

# Disturbance-mediated competition between perennial plants along a resource supply gradient

J. Stephen Brewer\*

Department of Biology, PO Box 1848, University of Mississippi, MS 38677-1848, USA

## Summary

1. Traditional views of ecological disturbance emphasize the role that physical disturbances play in reducing competition between populations and maintaining species coexistence. I present an alternative view that employs a simple Lotka–Volterra model to demonstrate how disturbance resistance, disturbance resilience and resource storage can increase competition between individual perennial plants of similar growth form along a resource supply gradient.
2. In contrasting the growth of individual genets of two hypothetical species, I assumed that traits associated with inherently low module (i.e. plant part) mortality in infertile soils resulted in greater resource storage, but traded off with maximum potential net photosynthesis rates and thus disturbance resilience.
3. The species with more persistent modules (the ‘persistent’ species) and greater storage produced larger genets and displaced the other species at low gross resource supplies as a result of pre-emption.
4. The species with the greater net photosynthesis rate (the ‘resilient’ species) gained a size and competitive advantage with increasing gross resource supply, provided senescence of its modules was sufficiently low or there was a constant and equivalent rate of damage to portions of the genets of both species.
5. Selection for disturbance resistance was greater in the persistent species than in the resilient species, which in turn increased the former’s competitive ability in moderately resource-rich, disturbance-prone environments.
6. *Synthesis.* Both resistance and resilience to disturbance potentially increase a species’ competitive ability by allowing that species to interfere with the recovery of its competitors from disturbance. Contrary to the view that disturbances must be eliminated from competition experiments to accurately measure the potential for competition to structure plant communities, I conclude that the opposite is true.

**Key-words:** clonal growth, competition, disturbance, life history, modular demography, plant–plant interactions, resilience, resistance, storage, stress tolerance

## Introduction

Despite more than 30 years of intense interest in resource competition and disturbance-mediated coexistence, competitive interactions along resource supply gradients in naturally disturbed (i.e. real) landscapes remain poorly understood (Platt & Connell 2003; Miller *et al.* 2005). One possible reason is inadequate attention to how disturbances realistically affect competitive interactions along resource supply gradients. Physical disturbances are hypothesized to maintain species diversity by reducing population densities (and thus competition) and providing opportunities for colonization by fugitive

species (Dayton 1971; Grubb 1977; Connell 1978; Sousa 1980). There is increasing evidence, however, that many physical disturbances in plant communities (e.g. wind damage, wave damage, ice damage, fire, burial by plant debris or sediment) cause little mortality of entire adults and thus provide relatively few opportunities for colonization or recruitment from seed (Hartnett 1987; Boucher *et al.* 1990; Collins, Glenn & Gibson 1995; Foster *et al.* 1997; Hodgkinson 1998; Bond & Midgley 2001; Platt & Connell 2003). Even when adult mortality by disturbances is significant, the extent of mortality often varies among species, which in turn may influence species composition to a greater extent than interspecific differences in seedling recruitment (Foster *et al.* 1997; Brewer, Levine & Bertness 1998; Bond & Midgley 2001). Three potentially important but

\*Correspondence author. E-mail: jbrewer@olemiss.edu

largely unappreciated effects of such disturbances as they relate to plant competition are: (i) disturbances can give disturbance-resistant species an immediate size advantage, (ii) disturbances can increase net resource supply and allow rapidly growing disturbance-resilient individuals to interfere with the recovery of slower-growing individuals from disturbance and (iii) the degree to which disturbances favour either resistant or resilient species may depend on habitat productivity (gross resource supply). Accurate predictions of the effects of natural disturbances on communities must therefore account for the potential for disturbances to increase the competitive advantage of resilient or resistant species over others in relation to habitat productivity. I call the potential for increased competitive exclusion following disturbance the disturbance-mediated competition hypothesis (or DMCH), which is offered as an alternative to hypotheses of disturbance-mediated coexistence.

To understand how disturbances influence plant competition along productivity gradients, I argue that three issues require more attention: (i) how the longevity of plant parts (i.e. leaves, roots, tillers and ramets) relates to resource storage and pre-emption at low resource supplies, (ii) how interspecific differences in resilience of individual plants to non-lethal disturbances influence competitive outcomes along resource supply gradients and (iii) how storage indirectly affects competitive outcomes along resource supply gradients by selectively favouring increased disturbance resistance. I therefore argue that it is necessary to examine interspecific trade-offs between resource storage and disturbance resilience and between disturbance resilience and disturbance resistance.

Although resource storage is widely recognized to increase tolerance of environments characterized by low resource availability (Grime 1979; Chapin, Schulze & Mooney 1990), it could also give a species a competitive advantage in these environments by enabling it to pre-empt resources (Brewer 2003; Craine, Fargione & Sugita 2005; Semchenko, Zobel & Hutchings 2010). This is because storage requires the production of persistent plant parts, which occupy and consume space and associated resources for longer periods of time than do less persistent plant parts (Brewer 2003; Semchenko, Zobel & Hutchings 2010). Ecologists have long recognized that tolerance of low resource supplies and competitive ability are not mutually exclusive (Goldberg 1990). Nevertheless, the relative importance of resource concentration reduction and pre-emption as mechanisms by which one species displaces another at low resource supplies remains a point of contention (Brewer 2003; Craine, Fargione & Sugita 2005; Dybzinski & Tilman 2007). Perhaps a demonstration of how resource storage by individual plants leads to increased pre-emption (and thus competitive dominance) could help clarify this issue.

Conservative resource use and storage often trade-off with maximum photosynthetic rates (Grime & Hunt 1975; Chapin, Schulze & Mooney 1990), the latter of which can affect the rate of recovery of individual plants from disturbances (i.e. disturbance resilience). Species that are resilient to disturbance potentially gain a competitive advantage by rapid exploitation of unoccupied patches (Semchenko, Zobel & Hutchings 2010) and interfering with recovery of slower-growing species from

disturbance. The effectiveness of such a strategy, however, may depend on site productivity (i.e. gross resource supply). Gradients in gross resource supply among sites are often strongly linked to soil fertility gradients. Within a site, disturbances potentially increase net resource supply by increasing the availability of light and/or soil resources. Hence, if rates of photosynthesis are strongly limited by both light and soil fertility, then the competitive advantage of disturbance-resilient species is predicted to increase with native soil fertility and with disturbances that kill portions of genets.

