$$C_x = \frac{B_{NC}}{B_C} = \frac{\gamma R_x(0) + B_s}{\gamma R_x(0) + n_x B_s} n_x. \quad (5)$$

Providing $n_x > 1$, the partial derivative $\partial C_x / \partial R_x(0)$ is positive, and so even if all model parameters (γ, n_x, B_s) are unaffected by resource availability, the intensity of competition will increase with resource availability. This is a consequence of the initial biomass, $n_x B_s$ influencing the total biomass produced, $\gamma R_x(0) + n_x B_s$ making C_x a nonlinear function of $R_x(0)$. Removing this effect, eqn 5 simplifies to $C_x = n_x$, which is independent of $R_x(0)$. As the biomass at the end of the experiment is generally much greater than that at the beginning, $\gamma R_x(0) \gg n_x B_s$, eqn 5 simplifies to $C_x \approx n_x$. In the case where C_x is not a function of $R_x(0)$, whether the intensity of competition increases or decreases depends on how n_x varies with resource availability. If density dependence acts primarily on fecundity, then at higher resource levels we expect plants to achieve greater mass and so have higher fecundity, resulting in n_x increasing with resource levels, as in Kadmon's study of *Stipa capensis* (Kadmon 1993, 1995). When there is density-dependent mortality, the interpretation of n_x is more complicated. For annuals, n_x is the number of competitors before the action of density dependence, as this is the level of competition experienced by individuals within the community; studies where n_x is estimated from the density at the end of the experiment will therefore underestimate the intensity of competition. In perennial communities, where the density of competitors develops over several years, n_x can be interpreted as the density of competitors after density-dependent mortality, as this reflects the level of competition experience by an individual introduced into the current community.

For perennial communities, however, the density of competitors is less important than their biomass, and so to explore this, we will assume that single seedlings are introduced into cleared and intact vegetation (Wilson & Tilman 1991). In this case, if seedlings and established ramets have the same uptake and conversion parameters (β, γ), then any initial differences in biomass will be preserved (eqn 2), and so

$$C_x = \frac{\gamma R_x(0) + B_s}{B_s / (B_s + B_{r,x}) \gamma R_x(0) + B_s}, \quad (6)$$

where B_s is the biomass of a seedling and $B_{r,x}$ is the total biomass of perennial ramets within a site. $\partial C_x / \partial R_x(0) > 0$ providing $B_{r,x} > 0$, and so we expect the intensity of competition to increase with resource availability, even when resource availability does not affect any of the model parameters. As in the previous case, eqn 5, this is a consequence of the initial seedling mass, B_s influencing the final the total biomass produced, removing this effect leads to $C_x = (B_s + B_{r,x}) / B_s$, which is independent of $R_x(0)$. If as is reasonable, we assume $\gamma R_x(0) \gg B_s$, and $B_{r,x} \gg B_s$, then eqn 6 simplifies to $C_x \approx B_{r,x} / B_s$. So in this case, the impact of competition on plant performance is proportional to the initial ramet biomass. As we would expect initial ramet biomass to increase with resource availability, and seedling mass is constant, this results in the impact of competition increasing with resource availability.

These simple models assume the effects of weeding do not change the spatial scale of competition, so competition is restricted to within sites of constant size over the gradient. This seems unlikely because at high resource levels plants grow rapidly and so can exploit resources over a larger area when freed from competition (Gorham 1979). For the simple thinning experiment described above (eqn 4), let the number of sites over which plants can exploit resources when freed from competition be A_x and so $B_{NC} = A_x \gamma R_x(0) + B_s$. In competition, plants interact within a site as before and so

$$C_x = \frac{B_{NC}}{B_C} = \frac{A_x \gamma R_x(0) + B_s}{\gamma R_x(0) + n_x B_s} n_x \quad (7)$$

which simplifies to $C_x \approx A_x n_x$ when $\gamma R_x(0) \gg n_x B_s$. So we identify a new mechanism influencing the effects of productivity on competition, namely that in high-productivity sites, maximum potential plant size is greater, which increases the benefit from weeding and results in the effects of competition increasing with resource levels.

