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Resource competition and fire-regulated nutrient demand in carnivorous plants of wet pine savannas

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Abstract

Question: What are the mechanisms by which fire reduces competition for both a short-lived and a long-lived species in old-growth ground-cover plant communities of wet pine savannas (originally *Pinus palustris*, replaced by *P. elliottii*)?

Location: Outer coastal plain of southeastern Mississippi, USA.

Methods: I reviewed previous competition experiments and proposed a new hypothesis to explain the relationship between fire, competition, and species co-existence in wet longleaf pine savannas. The first study is about growth and seedling emergence responses of a short-lived carnivorous plant, *Drosera capillaris*, to reduction in below-ground competition and above- plus below-ground competition. The second study deals with growth and survival responses of a long-lived perennial carnivorous plant, *Sarracenia alata*, to neighbour removal and prey-exclusion to determine if a reduction in nutrient supply increased the intensity of competition in this nutrient-poor system.

Results: Fire increased seedling emergence of the short-lived species by reducing above-ground competition through the destruction of above-ground parts of plants and the combustion of associated litter. Prey exclusion did not increase competitive effects of neighbours on the long-lived species. However, because the experiment was conducted in a year without fire, shade reduced nutrient demand, which may have obviated competition for soil nutrients between *Sarracenia alata* and its neighbours.

Conclusion: Repeated fires likely interact with interspecific differences in nutrient uptake to simultaneously reduce both above-ground competition and competition for nutrients in old-growth ground cover communities in pine savannas. Restoration practitioners should consider the possibility that the composition of the plant community is just as important as fire in ensuring that frequent fires maintain species diversity.

Keywords: Co-existence; Diversity; Litter; Niche complementarity; Phenotypic plasticity; *Pinus elliottii*; *Pinus palustris*.

Nomenclature: Clewell (1985) and Schnell (1976).

Introduction

Managing biodiversity in fire-dependent ecosystems requires an understanding of the link between soˇ□idÛ differences and the effects of fire on competitive interactions. Old-growth ground cover plant communities of longleaf pine (*Pinus palustris*) ecosystems are among the most diverse in North America (Peet & Allard 1993). In 1983, Walker & Peet proposed several hypotheses to explain this extraordinary plant species diversity in *Pinus palustris* savannas. One hypothesis was that frequent fires reduced the intensity of competition between plants. In theory, when combined with the low growth rates of plants growing in nutrient-poor soils, frequent low-severity disturbances such as fire could be important in maintaining species diversity by reducing rates of competitive displacement (*sensu* Huston 1979). Hence, frequent fires maintain a non-equilibrium co-existence of species in pine savannas (Walker & Peet 1983). Another hypothesis was that substantial interspecific differences in resource use (i.e. niche complementarity; e.g., phenological variation) could maintain an equilibrium co-existence of plant species (Newman 1973). Until recently there has been no attempt to examine the mechanisms associated with the effects of fire and niche complementarity on species co-existence in pine savannas. This paper describes attempts to answer the following two questions: 1. Does fire reduce the intensity of competition between plants and if so by what mechanism(s)? 2. Do differences in nutrient use between carnivorous pitcher plants and their non-carnivorous neighbours (i.e., nutrient-niche complementarity) contribute to co-existence of these species in pine savannas?

Then it is explained why fire-mediated co-existence and niche complementarity are not mutually-exclusive hypotheses and why recognizing the link between fire and niche complementarity is crucial to understanding the role that fire plays in maintaining biodiversity and ecosystem function.

Material and Methods

The study system

Fire-maintained wet pine savannas in southeastern Mississippi (USA) are essentially wetlands with a sparse scattering of trees. The sparse tree canopy was originally dominated in the overstorey by *Pinus palustris* (longleaf pine) (Hilgard 1860; Harper 1914), but this species was largely replaced by *Pinus elliottii* (slash pine) following logging and fire suppression in the early to mid-20th century. Nevertheless, the incredibly rich ground cover vegetation is essentially old-growth, with a species composition that is very similar to that found by Eugene Hilgard in the mid-19th century.