In contrast to traits that promote disturbance resilience, plant traits that confer higher disturbance resistance (e.g. effective resprouting from below-ground reserves) are often associated with species that grow slowly, use resources conservatively and exhibit prolonged storage (Grime 1979; Midgley 1996). Because prolonged storage requires the production of persistent plant parts, these parts potentially remain vulnerable to physical disturbances such as wildfires or attack by herbivores for longer periods of time than do ephemeral plant parts (Coley, Bryant & Chapin 1985; Bazzaz *et al.* 1987; Christensen 1993). Furthermore, because storage often trades off with maximum photosynthetic rates (Grime & Hunt 1975; Chapin, Schulze & Mooney 1990), recovery from disturbance may be slower unless stored reserves are protected or defended (Coley, Bryant & Chapin 1985; Bond & Midgley 2001). If resistance to a given disturbance (e.g. fire) is greater in species with greater storage than in resilient species, then increased frequencies or intensities of such disturbances throughout a soil fertility gradient could allow the former species to expand into habitats of somewhat higher resource supply (Surrette, Aquilani & Brewer 2008). Conversely, maintenance of disturbances that damage all species more or less equally should give disturbance-resilient species a competitive advantage over species that sacrifice high photosynthetic rates in favour of greater resource storage.

In this study, I examined an interspecific trade-off between resource storage and disturbance resilience and its effect on competitive outcomes and disturbance resistance along a resource supply gradient. I considered the effects of resource storage, disturbance resistance and disturbance resilience on the growth and size of individual plants with modular construction (i.e. plants that grow by increasing the number of ramets, tillers, branches, roots or leaves; Harper 1977), thereby permitting the use of the familiar Lotka–Volterra competition equations. I examined changes in competitive outcomes with increasing gross resource supply, with and without disturbances having non-selective lethal effects (density-independent module mortality), and with and without disturbances having differential effects on module mortality. I assumed that resource storage was associated with inherently low module mortality (persistence), which potentially provided a size advantage at low gross resource supplies, but traded off with maximum net photosynthesis rates and thus disturbance resilience. I hypothesized that resource storage increased competitive ability in environments with low gross resource supplies and that disturbance resilience increased competitive ability in environments with high gross resource supplies. I also hypothesized that the competitive outcomes predicted by the

trade-off between resource storage and disturbance resilience selectively favoured greater disturbance resistance in species with greater storage. I predicted that such an increase in disturbance resistance would improve the competitive ability of these species in moderately resource-rich, disturbance-prone environments. The current treatment differs from but complements another recent treatment of a disturbance resistance–resilience trade-off (Miller & Chesson 2009) in that it focuses specifically on how the resistance–resilience trade-off interacts with resource supply to influence competitive dominance rather than how such a trade-off maintains species coexistence via a storage effect in a patchy environment.

### Modelling plant size and competition along a resource supply gradient

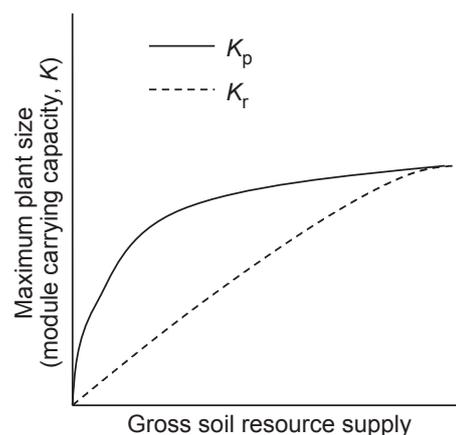
The basic premise of the model is that the species that produces a sufficiently larger genet in the face of sub-lethal disturbances at a given gross resource supply will be the superior competitor (see also Sackville Hamilton, Schmid & Harper 1987). Consider two individual adult perennial plants of similar growth form growing together with intermixed ramets and assume that an interspecific trade-off exists between module longevity (which is assumed to be necessary for resource storage) and maximum net photosynthesis rate (measured in module equivalents and assumed to be a positive function of photosynthetic rate per gram of leaf when resources are abundant). An individual of each species is treated as a population of modules or plant parts (a genet). There is no seed production, seedling recruitment or senescence of genets. Mortality of a perennial and potentially immortal genet results from the extinction of the module population.

#### MODULE LIFE HISTORY AND THE RELATIONSHIP BETWEEN COMPETITION AND RESOURCE SUPPLY

Before explicitly considering the effects of disturbances on competition, let's first consider how interspecific differences in module life history influence competitive interactions. Let the species with high module longevity be the 'persistent' species (species p) and the species with high module birth rate be the 'resilient' species (species r). Assume that a certain fraction of the module mortality rate (per year) is caused by senescence and does not vary with density and is species specific, whereby  $s_p$  (senescence rate of the persistent species)  $<$   $s_r$  (senescence rate of the resilient species). The rationale for assuming that senescence is density-independent is based on the notion that modules that are already established at a given spot are likely to resist displacement by later-arriving modules (the condition described as pre-emption). In addition, because storage requires persistent organs (modules), the species that produces more persistent modules is likely to be more effective at storing resources. Assume that the maximum net photosynthesis rate or  $r_i$  (in units module per module per year) is greater in the resilient species than in the persistent species. Although  $r_i$ , itself, is assumed to be a maximum potential rate and is density-independent, the realized net photosynthesis rate (see

below) is assumed to decline with increasing density and competition as net resource supply decreases. Realized net photosynthesis rates can become negative at high densities if photosynthesis rates are lower than respiration rates. I assume that the module carrying capacity of each species,  $K_i$  (i.e. the maximum expected plant size in a given environment in the absence of interspecific competition), is a function of: (i) the gross soil resource supply of a given environment and (ii) the ability to maintain size during periods of resource scarcity (Grime & Hunt 1975). Consistent with classic life history theory for populations (e.g. Cody 1966; Williams 1966), I assume that greater storage allows genets of the persistent species to better maintain size during periods of resource scarcity. Because storage requires persistent organs (modules), I assume that the species that produces more persistent modules is likely to be more effective at storing resources. The benefit of greater storage is accomplished in the model by assigning a higher module carrying capacity to the persistent species than to the resilient species (i.e.  $K_p > K_r$ ) at low gross resource supplies (Fig. 1). Module carrying capacity of both species increases with gross soil resource supply, but carrying capacities of the two species converge as the average of  $K_p$  and  $K_r$  increases (Fig. 1). This convergence in  $K$  with increasing gross resource supply is based on the assumption that the advantage of resource storage diminishes as periods of resource scarcity become less frequent. The gradient in gross resource supply envisioned here is a soil fertility gradient. In ecosystems other than forests (e.g. grasslands, woodlands and savannas), I assume that tree density is kept low (and gross light levels kept high) throughout the fertility gradient by disturbances such as fire, grazers or non-resource-related factors that limit tree establishment, but not by soil resource supply. The net supply of light to a given module is assumed to be density dependent.