These results have been derived assuming that all the resources have been consumed; however, using eqn 3 we can obtain an expression for the time course of competition intensity, $C_x(t)$. In the thinning experiment, (eqn 5), this is given by

$$C_x(t) = \frac{(\gamma R_x(0) + B_s)(\gamma R_x(0) + n_x B_s \exp(\beta \phi t))}{(\gamma R_x(0) + n_x B_s)(\gamma R_x(0) + B_s \exp(\beta \phi t))}$$

and so $C_x(0) = 1$ and as $t \rightarrow \infty$ we obtain

$$\lim_{t \rightarrow \infty} C_x(t) = \frac{(\gamma R_x(0) + B_s)}{(\gamma R_x(0) + n_x B_s)} n_x$$

which if $\gamma R_x(0) \gg n_x B_s$ simplifies to $\lim_{t \rightarrow \infty} C_x(t) \approx n_x$ as expected.

We have derived the result for the single-species case using a simple resource model as this makes the underlying assumptions explicit, and allows development and analysis of the more complex two-species case. However, some of the results may be derived heuristically as follows. At any point on the productivity gradient, plants compete for available resources (e.g. soil nutrients, water, light etc.) and convert these to biomass. If we assume that the law of constant final yield (Harper 1977) holds over all densities and competition is symmetrical then $B_{NC} = K$ and $B_C = K / n_x$ where K is the constant final yield, which means that $C_x = n_x$, which is independent of the details of the underlying model for resource competition. This simple heuristic model can be extended to allow for the important case where single plants cannot exploit all available resources, either because (1) there is an upper bound on plant size, (2) the duration of the experiment is too short or (3) isolated plants have reduced performance (Callaway 1995), in which case the law of constant final yield will not hold over all densities. We can capture this idea by assuming a single plant can exploit some fraction α_x of available resources, and so $C_x = \alpha_x n_x$. In the case where there is an upper bound on plant size, we would expect α_x and hence the intensity of competition to decline with resource availability. As growth rate increases with resource availability, we would expect over the fixed duration of an experiment the fraction of resources consumed to increase with initial resource availability. For example, in eqn 1, the time for resources to be depleted by 50% decreases with initial resource availability. Therefore, if the duration of the experiment is such that not all resources are consumed, then α_x and

hence the intensity of competition will increase with resource availability. Finally, if positive interactions are more prevalent at low resource availability (Maestre *et al.* 2009), then we would expect α_x and hence the intensity of competition to increase with resource availability.

An application

To illustrate the models, we will revisit Kadmon's classic study of the effects of natural and artificial water gradients on productivity and the intensity of competition in *Stipa capensis* (Kadmon 1993, 1995); which has been previously been reanalysed (Brooker & Kikvidze 2008; Rees *et al.* 2012). In the experiment, plots were either controls (natural density of competitors) or thinned to a single individual, and there were three habitats, each with two water-addition treatments and a control (no water added). *Stipa capensis* made up 90% of all individuals within the quadrats by numbers and biomass (Kadmon *pers comm.*), and so the study can be reasonably treated as a single-species study.

In the derivation of eqn 5, we assumed *per capita* performance declines with the density of competitors, n_x , eqn 4, and this seems reasonable for the two water-addition treatments, Fig. 2a. For these treatments, we therefore expect $C_x \approx n_x$ and this indeed provides an excellent description of the data Fig. 2b. There was no significant difference between the slopes in the two water-addition treatments ($t = 2.06$, d.f. = 3, $P > 0.1$) and so we combined these treatments. The slope of the relationship between C_x and n_x in the combined water-addition treatments was 0.97, which was not significantly different from 1 ($t = 0.6$, d.f. = 5, $P > 0.5$), as predicted. In both control and water-addition treatments the intercepts were not significantly different from 0, as predicted. In the control treatment (no water added), the slope was 0.5, which was significantly different from 1 ($t = 7.1$, d.f. = 5, $P < 0.001$).

Multispecies dynamics

Over natural productivity gradients, the relative abundances of the species will vary, which will change the competitive environment (Wilson & Tilman 1991). In contrast, on experimental productivity gradients the relative abundances are often fixed (Mahmoud & Grime 1976; Campbell & Grime 1992; Carlyle *et al.* 2010). To

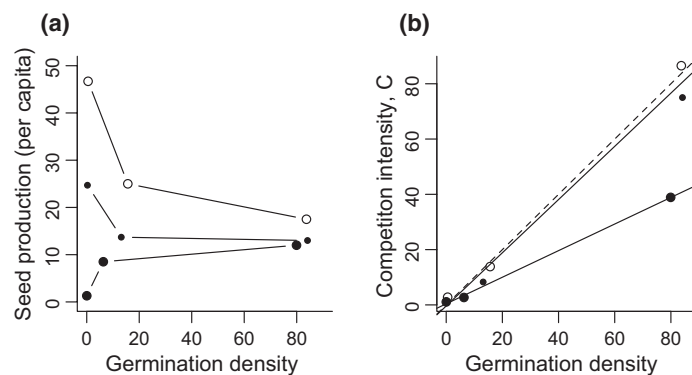


Figure 2 Relationships between (a) *per capita* fecundity and (b) competition intensity and the density of seedlings (per 100 cm²) for *Stipa capensis*, data from Kadmon (1993, 1995). The solid lines in (b) are the fitted relationships for the control and water-addition treatments, the dashed line is the theoretical prediction, eqn 5. Open circles, +80mm water addition; small, closed circles +30mm water addition; large, closed circles control.

