# Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand

MARK A. DAVIS, KEITH J. WRAGE* and PETER B. REICH*

*Department of Biology, Macalester College, St Paul, MN 55105, USA; and *Department of Forest Resources, University of Minnesota, St Paul, MN 55108, USA*

**Summary**

**1** We measured competition intensity (CI) between herbaceous vegetation and tree seedlings (*Quercus macrocarpa* and *Q. ellipsoidalis*) along an experimental moisture–light gradient. Contrasting theories were tested by comparing variation in competition intensity to changes in neighbour biomass and resource supply and demand.

**2** CI based on survival was inversely correlated with net soil water supply (gross supply minus demand by herbaceous vegetation). CI was not positively correlated with either gross resource supply or neighbour biomass, contrary to predictions of Grime's triangular model for plant strategies.

**3** Many of the inconsistencies and conflicting results that have characterized the recent literature on plant competition could be eliminated if changes in competition intensity along a resource gradient are compared with changes in net resource supply rather than changes in productivity or neighbour biomass.

**4** Tree seedling success in savannas and grasslands may be strongly influenced by the intensity of competition from herbaceous vegetation. Factors that reduce soil water content are likely to increase competition intensity (and reduce seedling success) in these environments, while factors that increase soil water content will favour seedling success through decreased competition for water with herbaceous vegetation.

*Keywords:* competition, grassland, *Quercus*, resource demand, resource gradients, resource supply, savanna, tree regeneration

*Journal of Ecology* (1998) **86,** 652–661

## Introduction

The extent to which competitive interactions among plant species vary along resource gradients has been the subject of much debate (Grime 1973, 1979; Grubb 1985; Tilman 1988). Grime's C-S-R model states that the intensity of competition (C) increases as disturbance (R) and stress (S) decline (Grime 1979, 1985, 1988), or comparably that competition intensity increases with increasing resource abundance, productivity and neighbour biomass (Grime & Hodgson 1987; Keddy 1989). This theory and the variants presented by others (Southwood 1977; Greenslade 1983), and the C-S-R theory, are consistent with the traditional *r/K* selection theory (MacArthur & Wilson 1967). Results of field studies have been mixed, with some supporting the C-S-R theory (Gurevitch 1986;

Reader & Best 1989) and some refuting it (Watkinson 1982; McGraw & Chapin 1989; Tilman & Cowan 1989).

Some investigators have argued that competition intensity may be high even in stressful and unproductive environments (Newman 1973; Grubb 1985; Tilman 1988) and, under some conditions, may be low in very productive environments (Taylor *et al.* 1990). We propose that what matters to an individual plant is not so much a change in gross resource supply or change in abundance of its competitor, but the extent to which resource availability is affected by changes in supply and demand. Thus, we theorize that competition intensity should be inversely correlated with net resource supply (gross supply minus use by a competitor). Unlike the C-S-R theory, the supply minus demand (S-D) theory does not predict that competition intensity will necessarily correlate with resource abundance or neighbour biomass.

Competition between herbaceous vegetation and

Correspondence: M. A. Davies (fax 612 696 6443; e-mail davis@macalester.edu).

woody seedlings for soil water is believed to influence strongly tree and shrub establishment in grasslands and savannas throughout the world (Walker *et al.* 1981; Knoop & Walker 1985; Archer *et al.* 1988; Harrington 1991; Belsky 1994; Breshears *et al.* 1997; Scholes & Archer 1997). Knowing how competition intensity between herbaceous vegetation and tree seedlings varies with changes in soil water availability should help us better understand the establishment phase for trees in these environments. The purpose of this study was to measure competition intensity (CI) between herbaceous vegetation and tree seedlings along an experimental moisture–light gradient, and by relating variation in CI to changes in neighbour biomass and resource supply and demand, to test the contrasting predictions made by the S-D and C-S-R theories.