We can represent the growth of a single genet from each of the two species in competition with one another using a



**Fig. 1.** Assumed relationship between maximum plant size in a given environment (module carrying capacity) and gross soil resource supply for a species well developed resource storage capacity (the persistent species, species p) and a species capable of high maximum net photosynthesis rates (the resilient species, species r).

modified version of the familiar Lotka–Volterra competition equations:

$$\frac{\Delta N_p}{\Delta t} = r_p N_p \left(1 - \frac{N_p}{K_p} - c_{pr} \frac{N_r}{K_p}\right) - s_p N_p \quad \text{eqn 1}$$

$$\frac{\Delta N_r}{\Delta t} = r_r N_r \left(1 - \frac{N_r}{K_r} - c_{rp} \frac{N_p}{K_r}\right) - s_r N_r \quad \text{eqn 2}$$

where  $c_{pr}$  is the per module competitive effect of the resilient species on the persistent species and  $c_{rp}$  is the per module competitive effect of the persistent species on the resilient species. The per-capita realized net photosynthesis rate is equal to  $r_i$  multiplied by the feedback term in parentheses in eqns 1 and 2.

Assuming  $c < 1$ , the equilibrium module densities of each species can be obtained by setting  $\Delta N/\Delta t = 0$  and simplifying to obtain:

$$\hat{N}_p = K_p \left(1 - \frac{s_p}{r_p}\right) - c_{pr} N_r \quad \text{eqn 3}$$

$$\hat{N}_r = K_r \left(1 - \frac{s_r}{r_r}\right) - c_{rp} N_p \quad \text{eqn 4}$$

If we assume that both  $s_r/r_r$  and  $s_p/r_p$  are less than 1, and let the growth constant,  $g_i$ , equal  $1 - s_i/r_i$ , assume  $c_{rp} = c_{pr} = c$ , and substitute the equilibrium density of the competing species into eqns 3 and 4, we get

$$\hat{N}_p = \frac{g_p K_p - c g_r K_r}{1 - c^2} \quad \text{eqn 5}$$

$$\hat{N}_r = \frac{g_r K_r - c g_p K_p}{1 - c^2} \quad \text{eqn 6}$$

The species that produces the larger genet at equilibrium within a patch (i.e. has the greater  $\hat{N}$ ) depends on  $g$ ,  $c$  and  $K$ . At low resource supplies, we assume that  $K_p > K_r$ . Therefore, the persistent species will have a size advantage over the resilient species at low resource supplies, provided that any growth advantage that the resilient species might have over the persistent species (i.e.  $g_r/g_p$ ) is sufficiently low. The conditions necessary for the persistent species to competitively exclude the resilient species can be found by setting  $\hat{N}_r \leq 0$  in eqn 6 and simplifying. If the disparity between  $K_p$  and  $K_r$  is great enough such that  $K_p g_p / K_r g_r \geq 1/c$ , the persistent species will competitively exclude the resilient species.

The advantage that the persistent species has at low resource supplies results from competition and not from the resilient species' inability to persist in monoculture. Recall that we assumed that both  $s_p/r_p$  and  $s_r/r_r$  were less than 1. Persistence of either species in monoculture simply requires that  $s_i < r_i$ . On the other hand, competitive superiority of the persistent species at low resource supplies does not result from the competitive superiority of individual modules because we assumed that  $c_{pr} = c_{rp}$  and  $c$  does not change with resource supply. We could relax this assumption and make  $c$  contingent upon allocation to roots or stems, which could make a given ramet a better competitor for either soil resources or light, respectively, as predicted by the resource-ratio hypothesis for higher plants

(i.e. ALLOCATE; Tilman 1988). Irrespective of any ramet-level differences in competitive ability, however, the higher module carrying capacity of the persistent species results in the persistent species having a higher gross (i.e. per genet) competitive effect on the resilient species. The ratio  $K_p g_p c / K_r g_r$  can be thought of as a per genet competition coefficient (for the effect of the persistent species on the resilient species). The greater this value is the greater the competitive effect of the persistent species on the resilient species at the level of the genet population, all else equal. Given the assumption that  $K_p - K_r$  decreases with increasing resource supplies (average  $K$ ), the benefit of resource storage diminishes, and the ability of the persistent species to out-compete the resilient species decreases with increasing resource supplies.

The advantage that the resilient species has over the persistent species at high resource supplies results from interspecific differences in intrinsic growth rates ( $g_i$ ). Given that  $g_r$  is sufficiently greater than  $g_p$ , the competitive advantage that the resilient species has over the persistent species should increase with resource supply, as  $K_r$  approaches  $K_p$  and thus the advantage of resource storage diminishes. The prediction that interspecific differences in  $g_i$  affect competitive outcomes is based on the assumption that the realized net photosynthesis rate is density dependent but senescence is not. If all mortality were assumed to be density dependent and  $c_i$  was the same for both species, the competitive outcome would depend only on differences in  $K_i$ .