Wet pine savannas are useful study systems because:
1. The relatively pristine ground-cover communities have not experienced severe (i.e. lethal) disturbances. Plots discussed in this paper are at sites that have not been ditched or bedded or cultivated. The most important disturbances to the ground-cover of these systems are fires and crayfish burrowing (Brewer 1999a; b). Although fires are lethal to the seedlings of some trees (e.g. *Pinus elliottii*; Brewer unpubl.) and destroy above-ground parts of most herbs, neither type of disturbance causes significant mortality of most herbaceous plants or low shrubs. Hence, I reasoned that fire likely reduced above-ground competition, and the potential for below-ground competition was high after fire.
2. Wet pine savannas occur on nutrient-poor soils and are dominated by long-lived, slow-growing perennial grasses, sedges, and forbs. Consistent with the predictions of Newman (1973) and Tilman (1988), in the absence of niche complementarity, competition for nutrients would be expected to be intense in this system. Alternatively, slow plant growth may result in low rates of competitive displacement (Grime 1973; Huston 1979). 3. Wet pine savannas depend on frequent fires to maintain species diversity (Walker & Peet 1983; Glitzenstein et al. 2003). Despite the fact that fires cause very little mortality of ground-cover vegetation, they nonetheless appear to improve conditions for some species.
4. Wet pine savannas are a prime habitat for a variety of carnivorous plants. The value of studying carnivorous plants is twofold: (1) carnivorous plants are suspected of being particularly vulnerable to reductions in fire frequency (Roberts & Oosting 1958; Walker & Peet 1983; Barker & Williamson 1988; Brewer 1999a; Glitzenstein et al. 2003); (2) carnivorous plants co-occur with non-carnivorous plants in pine savannas, but they appear to occupy a different 'nutrient niche'. Examining the responses of carnivorous plants to fire, neighbour removal, and nutrient-niche manipulation provides a unique opportunity to test the effects of fire and niche complementarity on competitive interactions.

Here, the results of two experiments (Brewer 1999a, 2003a) are reviewed, which examined the mechanisms of fire effects and nutrient-niche complementarity, respectively.
Details of the experimental designs are provided in those papers.

How does fire reduce competition? Effects of fire and competition on Drosera capillaris (Brewer 1999a)

The effects of fire and competition on recruitment of pink sundews were assessed by examining the effects of live neighbours, standing dead, and litter on seedling densities within burned and unburned sites. Two different types of competition-reduction treatments were imposed to partition the effects of competition from live vegetation from the inhibitory effects of standing dead plant material and litter on sundews. The experimental design included an undisturbed reference (full competition), vegetation treated with herbicide but with dead material left in place (below-ground competition reduced), and vegetation treated with herbicide and removed (no competition). In December, plots were censused to obtain 'pre-fire' estimates of seedling densities and re-censused in March, May, and August to obtain 'post-fire' records of seedling densities.

Do pitcher plants and non-carnivorous plants occupy different nutrient niches? Effects of prey exclusion and neighbour removal growth and allocation patterns in pitcher plants (Brewer 2003a)

It was assumed that if carnivorous plant growth were primarily nutrient limited and if nutrient-niche complementarity between carnivorous plants and their neighbours were important for species co-existence, then removal of neighbours should have only a modest effect on the growth of carnivorous plants. Furthermore, if prey capture enabled carnivorous plants to avoid below-ground competition for nutrients, then prey exclusion would have its greatest effect on growth when neighbour vegetation was left intact, resulting in a significant neighbour reduction × prey exclusion interaction.

To test the niche complementarity hypothesis, a field experiment was established using intact mixtures of established pitcher plants, *Sarracenia alata* (trumpet pitcher plant), and non-carnivorous plants within square plots of 0.25 m^2. *Sarracenia alata* produces pitchers which are leaves modified to capture insect prey, which provide an additional source of N and P, both of which are limiting nutrients in pitcher plants

(Christensen 1976). I used press (i.e. repeated and sustained) reduction in neighbouring plants of juvenile pitcher plants crossed with prey exclusion to test the hypothesis that excluding prey from pitcher plants would have a greater effect on growth when neighbours were left intact (due to below-ground competition for nutrients).

Four treatment combinations ($n = 20$) at each of two sites were possible: Neighbours Intact/Pitcher Open, Neighbours Reduced/Pitchers Open, Neighbours Intact/Pitchers Starved, and Neighbours Reduced/Pitchers Starved.