explore the effects of multispecies competition, we will therefore assume there are two species, one fast- and one slow-growing, and that either, (1) both are equally abundant across the productivity gradient, or (2) the slow-growing species dominates at low resource levels, whereas the fast-growing one is dominant at high resource levels. For each of these scenarios, we then simulate the competitive dynamics (eqn 1) and explore how the intensity of competition changes. As in the single-species case, we measure the intensity of competition using $C = B_{NC}/B_C$, where B_{NC} is biomass in no competition, and B_C is biomass in competition.

To isolate the effects of multispecies competition and changes in community composition on competitive intensity, we will assume that (1) the number of competitors, n_x , within a site and (2) number of sites from which plants can exploit resources, A_x , when freed from competition, does not vary over the gradient. When the relative abundance of the two species varies, the fraction of slower growing species was set at $\min(R_x(0))/R_x(0)$, which equals 1 at the lowest resource availability, and so the slow-growing species dominates at the low resource availability and the fast-growing species at high resource availability.

When all resources are consumed, the simulations (Fig. 3a) show that the competitive intensity experienced by the slow-growing species (poor competitor) increases with resource availability both when its initial abundance varies along the gradient and when it is fixed. The curves cross because at low resource availability the ini-

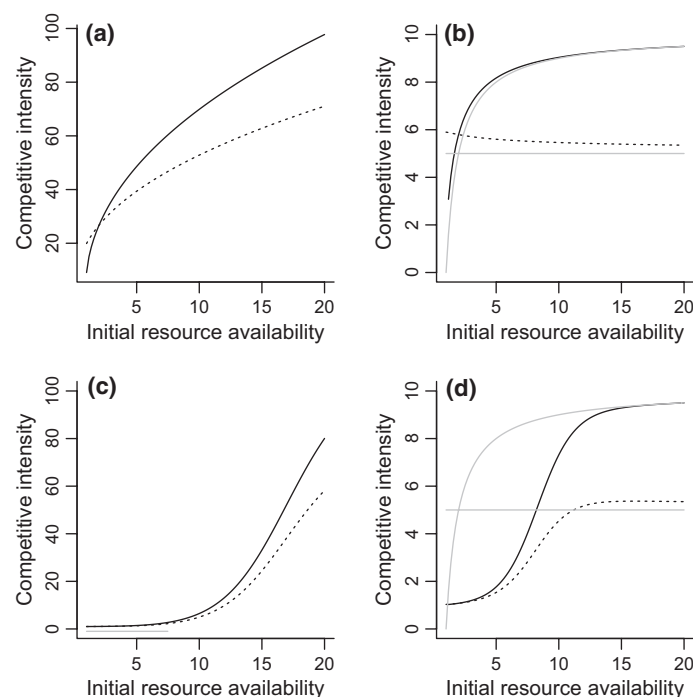


Figure 3 Effects of resource availability on competition intensity for species that (a) grow slowly and (b) grow fast. The solid lines indicate that the slow-growing species dominates at low resource availability, whereas the dotted lines indicate that both species were equally abundant across the gradient. Grey lines in (b) and (d) are the single-species results. In (c) and (d), we fix the duration of the experiment so not all resources are consumed. Duration (a) and (b) 100 time units; (c) and (d) 1 time unit. The grey line in (c) indicates where the slower growing species experiences less intense competition. For the fast-growing species, $\beta = 0.9$, $\gamma = 0.9$, and the slow-growing species $\beta = 0.5$, $\gamma = 0.9$; $n_x = 10$, and initial seedling mass 0.01.

tial abundance of the fast-growing species (good competitor) is greater in the fixed-abundance scenario, resulting in an increase the intensity of competition. In contrast, at high resource availability, the relative abundance of the fast-growing species is greater when relative abundance varies, and so the intensity of competition experienced by the slow-growing species is greater compared with the fixed relative-abundance scenario.