#### THE EFFECT OF DIFFERENCES IN DISTURBANCE RESILIENCE ON COMPETITION ALONG A RESOURCE SUPPLY GRADIENT

Aside from interspecific differences in  $K$  and  $g$ , another parameter that could influence the competitive outcome between genets is the overall level of density-independent module mortality resulting from disturbance; i.e. the overall intensity of disturbances that neither species can tolerate. These disturbances in effect damage a portion of each genet and thus are analogous to disturbances such as low-intensity fires or wind or ice damage. Such disturbances might damage only the above-ground portions of a clonal perennial herb or shrub (as in the case of fire) or might affect only a portion of the crown of a tree (as in the case of wind or ice damage). They do not kill entire genets. The effect of these disturbances can be explicitly incorporated into the Lotka–Volterra competition equations to determine competitive outcomes at equilibrium. In this case, disturbances occur at a constant rate (Hastings 1980). Here, we simply add an additional term to eqns 1 and 2 as follows:

$$\frac{\Delta N_p}{\Delta t} = r_p N_p \left(1 - \frac{N_p}{K_p} - c_{pr} \frac{N_r}{K_p}\right) - s_p N_p - d N_p \quad \text{eqn 7}$$

$$\frac{\Delta N_r}{\Delta t} = r_r N_r \left(1 - \frac{N_r}{K_r} - c_{rp} \frac{N_p}{K_r}\right) - s_r N_r - d N_r \quad \text{eqn 8}$$

In this case,  $d$  is the per-capita instantaneous death rate of modules resulting from disturbance [(i.e. density-independent

factors that cause damage and are unrelated to module life history as described in Gause 1934; Slobodkin 1961)]. Because  $d$  is an instantaneous rate, the model presented here does not explicitly address the issue of how the frequency of disturbances affects competitive displacement (as described by Huston 1979). Accordingly,  $d$  is a measure of disturbance severity. By severity I mean the instantaneous rate of density-independent module mortality due to tissue damage. Numerical simulations involving varying frequencies and severities of disturbances (the results of which are not shown here) revealed qualitatively similar predictions to those of the analytical model (as long as the frequency was the same for both species). In this example, neither species is more resistant to the types of disturbance quantified by  $d$ . Just as with eqns 1 and 2, we can set  $\Delta N/\Delta t$  equal to zero to obtain the equilibrium module densities for each species:

$$\hat{N}_p = K_p \left(1 - \frac{s_p}{r_p} - \frac{d}{r_p}\right) - c_{pr} N_r \quad \text{eqn 9}$$

$$\hat{N}_r = K_r \left(1 - \frac{s_r}{r_r} - \frac{d}{r_r}\right) - c_{rp} N_p \quad \text{eqn 10}$$

To determine the two species stable equilibrium (i.e.  $\hat{N}_p$  and  $\hat{N}_r > 0$ ), let the growth constant,  $g_i$ , equal  $1 - s_i/r_i$ , where  $g_i > 0$ , assume  $c_{rp} = c_{pr} = c < 1$ , and substitute  $\hat{N}_r = K_r (1 - s_r/r_r - d/r_r) - c_{rp} N_p$  for  $N_r$  in eqn 9 to obtain

$$\hat{N}_p = \frac{K_p(g_p - \frac{d}{r_p}) - cK_r(g_r - \frac{d}{r_r})}{1 - c^2} \quad \text{eqn 11}$$

Analogously, the two species stable equilibrium density for the resilient species is

$$\hat{N}_r = \frac{K_r(g_r - \frac{d}{r_r}) - cK_p(g_p - \frac{d}{r_p})}{1 - c^2} \quad \text{eqn 12}$$

Equations 11 and 12 reveal that the predicted size advantage one species has over the other in mixture is a function of  $d$  and differences in  $K$ ,  $r$  and  $g$ . With the addition of disturbance, we find that the resilient species will have a size advantage over the persistent species in mixture (i.e.  $\hat{N}_r > \hat{N}_p$ ) when  $0 < c < 1$ , provided that:

$$\frac{g_r - \frac{d}{r_r}}{g_p - \frac{d}{r_p}} > \frac{K_p}{K_r} \quad \text{eqn 13}$$

The left side of inequality 13 represents the rate of recovery from disturbance of the resilient species divided by the rate of recovery from disturbance of the persistent species. Therefore, the resilient species will have a size advantage over the persistent species if its relative advantage in terms of recovery from disturbance is greater than the relative advantage in maximum genet size of the persistent species over the resilient species as determined by gross resource supply (i.e.  $K_p/K_r$ ). The resilient species gains a competitive advantage because the more rapid recovery of the resilient species from disturbance allows it to interfere with the recovery of the persistent species from disturbance to a greater extent than *vice versa* [i.e.  $cK_r(g_r - d/r_r) > cK_p(g_p - d/r_p)$ ; see eqns 11 and 12].

The conditions necessary for the resilient species to competitively exclude the persistent species can be found by setting  $\hat{N}_p \leq 0$  in eqn 11 and simplifying. For  $g_i > d/r_i$  and  $0 < c < 1$ , the resilient species will competitively exclude the persistent species if

$$\frac{K_r(g_r - \frac{d}{r_r})}{K_p(g_p - \frac{d}{r_p})} \geq \frac{1}{c} \quad \text{eqn 14}$$