Above-ground parts of neighbours were repeatedly clipped within a 0.5 m × 0.5 m plot, combined with 'weeding' of neighbours within a 15-cm radius of the target pitcher plant within the plot to implement the press reduction in competition. Treatments were initiated in May and the prey exclusion treatment was sustained throughout the first growing season. In June 1999, all plants were excavated and the responses to the treatments were assessed by measuring survivorship, relative growth rate, and allocation to pitchers, rhizomes, and roots. No plants flowered during the study. In addition to measuring the performance of pitcher plants, I measured light levels and percent cover of seven common non-carnivorous species.

Results and Discussion

Fire stimulated recruitment of sundews by reducing above-ground competition.

The abundance of pink sundews was strongly recruitment limited, and recruitment appeared to be suppressed primarily by above-ground competition at all three sites (Brewer 1999a; Fig. 1). Pre-fire seedling densities were significantly higher in the no-competition subplots than in the other subplots ($F_{2,90} = 89.44$; $P < 0.0001$). The difference between the full-competition subplots and the subplots in which below-ground competition was reduced was less than the difference between no-competition subplots and subplots in which below-ground competition was reduced (Fig. 1).

When the same sites were revisited three months later (March 1997, one month after a fire at Site 3), a significant increase was found in recruitment at the recently burned site, Site 3 (Brewer 1999a; Fig. 1; census × competition-reduction × site interaction $F_{4,135} = 4.25$; $P = 0.003$). The difference seen between the control and the no-competition plots at the recently burned site resulted from the fact that fire created a short-lived reduction in competition, whereas the no-competition treatment created a sustained reduction in competition.

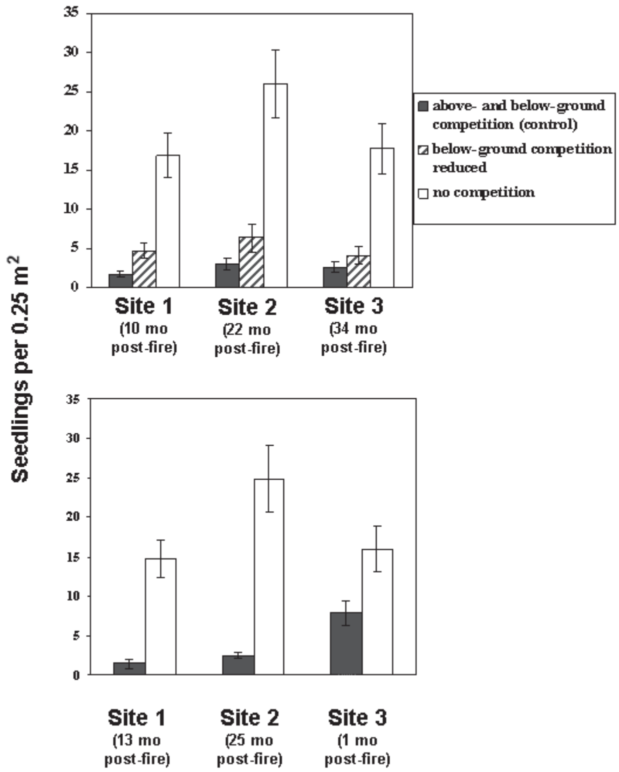

Fig. 1. Effects of competition-reduction treatments on seedling recruitment of *Drosera capillaris* in December 1996 (top) at three sites that had not been burned since February of 1996 and in March 1997 (bottom) at the same three sites, one month after a fire at Site 3 (Lige Branch). Error bars are ± 1 SE. Figure redrawn from Brewer (1999a).

Pitcher plants and their neighbours did not appear to occupy complementary niches in years without fire

Contrary to the prediction of the nutrient-niche complementarity hypothesis, removing neighbours had a very strong positive effect on pitcher plant growth (Brewer 2003a; Fig. 2; neighbour reduction $F_{1,133} = 11.2$; $P = 0.001$). Survivorship was not affected by the treatments. Most of the response of pitcher plants to neighbour removal could be attributed to increased allocation to pitchers (neighbour reduction $F_{1,134} = 9.01$; $P = 0.0032$). Pitcher plant growth appeared to be limited more by prey and thus nutrients when neighbours were removed (and thus when light was no longer limiting to growth), contradicting the niche-complementarity hypothesis. I suggest that light not nutrients limited the growth of pitcher plants when neighbouring plants were left intact. This statement is supported by a negative correlation between relative growth rate and light levels (photosynthetically-active photon flux density) in control plots ($r = -0.63$; $P < 0.0001$).