For the fast-growing species, the results are very different, Fig. 3b. First, the intensity of competition is much smaller, because fast growth (high $\gamma\beta$) confers a competitive advantage, and so the fast-growing species experiences a lower intensity of competition across the entire gradient. When relative abundance varies, we have a single species growing in isolation at each end of the productivity gradient, and so we recover our previous result that $C_x \approx n_x$. This means that C_x is bounded below by n_x for the slow-growing species, whereas for the fast-growing species, C_x is bounded above by n_x . When both species are at equal abundance along the gradient, C_x actually declines for the fast-growing species as productivity increases. The reason for this is that at high productivity, the ratio of final mass to initial mass is much greater, and so the fast-growing species can dominate the slow-growing species, resulting in the intensity of competition that it experiences being reduced. As the fast-growing species dominates the competitive dynamics, we can approximate C_x for the fast-growing species using the single-species result (eqn 5), see the grey lines in Fig. 3b. There is excellent agreement between the two approaches, with the largest discrepancies occurring at low resource availability.

Changing the duration of the simulated experiment, so that not all resources are consumed, results in broadly similar patterns (Fig. 3c and d). However, as the fraction of resources consumed increases with increasing initial resource availability, the simulations are more complicated to interpret. Reducing the duration of the experiment means that the intensity of competition experienced by both species is reduced particularly at low resource levels. The reason for this is that little growth occurs even when freed from competition, as a result of (1) the short duration of the experiment, (2) the low resource availability and (3) low $\gamma\beta$ for the slow-growing species, and so competition has little effect on performance, $C_x \approx 1$. For the slow-growing species, C_x is no longer bounded below by n_x , and so over some range of resource availability, (grey line in Fig. 3c) the slower growing species actually experiences *less* intense competition than the fast-growing one. As the resource levels increase, the dynamics of competition become faster and so the results of the short-term simulations and those where the resources are completely depleted become more similar (Fig. 3c and d).

Interestingly, we see a very similar pattern in the experiments of Campbell & Grime (1992). *Festuca*, the poor competitor, (minimum $C_x > 8$), experiences intense competition across the entire gradient, and the intensity of competition increases dramatically with productivity (maximum $C_x \approx 1600$), whereas in *Arrhenatherum*, the competitive dominant, the intensity of competition is largely unaffected by productivity (range of C_x over the productivity gradient 1.3–5.4), Fig. 4. See also Mahmoud & Grime (1976) where in a different, but similar experiment, the same pattern is found.

Impact of nonlinear resource uptake

There are many aspects of the competition model used (eqn 1) that can be modified to improve the biological realism. Perhaps the most

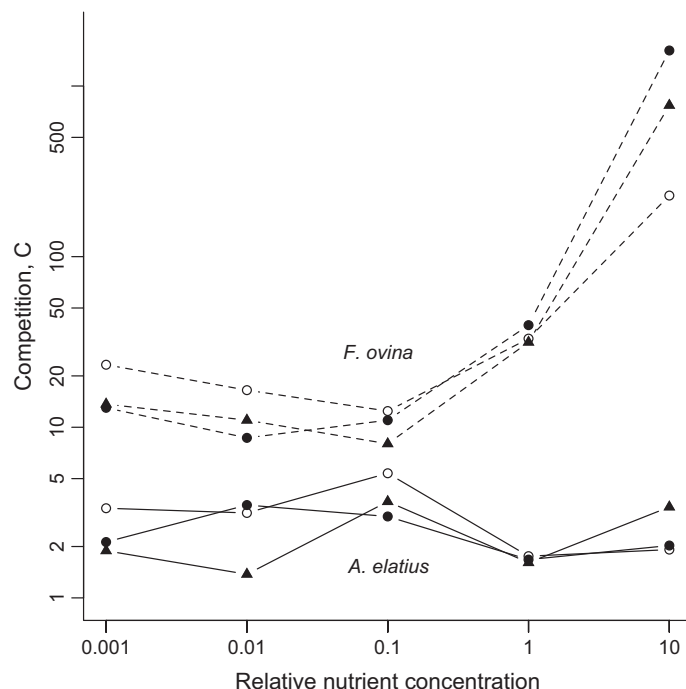


Figure 4 Effect of relative nutrient concentration on the intensity of competition in *Festuca ovina* (dashed lines) and *Arrhenatherum elatius* (solid lines), at three levels of disturbance (solid circles = 0, open circles = 75 and triangles = 150, higher numbers indicating more disturbance). Data from Campbell & Grime (1992).