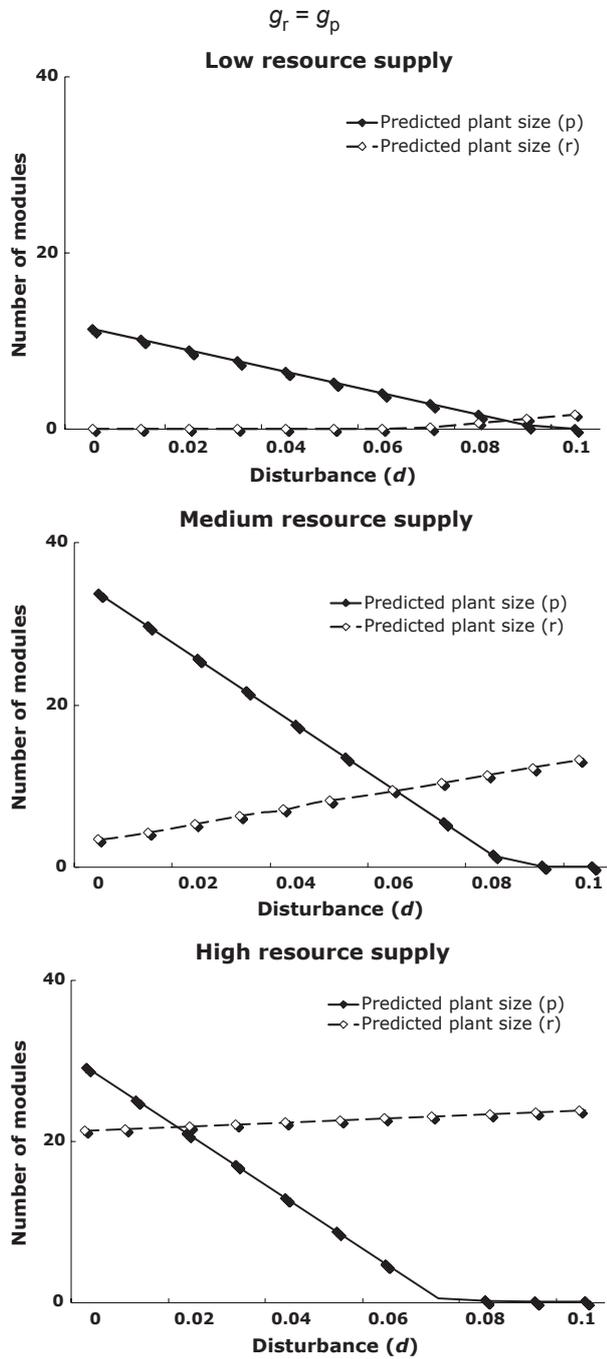
Whether or not a predicted size advantage will result in competitive displacement depends on  $c$ ; as  $c$  increases, the size advantage necessary for competitive displacement decreases. Assume for the moment that  $g_p = g_r$  and  $r_r > r_p$ . The competitive effect of the resilient species on the persistent species increases with increasing resource supply *and with increasing  $d$*  (as evident from the increasing predicted size ratio in Fig. 2). Sufficiently low disturbance is necessary for the persistent species to effectively compete with the resilient species at high resource supplies, whereas sufficiently high disturbance is necessary for the resilient species to effectively compete with the persistent species at low resource supplies (Fig. 2). The relationship between competition and resource supply therefore depends critically on the occurrence of density-independent module mortality to which neither species is adapted. However, if  $g_r$  is sufficiently greater than  $g_p$  (and  $c$  is sufficiently high), then the resilient species can displace the persistent species at high resource supplies, even in the absence of disturbance (Fig. 3).

#### THE EFFECT OF DIFFERENCES IN DISTURBANCE RESISTANCE ON COMPETITION ALONG A RESOURCE SUPPLY GRADIENT

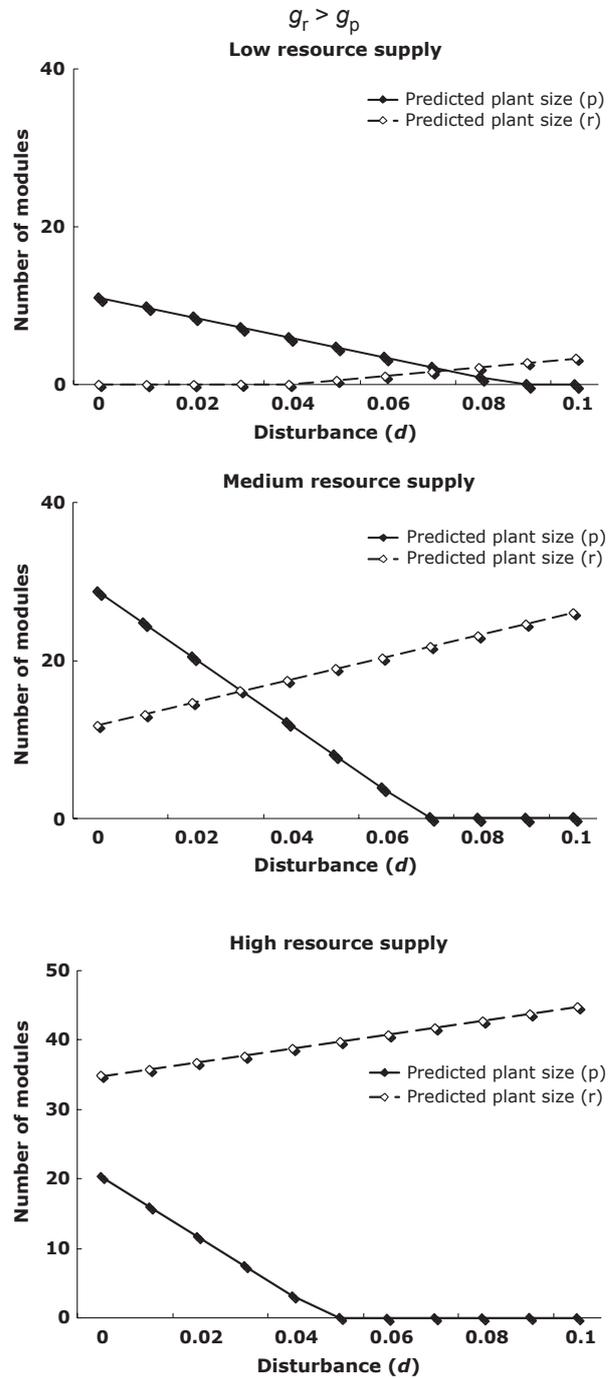
Examination of inequality 14 and Figs 2 and 3 reveals that an increase in  $d$  has a greater negative effect on the persistent species than on the resilient species. This is because  $r_p < r_r$ . It therefore stands to reason that the persistent species would benefit more from a reduction in disturbance than would the resilient species. If so, the selection pressure for increased disturbance resistance should be greater in the persistent species than in the resilient species. If the persistent species evolves greater resistance to a particular disturbance such as fire, then disturbance resistance could increase its competitive ability in more resource-rich environments that are also fire-prone.