## Materials and methods

### STUDY AREA

In spring 1995, a 2-year (two growing seasons) field study was established in an old field at Cedar Creek Natural History Area (CCNHA), Bethel, Minnesota, USA (45°24′N, 93°12′W). CCNHA is situated on the Anoka Sandplain, a glacial outwash area that is characterized by coarse textured soils that are low in nitrogen (Grigal *et al.* 1974). This area is located in the transition zone between the North American grasslands and the eastern deciduous forest. Prior to settlement by Europeans, oak savanna and barrens were the dominant vegetation types, with bur oak (*Quercus macrocarpa* Michx.) and northern pin oak (*Q. ellipsoidalis* E. J. Hill), being the two dominant tree species (Wovcha *et al.* 1995). Today, upland herbaceous-dominated communities at CCNHA include old fields and natural openings in remnant oak savanna/ woodlands. The study field is flat with deep sandy soils above a flat water table, and soil texture (coarse and well-drained) is quite uniform throughout the study field (P. B. Reich, unpublished data) due to the glacial outwash history and prior agricultural activity in the field. Mean soil N in the study area is 0.084% (R. Inouye, unpublished data). This is within the range of values found in openings of naturally occurring savannas and woodlands at CCNHA (M. A. Davis, unpublished data). Dominant grasses in the field are *Agropyron repens* L., *Bromus inermis* Leyss., *Poa pratensis* L., and common forbs include *Berteroa incana* L., *Ambrosia artemesiifolia* L. and *Physalis virginiana* Mill.

### EXPERIMENTAL DESIGN AND LAYOUT

A 3 × 2 × 2 factorial field experiment involving water, light and competition was conducted to test the hypothesis that intensity of competition between herbaceous vegetation and oak seedlings varies along a two-dimensional gradient of water and light. A light treatment was included because patches of canopy shade are present in savannas, and canopy shade is known to affect soil water content (Joffre & Rambal 1988; Ko & Reich 1993). The experiment consisted of 24 plots, each containing four subplots (1.5 × 1.5 m). The plots were laid out in three parallel lines running east–west with eight plots per line. Four metres separated plots within a line, and lines were 12 m apart. The experimental design included eight replicates, each replicate consisting of three adjacent plots from each line. The water treatments (dry, medium, wet) were each applied to one randomly selected plot within each replicate. The four subplots in a plot were randomly assigned to one of the four treatments involving light and competition – full sun with herbaceous vegetation present, full sun with herbaceous vegetation removed, shaded with herbaceous vegetation present, and shaded with herbaceous vegetation removed. Thus, the 96 subplots represented 12 different combinations of treatments (2 light × 2 competition × 3 water) (Fig. 1).

Within each subplot, four 2-year-old seedlings of each of *Q. macrocarpa* and *Q. ellipsoidalis* (with intact tap roots) were transplanted in late April 1995. They were planted alternately in two rows, with species order reversed in adjacent rows and adjacent subplots. Seedlings were spaced 30 cm apart in a row, with the two rows being 90 cm apart. Seedlings were obtained from the Minnesota Department of Natural Resources (MNDNR) and were planted by personnel from a professional tree nursery. A total of 384 seedlings of each species was planted. A small degree of mortality occurred in the first 2 weeks, and these were replaced by extra seedlings from the same MNDNR shipment. Surplus seedlings were planted in the same field near the plots: these were clipped at ground level in October 1996 to determine an allometric regression equation for woody shoot biomass for each species based on stem diameter and height. At the end of the experiment, we conducted a regression analysis of seedling biomass as a function number of surviving seedlings in a subplot. We found no negative correlations between biomass and seedling number for either species in any of the three water levels, and concluded that, owing to the spacing and small size of the seedlings, there was little competition between seedlings.