obvious is that we have assumed that the growth rate increases linearly with resource availability, whereas others have assumed nonlinear relationships, such as Michaelis–Menten (Tilman 1982). It is straightforward to modify eqn 1 to include Michaelis–Menten resource uptake,

$$\frac{dR}{dt} = - \sum_j \beta_j B_j(t) R(t) / (b_j + R(t))$$

$$\frac{dB_i}{dt} = \gamma_i \beta_i B_i(t) R(t) / (b_i + R(t)) \quad i = 1..N$$

where b_i is the resource concentration required for growth at half the maximum rate. The single-species results [eqns (5, 6)] are unchanged as a result of the inclusion of nonlinear resource uptake, as we have assumed all the resources are consumed, and this is not influenced by the dynamics of resource consumption. Modifying the multispecies simulations to include Michaelis–Menten resource uptake has a relatively minor effect on the relationship between competitive intensity and resource availability, Fig. 5. As expected, if the species with the lower maximum growth rate has the lower b then it has an additional advantage and so experiences less intense competition, compare Figs 3a and 5a, and has a greater impact on the species with the higher maximum growth rate, compare Figs 3b and 5b. When the species with the higher maximum growth rate has the lower b , then it has an additional advantage and so has a greater impact on the species with the slower maximum growth rate, compare Figs 3a and 5c, and experiences less intense competition, compare Fig. 3b and 5d. For a clear discussion of the relationships between various models of resource competition, see Huisman (1994).

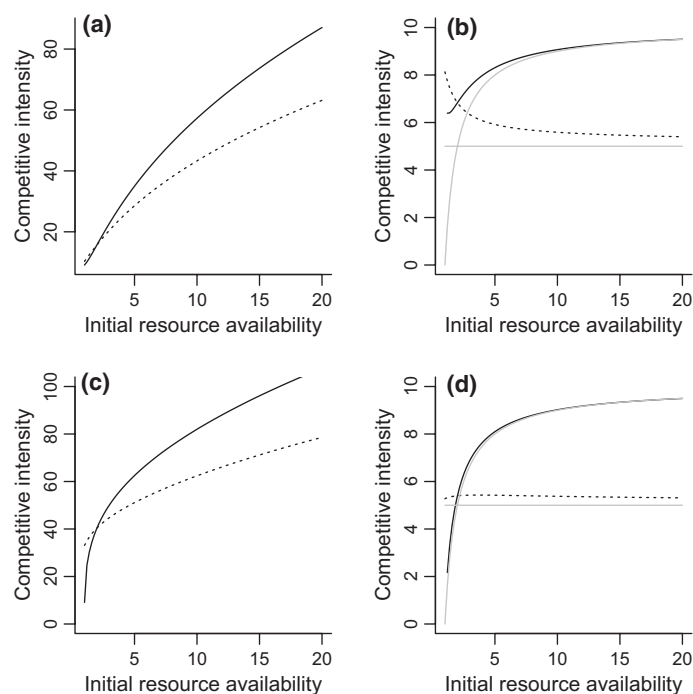


Figure 5 Effects of resource availability on competition intensity assuming nonlinear resource uptake for the slow-growing species (a, c) and the fast-growing species (b, d). The solid lines are from simulations where the slow-growing species dominates at low resource availability, whereas the dotted lines are from simulations where both species were equally abundant across the gradient. Grey lines in (b) and (d) are the single-species results, ignoring the presence of the slower growing species. Parameter values are the same as those in Fig. 3, slow species $b = 0.1$ in (a) and (b), and $b = 0.5$ in (c) and (d), fast-growing species has species $b = 0.5$ in (a) and (b), and $b = 0.1$ in (c) and (d).

DISCUSSION

We have demonstrated several processes that determine how the intensity of competition varies with resource availability. There are three basic ecological processes:

- (1) The nonlinearity of the competition eqns (5, 6); this occurs because the initial biomass influences the final productivity. When there is no effect of initial numbers or biomass on final productivity, eqns (5, 6) simplify to $C_{\infty} = n_{\infty}$ and $C_{\infty} = (B_s + B_{r,\infty})/B_s$, respectively, and so competition intensity is independent of resource availability, providing n_{∞} or $B_{r,\infty}$ do not vary along the gradient.
- (2) Changes in the number or biomass of competitors. If there are more competitors, either in terms of numbers or biomass, at higher resource levels, then the intensity of competition will increase with resource availability. In experiments on artificial gradients, the numbers or biomass of competitors is often fixed and so this effect cannot operate. In contrast, in experiments on natural productivity gradients, this effect could be important.
- (3) In high productivity sites, maximum plant size is greater, which increases the benefit from weeding as plants can exploit resources over a larger area, resulting in the effects of competition increasing with resource levels (eqn 7). We expect this to primarily occur in experiments in the field where plant growth is not limited by pot size.