To determine how greater disturbance resistance in the persistent species influences the competitive outcome between the two species, we can modify eqns 9 and 10 so that  $d$  is species specific (such that  $d_p < d_r$ ) and then solve for the two-species equilibrium as before. Doing so produces the following equations:

$$\hat{N}_p = \frac{K_p(g_p - \frac{d_p}{r_p}) - cK_r(g_r - \frac{d_r}{r_r})}{1 - c^2} \quad \text{eqn 15}$$



**Fig. 2.** Predicted relationship between plant size at competitive equilibrium (number of modules) and disturbance in three environments that differed in gross resource supply (average  $K$ ). Parameters are defined as follows:  $g$  is the senescence-adjusted growth rate ( $1-s/r$ );  $r$  is the maximum per module instantaneous growth rate,  $s$  is the module senescence rate,  $c$  is the competition coefficient,  $K$  is the maximum genet size expressed in terms of module density, and  $d$  is the instantaneous per module mortality rate from disturbance. Parameter values are as follows:  $g_p = g_r = 0.5$ ,  $r_p = 0.2$ ,  $r_r = 0.6$ ,  $s_p = 0.1$ ,  $s_r = 0.2$ ,  $c_{pr} = c_{rp} = 0.5$ ;  $K_{p-low} = 20$ ,  $K_{r-low} = 5$ ;  $K_{p-medium} = 70$ ,  $K_{r-medium} = 40$ ;  $K_{p-high} = 77.5$ ,  $K_{r-high} = 70$ .



**Fig. 3.** Predicted relationship between plant size at competitive equilibrium (number of modules) and disturbance in three environments that differed in gross resource supply (average  $K$ ).  $g$  is the senescence-adjusted growth rate ( $1-s/r$ );  $r$  is the maximum per module instantaneous growth rate,  $s$  is the module senescence rate,  $c$  is the competition coefficient,  $K$  is the maximum genet size expressed in terms of module density, and  $d$  is the instantaneous per module mortality rate from disturbance. Parameter values were as follows:  $g_p = 0.5$ ,  $g_r = 0.66$ ,  $r_p = 0.2$ ,  $r_r = 0.6$ ,  $s_p = 0.1$ ,  $s_r = 0.2$ ,  $c_{pr} = c_{rp} = 0.5$ ;  $K_{p-low} = 20$ ,  $K_{r-low} = 5$ ;  $K_{p-medium} = 70$ ,  $K_{r-medium} = 40$ ;  $K_{p-high} = 77.5$ ,  $K_{r-high} = 70$ .

$$\hat{N}_r = \frac{K_r(g_r - \frac{d_r}{r_r}) - cK_p(g_p - \frac{d_p}{r_p})}{1 - c^2} \quad \text{eqn 16}$$

The persistent species will have a size advantage over the resilient species in mixture when  $0 < c < 1$ , provided that:

$$(g_p - \frac{d_p}{r_p})K_p > (g_r - \frac{d_r}{r_r})K_r \quad \text{eqn 17}$$

The persistent species is predicted to have a size advantage over the resilient species when differences in  $K$  are large (i.e. when gross resource supply is low), when differences in  $g_i$  are relatively small and/or when  $d$  is either low or significantly lower for the persistent species than for the resilient species (i.e. when disturbance resistance is sufficiently greater in the persistent species than in the resilient species). The resilient species is expected to have a size advantage over the persistent species when differences in  $K$  are small (i.e. when gross resource supply is high), when  $g_r \ll g_p$  and/or when  $d$  is relatively high and similar for the two species. Greater resistance of the persistent species to disturbance potentially negates the advantage the resilient species has with respect to higher photosynthetic rate following disturbance. Consequently, disturbance resistance allows the persistent species to interfere with the recovery of the resilient species from disturbance, as evident by contrasting  $cK_p(g_p - d_p/r_p)$  with  $cK_r(g_r - d_r/r_r)$  in eqns 15 and 16.

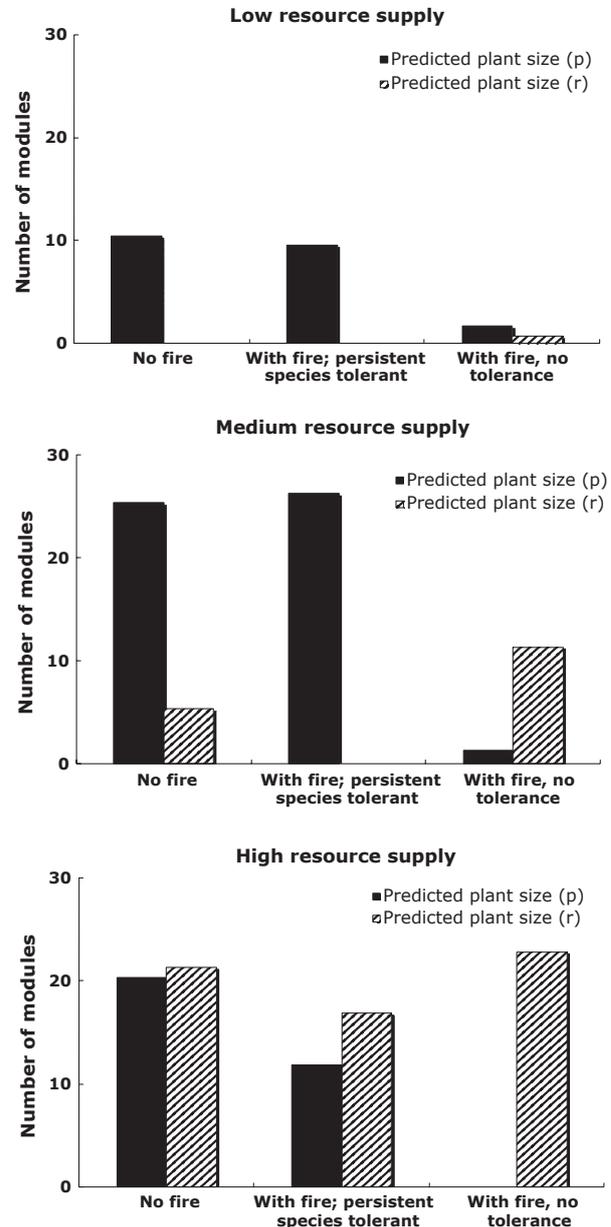
The conditions necessary for the persistent species to competitively exclude the resilient species can be found by setting  $\hat{N}_r \leq 0$  in eqn 16 and simplifying. For  $g_i > d_i/r_i$  and  $0 < c < 1$ , the persistent (and thus disturbance-resistant) species will competitively exclude the resilient species if

$$\frac{K_p(g_p - \frac{d_p}{r_p})}{K_r(g_r - \frac{d_r}{r_r})} \geq \frac{1}{c} \quad \text{eqn 18}$$

Examination of Fig. 4 shows how greater disturbance resistance (e.g. greater fire tolerance) in the persistent species could negate or reduce the competitive advantage the resilient species would otherwise have in resource-rich environments that are fire-prone. Conversely, in the case of fire suppression, such that  $d_p = d_r > 0$ , the resilient species could assume a competitive advantage over the persistent species, especially in areas of high resource supply (Fig. 4). Fire suppression (or the addition of fire) is predicted to result in competitive reversals in moderately productive habitats, whereas habitats with poor soils are predicted to be refugia for the persistent species during periods of fire suppression (Fig. 4). In highly resource-rich environments the benefits of fire tolerance are muted somewhat by the greater benefits of resilience to fire in these habitats. This suggests that there is a limit to the benefit of fire tolerance in resource-rich environments.