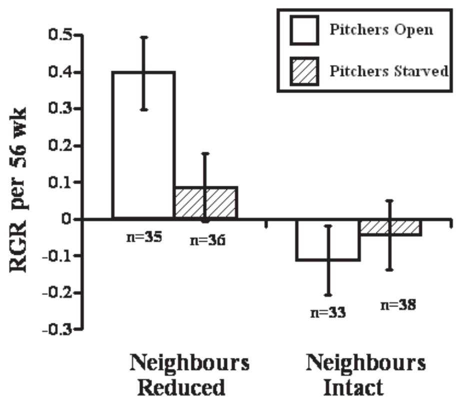

Fig. 2. Effects of neighbour reduction and prey exclusion on relative growth rate (g/g plant/56 wk) of *Sarracenia alata*. Error bars are ± 1 SE. Figure redrawn from Brewer (2003a).

Was nutrient-niche complementarity tested in this experiment? Considering the effect of light on nutrient use and its relevance to competition theory

An assumption of the second experiment was that pitcher plant growth was limited primarily by nutrients in this chronically nutrient-poor system. However, nutrient limitation of growth of this species occurred only when light was not limiting. Numerous studies have shown a positive relationship between investment in nutrient capture and light (Hunt & Burnett 1973; Gulmon & Chu 1981; Olff et al. 1990; Campbell et al. 1991; Jackson & Caldwell 1992; Brewer & Platt 1994a, b; Brewer 1995, 2003a; Zamora et al. 1998). The results of these studies may have some bearing on a contentious debate that started 30 years ago between Grime and Newman (Grime 1973; Newman 1973).

Grime argued that the intensity of competition in habitats with nutrient-poor soils should be relatively low, due to a low demand for nutrients and thus low rates of competitive displacement. Newman argued that the intensity of competition for nutrients should be relatively high in habitats with nutrient-poor soils, due to shortages in nutrients. Grime predicted that the intensity of competition for both light and nutrients should increase with soil fertility. Newman predicted that the intensity of competition for nutrients should decline with increasing soil fertility, whereas the intensity of competition for light should increase with increasing soil fertility. The most common approach to testing these competing hypotheses has been to examine the relationship between competition for light, competition for nutrients, and soil fertility. Experiments have produced mixed and conflicting results (e.g. Aerts et al. 1991; Putz & Canham 1992; Wilson & Tilman 1993; Twolan-Strutt & Keddy 1996; Cahill 1999; Brewer 2003b).

I argue that both light and nutrients are potentially limiting to plant growth in nutrient-poor wet savannas. Accordingly, it is suggested that both competition for light and competition for nutrients are important *at different times* in pine savannas. Results of the studies presented here indicate that competition for light is intense and competition for nutrients is not in years without fire. Above-ground vegetation reduces recruitment of light-demanding species (e.g. as in *Drosera capillaris*) while reducing the demand for nutrients by established plants of co-occurring species (as in *Sarracenia alata*). In contrast, I hypothesize that the intensity of competition for light is low and the potential for competition for nutrients is high in years in which a fire has occurred. Fires reduce above-ground competition, increase light availability, and stimulate recruitment in short-lived, seed-bank producing species such as *Drosera capillaris*, while at the same time, increasing demand for nutrients in long-lived species such as *Sarracenia alata*. To the extent that co-occurring species occupy the same nutrient niche, this increased demand for nutrients should result in an increased intensity of competition for nutrients.

The hypothesis that disturbance-mediated increases in light potentially *intensify* competition for nutrients in habitats with nutrient-poor soils has received little attention from ecologists and remains untested. Using carnivorous pitcher plants as a target species, one could test the effects of fire on the intensity of competition for nutrients by examining the three-way interaction between fire, prey-exclusion, and root exclusion. If fire increases nutrient demand in both pitcher plants and their non-carnivorous neighbours, then the negative effect of prey exclusion should be greatest at burned sites when the roots of neighbouring plants are left intact. Such a response would indicate that fire intensifies competition for nutrients unless countered by nutrient-niche complementarity.