We conjecture that processes 2 and 3 will be particularly important in studies on natural productivity gradients, and that these

effects explain why increases in the intensity of competition are often found (Gurevitch 1986; Wilson & Keddy 1986; Reader & Best 1989; Kadmon 1995; Twolan-Strutt & Keddy 1996; Sammul *et al.* 2000, 2006). In contrast, in studies where variation in productivity is generated experimentally, say by adding fertiliser, these effects will be much reduced, as there is little natural variation in the density or biomass of competitors or the density or biomass of competitors is fixed by the experimental design, and plant size is limited by pot or plot size (Mahmoud & Grime 1976; Fowler 1982; Wilson & Shay 1990; DiTommasso & Aarssen 1991; Campbell & Grime 1992; Carlyle *et al.* 2010).

In addition to these processes, aspects of the experimental design are also important. We divide these into two groups:

- (1) The species used to assess competition intensity. In single-species systems, an upper bound on plant size can result in the intensity of competition declining with initial resource availability, as the effect of freeing a plant from competition is reduced. Surprisingly in multispecies systems, the largest effects of changes in resource availability are generally seen in the slow-growing species, which in the context of these experiments is the weaker competitor (Fig. 3). In competitive dominants, much smaller changes in the intensity of competition are generally seen, and competition intensity can decrease with resource availability. This is a consequence of the competitive dominant achieving a greater suppression of the subdominant in high-resource environments (Fig. 3b).
- (2) The duration of the experiment. In short experiments, where not all resources are consumed, there are additional complications, which arise due to the fraction of resources consumed being a function of initial resource availability. In general, when growth increases with resource availability, we expect the fraction of resources consumed, and hence the intensity of competition, to increase with initial resource availability. The changing fraction of resources consumed can have counterintuitive effects in multispecies systems because the slow-growing species (competitive subdominant) has very little opportunity to grow even when freed from competition, and so can experience less intense competition compared with the fast-growing species, the competitive dominant.

The assumption that competition occurs for a single resource appears to be rather restrictive. However, the main conclusions (ecological processes 1–3 above) are likely to be very robust, as indicated by the heuristic derivation presented in the main body of the article, which only requires the assumptions that (1) the law of constant final yield (Harper 1977) holds over all densities and (2) competition is symmetrical. The available data suggest that competition for soil resources is generally symmetrical (Schwinning & Weiner 1998). Schwinning & Weiner (1998) also argue that competition for light may be symmetrical in low-density/biomass populations, as in many short-term experiments, suggesting that our assumption of symmetrical competition might be reasonable for many experimental studies. Whether asymmetrical competition influences the intensity of competition depends on (1) how the degree of asymmetry varies with resource availability and (2) the details of the experimental design. The degree of competitive asymmetry is thought to increase with resource availability, as competition for light is more intense in high-productivity environments (Twolan-Strutt & Keddy 1996; Wilson & Tilman 1996; Schwinning & Weiner 1998). This will result in the intensity of competition increasing with resource availability if the plants used to measure

the effects of competition are increasingly adversely affected as resource availability increases. For example, if seedlings sown into high-productivity plots are rapidly overtopped and suppressed. In contrast, in thinning experiments where performance in competition is calculated at the population level (i.e. dividing quadrat biomass by density) such effects are unlikely, as the sample used to calculate performance in competition will contain both dominant and suppressed individuals.

Many experimental studies are difficult to characterise in terms of the ideas of Grime and Tilman as the intensity of competition experienced by different species, *within* a study, show different responses to productivity (Mahmoud & Grime 1976; Fowler 1982; DiTommaso & Aarssen 1991; Campbell & Grime 1992; Turkington *et al.* 1993). In contrast, the simple resource competition theory presented here predicts substantial increases in the intensity of competition with productivity in the competitive subordinates, and much weaker responses in the dominants (Fig. 3), as seen in several experimental studies (Mahmoud & Grime 1976; Campbell & Grime 1992). The interpretation of the results of Campbell & Grime (1992) presented here differs from that of the original authors, as a result of using a different competition index. The original authors used RCI ($(B_{NC}-B_C)/B_{NC} * 100$), which is very insensitive to changes in the intensity of competition when competition has a large impact on plant performance. For example, when $C = 100$, $RCI = 99$, whereas when $C = 200$, $RCI = 99.5$, making it very difficult to detect changes in the intensity of competition (Oksanen *et al.* 2006).