## Discussion

In this paper, I explicitly developed the argument that interspecific differences in resource storage and the occurrence of disturbances (destruction of biomass) potentially result in the competitive exclusion of one plant by another by increasing



**Fig. 4.** Predicted effects of two hypothetical fire regimes (with fire, without fire) and interspecific differences in fire tolerance on competition between a persistent and a resilient species. Low resource supply = Average  $K$  of 12.5 modules. Medium resource supply = Average  $K$  of 55 modules. High resource supply = Average  $K$  of 73.8 modules. Parameters of the competition equations are the same as in Figure 2. Values of  $d$  (instantaneous rate of module mortality due to disturbance) are as follows: No Fire –  $d_p = d_r = 0.02$ ; With Fire and Tolerance in Persistent Species –  $d_p = 0.02$ ,  $d_r = 0.08$ ; With Fire and No Tolerance –  $d_p = 0.08$ ,  $d_r = 0.08$ .

interspecific differences in plant size. In particular, I showed how enhanced storage of resources can result in the competitive exclusion of species with reduced capacity for resource storage in resource-poor environments and how the occurrence of damage to portions of the genet that no species can resist can result in the competitive exclusion of species with low growth rates in resource-rich environments. In addition, I

showed how competition between a species with high resource storage and a disturbance-resilient species can select for greater disturbance resistance in the species with greater resource storage. As a result, disturbances increase the competitive effect of the species with high resource storage on the resilient species. These predictions run counter to the prevailing view among ecologists that disturbances prevent competitive exclusion, especially in resource-rich environments (Burke & Grime 1996) and the view that resource storage trades off with competitive ability (Grime 1979). In contrast to previous considerations of disturbance, I assumed that disturbances differentially affected the sizes and recovery rates of individual established plants rather than the mortality of established adults and subsequent recruitment by juveniles (Grubb 1977). I consider three important predictions of the model presented here, discuss the available evidence in support of the hypothesis, and suggest future research needed to test the hypothesis.

PREDICTION 1: RESOURCE STORAGE PROVIDES A COMPETITIVE ADVANTAGE WHEN RESOURCE SUPPLIES ARE LOW

An important prediction of the DMCH is that a species that effectively stores resources can out-compete a disturbance-resilient species at low nutrient supplies. This prediction results from the model assumption that interspecific differences in competitive ability are more a function of the ability to maintain genet size at low resource supplies than of interspecific differences in ramet competitive ability. Consequently, greater tolerance of low resource supplies (i.e. greater stress tolerance, to use Grime's terminology) *could explain* competitive superiority of stress tolerant species over less stress tolerant species at low resource supplies (Goldberg 1990; Brewer 2003). In contrast to the predictions of the resource-ratio hypothesis for higher plants (i.e. ALLOCATE; Tilman 1988), competitive superiority at low soil resource supplies need not be related to allocation to roots. Because effective storage requires the production of persistent modules (e.g. tillers, ramets), increased ramet persistence, irrespective of root allocation, could lead to greater pre-emption and thus a competitive advantage in infertile soils (Semchenko, Zobel & Hutchings 2010). As gross resource supply increases (and module carrying capacities converge; Fig. 1), interspecific differences in growth rates ( $g$ ) become relatively more important in determining genet size and thus competitive ability, provided that realized net photosynthesis rates are density dependent and module senescence rates ( $s_i$ ) are not (compare Figs 2 and 3 for no disturbance). In a 3-year field experiment, I examined the effect of nutrient addition on competition between two long-lived clonal perennial plants (*Juncus roemerianus*, a species with more persistent tillers) and *Spartina alterniflora* (a species with less persistent tillers but that exhibited higher tillering and clonal growth rates, which were strongly limited by nutrients). The two species occurred in adjacent zones that differed in nutrient supply from tides (Brewer 2003). I found that *J. roemerianus* had a competitive advantage in the low nutrient zone. Nutrient addition allowed *S. alterniflora* to increase its ability to vegetatively

colonize openings in the *Juncus*-dominated zone, but it did not reduce below-ground competition (i.e. the log reduction in shoot densities of *S. alterniflora* by below-ground parts of *J. roemerianus* neighbours). This result suggested that greater tolerance of low nutrient supplies enabled *J. roemerianus* to maintain larger genets than *S. alterniflora* in the low nutrient zone, thereby giving *J. roemerianus* a competitive advantage. Hence, despite having similar genet life histories, competitive interactions between these two species appeared to have been driven by differences in plant part (e.g. tiller) life histories. Future research on the relationship between competition and productivity must account for interspecific differences in plant part life history (i.e. leaf or tiller longevity, tillering rates), not just differences in plant life history (i.e. genet longevity, reproductive effort, seed size).