The results of experiments that test the effects of light on the intensity of competition for nutrients could be generally relevant to competition and diversity theory. Carnivorous plants are not the only plants that allocate carbon to specialized structures to enhance nutrient capture. For example, legumes, myrtles, and mycorrhizal species may benefit from increased light and photosynthesis rates after a fire by maintaining an adequate supply of carbon to nitrogen-fixing and nutrient-capturing symbionts. In theory, the cost-benefit model developed by Givnish et al. (1984) to explain carnivory in plants should apply equally well to plants with nitrogen-fixing endosymbionts, mycorrhizal plants, and hemiparasites (which when combined account for the majority of pine savanna plants). If plants adapted to nutrient-poor soils suppress nutrient demand when shaded (to

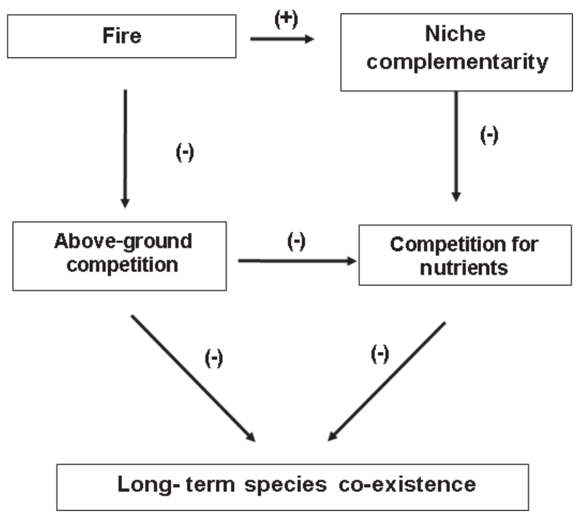

Fig. 3. Hypothetical conceptual model of the interactions between fire, niche complementarity, competition intensity, and plant species co-existence in wet pine savannas.

conserve resources), and plants adapted to nutrient-rich soils do not, then one would expect to see intermittent competition for nutrients in infertile soils and continuous competition for nutrients in fertile soils. Intermittent demand for nutrients may lead to lower rates of competitive displacement in habitats with nutrient-poor soils and thus higher species diversity. Nevertheless, assuming there are occasional periods of intense demand for nutrients (e.g. when light is not limiting), niche complementarity among species may be required for long-term species co-existence in habitats with low soil fertility. Different species potentially acquire nutrients in a variety of complementary ways (Newman 1973). In contrast, the continuous demand for nutrients needed for plants to 'grow out of' local areas of resource depletion in productive habitats may select for herbaceous perennials capable of rapid growth and clonal expansion, thereby limiting the number of species that could persist in such habitats (Grime 1979). Hence, contrasting selection pressures in habitats that differ in soil fertility may provide an evolutionary explanation for observed relationships between soil fertility and diversity.

In conclusion, I argue that ecologists will not fully understand the mechanisms of species co-existence in pine savannas and their relation to ecosystem function without studying the effects of fire on niche complementarity. Although fire reduces above-ground competition, it has the potential (in the absence of niche complementarity) to intensify competition for nutrients by increasing nutrient demand (Brewer 1999c; Fig. 3). Without niche complementarity to reduce the intensity of competition for nutrients when light is not limiting to growth, the reduction of above-ground competition by frequent fires may not be sufficient to maintain long-term species co-existence. In the absence of niche complementarity, frequent fires might result in unsustainable nutrient losses (Christensen 1993) and increased vulnerability to invasion by non-native species (Stohlgren et al. 2001). Likewise, without frequent fires, nutrient-niche complementarity might be irrelevant, because nutrient demand would remain very low during prolonged fire-free intervals, during which time, above-ground competition and encroachment by woody species would reduce species diversity. When studying competitive mechanisms in pine savannas, ecologists need to resist the false dichotomy of disturbance-mediated vs. niche-mediated co-existence and focus on the effects of fire on interspecific differences and their relation to species co-existence.

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