The theory presented here provides a simple framework for interpreting the results of short-term competition experiments on both natural and artificial productivity gradients. It would be interesting to assess when the mechanisms described in the main body of the article operate in field systems, and which are most important. The addition of nutrients is known to increase the biomass of competitors, and this effect seems to be smaller in nutrient-poor habitats (DiTommaso & Aarssen 1989). This suggests increases in the intensity of competition in high nutrient/productivity environments, however, in some systems there is a negative correlation between shoot biomass and nutrient concentrations (Vermeer & Berendse 1983) making the quantification of this relationship critical. Quantifying this relationship allows a direct test of the theory presented (eqn 6) and so holds out the possibility of a relatively simple predictive theory linking measures of the intensity of competition with ecosystem-level properties.

ACKNOWLEDGEMENTS

I would like to thank Steve Ellner for advice, and NERC for funding (NE/H020802/1).

REFERENCES

- Belcher, J.W., Keddy, P.A. & Twolan-Strutt, L. (1995). Root and shoot competition intensity along a soil depth gradient. *J. Ecol.*, 83, 673–682.
- Brooker, R.W. & Kikvidze, Z. (2008). Importance: an overlooked concept in plant interaction research. *J. Ecol.*, 96, 703–708.
- Callaway, R.M. (1995). Positive interactions among plants. *Bot. Rev.*, 61, 306–349.
- Campbell, B.D. & Grime, J.P. (1992). An experimental test of plant strategy theory. *Ecology*, 73, 15–29.
- Carlyle, C.N., Fraser, L.H. & Turkington, R. (2010). Using three pairs of competitive indices to test for changes in plant competition under different resource and disturbance levels. *J. Veg. Sci.*, 21, 1025–1034.
- Chesson, P. (2008). Quantifying and testing species coexistence mechanisms. In: *Unity in Diversity: Reflections on Ecology after the Legacy of Ramon Margalef*. (eds Vallarres, F., Camacho, A., Elosegui, A., Gracia, C., Estrada, M., Senar, J.C. & Gili, J.M.). Fundacion BBVA, Bilbao, pp. 119–164.
- Dahlgren, J.P. & Ehrlén, J. (2011). Incorporating environmental change over succession in an integral projection model of population dynamics of a forest herb. *Oikos*, 120, 1183–1190.
- DiTommaso, A. & Aarssen, L.W. (1989). Resource manipulations in natural vegetation - a review. *Vegetatio*, 84, 9–29.
- DiTommaso, A. & Aarssen, L.W. (1991). Effect of nutrient level on competition intensity in the field for 3 coexisting grass species. *J. Veg. Sci.*, 2, 513–522.
- Fowler, N. (1982). Competition and coexistence in a North-Carolina grassland.3. mixtures of component species. *J. Ecol.*, 70, 77–92.
- Freckleton, R.P., Watkinson, A.R. & Rees, M. (2009). Measuring the importance of competition in plant communities. *J. Ecol.*, 97, 379–384.
- Gibson, D.J. (1988). The maintenance of plant and soil heterogeneity in dune grassland. *J. Ecol.*, 76, 497–508.
- Goldberg, D. & Novoplansky, A. (1997). On the relative importance of competition in unproductive environments. *J. Ecol.*, 85, 409–418.
- Goldberg, D.E., Rajaniemi, T., Gurevitch, J. & Stewart-Oaten, A. (1999). Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology*, 80, 1118–1131.
- Gorham, E. (1979). Shoot height, weight and standing crop in relation to density of monospecific plant stands. *Nature*, 279, 148–150.
- Grace, J.B. (1991). A clarification of the debate between grime and tilman. *Funct. Ecol.*, 5, 583–587.
- Grace, J.B. (1993). The effects of habitat productivity on competition intensity. *Trends Ecol. Evol.*, 8, 229–230.
- Grime, J.P. (1977). Evidence for existence of 3 primary strategies in plants and its relevance to ecological and evolutionary theory. *Am. nat.*, 111, 1169–1194.
- Grime, J.P. (2002). *Plant Strategies, Vegetation Processes, and Ecosystem Properties*, 2nd edn. John Wiley & Sons Ltd, Chichester.
- Grubb, P.J. (1985). Plant populations and vegetation in relation to habitat, disturbance and competition: problems of generalization. In: *The Population Structure of Vegetation*. (ed White, J.). Dr. W. Junk, Dordrecht, The Netherlands, pp. 595–611.
- Gurevitch, J. (1986). Competition and the local-distribution of the grass stipa-neomexicana. *Ecology*, 67, 46–57.
- Harper, J.L. (1977). *Population Biology of Plants*. Academic Press, London.
- Huisman, J. (1994). The models of berendse and tilman - 2 different perspectives on plant competition. *Funct. Ecol.*, 8, 282–288.
- Kadmon, R. (1993). Population-dynamic consequences of habitat heterogeneity - an experimental-study. *Ecology*, 74, 816–825.
- Kadmon, R. (1995). Plant competition along soil-moisture gradients - a field experiment with the desert annual *stipa capensis*. *J. Ecol.*, 83, 253–262.
- Keddy, P.A. (1991). *Competition*. Chapman & Hall, London.
- Maestre, F.T., Callaway, R.M., Valladares, F. & Lortie, C.J. (2009). Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *J. Ecol.*, 97, 199–205.
- Mahmoud, A. & Grime, J.P. (1976). Analysis of competitive ability in 3 perennial grasses. *New Phytol.*, 77, 431–435.
- Newman, E.I. (1973). Competition and diversity in herbaceous vegetation. *Nature*, 244, 310–310.
- Oksanen, L., Sammul, M. & Magi, M. (2006). On the indices of plant-plant competition and their pitfalls. *Oikos*, 112, 149–155.
- Reader, R.J. & Best, B.J. (1989). Variation in competition along an environmental gradient - *Hieracium-floribundum* in an abandoned pasture. *J. Ecol.*, 77, 673–684.
- Reader, R.J., Wilson, S.D., Belcher, J.W., Wisheu, I., Keddy, P.A., Tilman, D. *et al.* (1994). Plant competition in relation to neighbor biomass - an intercontinental study with *Poa pratensis*. *Ecology*, 75, 1753–1760.
- Rees, M., Childs, D.Z. & Freckleton, R.P. (2012). Assessing the role of competition and stress: a critique of importance indices and the development of a new approach. *J. Ecol.*, 100, 577–585.