PREDICTION 2: DISTURBANCE RESILIENCE INCREASES COMPETITIVE ABILITY OF PLANTS WITH HIGH PHOTOSYNTHESIS RATES

Contrary to the generally accepted view that disturbances must be eliminated from competition experiments to accurately measure the potential for competition to structure plant communities, I suggest that the opposite is true. Most long-term competition experiments purposely exclude any type of disturbance, or when disturbances are incorporated, their interaction with competition is generally not monitored over the long term. Long-term competition experiments that exclude disturbances (e.g. Dybzinski & Tilman 2007) have found that species with the lowest minimum resource requirements (i.e. the lowest  $R^*$ ) are better competitors than disturbance-resilient species with high clonal growth rates. Although not designed to test effects of disturbances on competition, several studies of natural disturbances provide suggestive evidence of increased competitive effects of one or more species on others following disturbance, especially under conditions of high resource availability (Collins, Glenn & Gibson 1995; Brose, Van Lear & Cooper 1999; Rajaniemi, Allison & Goldberg 2003; Gagnon & Platt 2008). One experimental study with old-field plants found that when light was not limiting (as might be expected in early successional or moderately disturbed habitats), the competitive effects of roots of neighbouring plants on target species increased with increasing soil fertility (Rajaniemi, Allison & Goldberg 2003). This result suggests that high growth rates of perennial plants in productive habitats such as recently disturbed fields on fertile soils can result in increased below-ground competition. Other studies have provided suggestive evidence of increased competitive effects of mesophytic and floodplain tree species on xerophytic tree species following canopy gap formation in fire-suppressed forests (Abrams 1992; Brose, Van Lear & Cooper 1999; Surrlette, Aquilani & Brewer 2008). Damage to canopy trees in these forests increases light levels (net resource supply) and thus provides a growth opportunity for smaller stems, which could be seedlings, saplings, stump sprouts, root sprouts or branches from downed (but living) trees. The model presented here assumes no seed production and therefore treats the growth of advance

recruits (i.e. large seedlings and saplings) as if it were equivalent to the growth of root or stump sprouts or branches following damage to the crown. Early successional species (e.g. *Liriodendron tulipifera*, *Liquidambar styraciflua*) and some shade-tolerant species (e.g. *Acer rubrum*) grow more rapidly in response to canopy gaps in fire-suppressed upland forests than do shade-intolerant, fire-tolerant *Quercus* spp. (Brose, Van Lear & Cooper 1999; Brewer 2001; Albrecht & McCarthy 2006; Iverson *et al.* 2008). The inability of oaks to effectively compete in canopy gaps is therefore explained better by their lack of disturbance resilience than by their lack of shade tolerance (at least on drier sites; Iverson *et al.* 2008). The competitive advantage that mesophytic species have over oaks in canopy gaps appears to be greater at more productive sites than at poorer sites (Abrams 1992; Brose, Van Lear & Cooper 1999; Iverson *et al.* 2008), which is also consistent with the DMCH. In productive upland soils in the Piedmont of the south-eastern USA, the tree species that has the greatest competitive effect on fire-tolerant oaks is *L. tulipifera*, a species known for its ability to respond rapidly to canopy gaps (Brose, Van Lear & Cooper 1999). In less productive upland areas of the Piedmont, however, oaks are better able to compete with mesophytic gap responders in fire-suppressed stands, provided there are sufficiently large canopy gaps (Brose, Van Lear & Cooper 1999).

PREDICTION 3: DISTURBANCE RESISTANCE  
INCREASES COMPETITIVE ABILITY OF PLANTS  
ADAPTED FOR RESOURCE STORAGE

The DMCH predicts that selection favouring disturbance resistance is greater in species that sacrifice high maximum net photosynthetic rates in favour of increased storage (i.e. persistent species) than in species that sacrifice storage in favour of increased maximum net photosynthetic rates (resilient species). The resulting interspecific differences in disturbance resistance may allow persistent species to expand into moderately resource-rich, disturbance-prone environments. The extent of this expansion is limited, however, by competition with resilient species because resilience is more beneficial in resource-rich environments. Also, the hypothesis predicts that suppression of disturbances that the persistent species can tolerate but the resilient species cannot will reduce and possibly reverse the competitive advantage of the persistent species over the resilient species, especially within environments that are moderately resource-rich.

Responses of mesophytic tree species and fire-tolerant oaks to canopy gaps and low-intensity fires illustrate the potential for disturbance resistance to influence competitive interactions. High below-ground allocation and storage in understory oaks permits tolerance of fire as well as dry and nutrient-poor soils. In fire-prone landscapes, there is considerable evidence that tolerance of low-intensity fires is positively associated with tolerance of low nutrient (or low moisture) soils (Christensen 1993). Indeed, some adaptations for fire tolerance (below-ground storage, fire-stimulated flowering) may also be adaptations for tolerance of low resource supplies (Kellman 1984; Brewer 1995). Repeated or relatively intense fires reduce the

sizes of genets of rapidly growing gap responders to a greater extent than for fire-tolerant oaks (e.g. through greater top-kill and depletion of limited stored reserves or complete-kill of stems), thereby potentially giving the disturbance-resistant oaks a competitive advantage (Johnson, Shifley & Rogers 2002; Iverson *et al.* 2008). The potential competitive advantage is also evident from more rapid regrowth of fire-damaged oak saplings (presumably from stored reserves) compared to that of their mesophytic competitors (Larsen & Johnson 1998; J.B. Cannon and J. S. Brewer, unpublished data).

In contrast to the situation seen today at fire-suppressed productive sites, upland oaks dominated and successfully regenerated within these stands prior to fire suppression (Surrette, Aquilani & Brewer 2008). Hence, as predicted by the DMCH, frequent fires allowed xerophytic oaks to effectively compete with and perhaps displace mesophytic species at moderately productive sites in the past (Surrette, Aquilani & Brewer 2008), an effect that has been reversed by modern fire suppression. This result is consistent with the results of a general survey of resprouting of woody plants along productivity gradients in Australia, which suggested that resprouting was more important in increasing competitive ability in moderately productive habitats than in unproductive habitats (Clarke *et al.* 2005). Although it is commonly assumed that the absence or low abundance of mesophytic species from fire-prone uplands is solely the result of their lack of fire tolerance (Brewer 2001), the DMCH predicts that competitive displacement by fire-tolerant species could play an important role. More studies that examine interactions between competition and realistic physical disturbances are needed.

## Acknowledgements

I thank Jason Hoeksema, Jeff Cannon and three anonymous reviewers for helpful comments on the manuscript. The ideas for this paper were inspired in part by twenty years of data and observations on the effects of natural disturbances (fire, burial by plant debris, storm surges and wind damage) on plants and, more recently, by data and observations associated with a study of tornado damage and salvage logging. This work was funded by a Joint Venture between the University of Mississippi and USDA Forest Service Southern Research Station, Center for Bottomland Hardwoods Research (08-JV11330127-030), P.I., J.S.B.

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Received 11 November 2010; accepted 21 April 2011

Handling Editor: Thomas Kitzberger