- Sammul, M., Kull, K., Oksanen, L. & Veromann, P. (2000). Competition intensity and its importance: results of field experiments with *Anthoxanthum odoratum*. *Oecologia*, 125, 18–25.
- Sammul, M., Oksanen, L. & Magi, M. (2006). Regional effects on competition-productivity relationship: a set of field experiments in two distant regions. *Oikos*, 112, 138–148.
- Schwinning, S. & Weiner, J. (1998). Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia*, 113, 447–455.
- Sears, A.L.W. & Chesson, P. (2007). New methods for quantifying the spatial storage effect: an illustration with desert annuals. *Ecology*, 88, 2240–2247.
- Taylor, D.R., Aarssen, L.W. & Loehle, C. (1990). On the relationship between r/k selection and environmental carrying-capacity - a new habitat templet for plant life-history strategies. *Oikos*, 58, 239–250.
- Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton University Press, Princeton, New Jersey.
- Tilman, D. (1987). The importance of the mechanisms of interspecific competition. *Am. nat.*, 129, 769–774.
- Tilman, D. (1988a). On the meaning of competition and the mechanisms of competitive superiority. *Funct. Ecol.*, 1, 304–315.
- Tilman, D. (1988b). *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, New Jersey.
- Turkington, R., Klein, E. & Chanway, C.P. (1993). Interactive effects of nutrients and disturbance - an experimental test of plant strategy theory. *Ecology*, 74, 863–878.
- Twolan-Strutt, L. & Keddy, P.A. (1996). Above- and belowground competition intensity in two contrasting wetland plant communities. *Ecology*, 77, 259–270.
- Vermeer, J.G. & Berendse, F. (1983). The relationship between nutrient availability, shoot biomass and species richness in grassland and wetland communities. *Vegetatio*, 53, 121–126.
- Weiner, J. (1990). Asymmetric competition in plant-populations. *Trends Ecol. Evol.*, 5, 360–364.
- Wilson, S.D. & Keddy, P.A. (1986). Measuring diffuse competition along an environmental gradient - results from a shoreline plant community. *Am. nat.*, 127, 862–869.
- Wilson, S.D. & Shay, J.M. (1990). Competition, fire, and nutrients in a mixed-grass prairie. *Ecology*, 71, 1959–1967.
- Wilson, S.D. & Tilman, D. (1991). Components of plant competition along an experimental gradient. *Ecology*, 72, 1050–1065.
- Wilson, S.D. & Tilman, D. (1996). Plant competition and resource availability in response to disturbance and fertilization. *Ecology*, 74, 599–611.

Editor, Jerome Chave

Manuscript received 21 September 2012

First decision made 21 October 2012

Manuscript accepted 23 October 2012