### TREATMENTS

#### Light

A shade treatment was imposed using commercial black shade cloth with a shading effect of 80%, which mimics a common shade effect in tree-covered areas of the oak savanna/woodland at CCNHA. The shade cloth was positioned so that the top was *c.* 75 cm above the ground. In order to allow air flow through
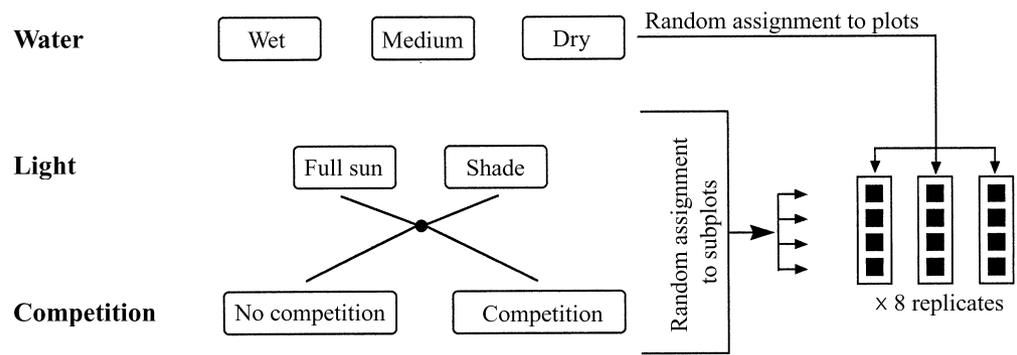
**Fig. 1** Plot layout and design of the experiment.

shaded subplots, the north side of the shade cloth stopped about 50 cm above the ground, and the sides facing east and west stopped a few centimetres above the ground. Prior measurements of air temperatures in similar shade cloth structures revealed no difference compared to air temperatures in shaded areas in the oak woodland at CCNHA (Davis *et al.* 1995). The mesh screen easily allowed rain water to drip through. Shade treatments were begun in early July 1995. The shade cloths were removed in mid-October 1995, and replaced in early May 1996, the time of oak leaf out at CCNHA in that year. They remained in place until the end of the study, September 1996.

*Water*

The three water treatments were applied during the second summer (1996) of the experiment. Water treatments were not imposed until the second year in order to give seedlings a full year to establish themselves and to minimize any transplant effect. The purpose of the water treatments was to create three soil water regimes – dry, medium and wet. We sought to maintain soil water in the dry and wet treatments consistently lower or higher, respectively, than that in the medium plots. Treatments to reduce or increase soil water in plots were applied as needed to meet these goals, as determined by weekly soil water measurements (percentage soil water) of full sun, unweeded plots.

Dry conditions were created by pulling a 6-ml plastic tarp (30 × 6 m) over plots immediately prior to a rainfall, and removing it after the rain ended throughout the period 1 June–31 August 1996. The rain tarps effectively excluded rain from the plot as well as from a 1.5-m buffer area around the plot. Since the aim was to create drier than ambient soil conditions, but not to eliminate water input completely, the rain tarps were not applied during every precipitation event during summer 1996. During summer 1996, the study site received 215 mm of rainfall, whereas dry plots received 85 mm of rainfall.

Wet conditions were created by using an irrigation system of flat sprinkler hoses. Water was supplied from a nearby well. Output from the sprinkler hoses was *c.* 13 mm h$^{-1}$. The sprinklers were turned on for periods ranging from 0.75 to 9 h throughout summer 1996, whenever it was determined by the soil water measurements that additional water input was needed to keep soil water levels above those in the medium plots. Wet plots received an estimated total amount of water input (precipitation plus irrigation) of 820 mm during the 3-month period. Medium water conditions were created primarily by exposing plots to ambient rainfall, but medium water plots received an additional 13 mm of water during an especially dry period for a total of 228 mm. Although summer 1996 was relatively dry, the total amount of water input in the medium plots (rainfall plus irrigation) fell within the 33-year standard deviation of precipitation levels for June–August. The dry and wet treatments produced soil water levels typical of those found in drought or wet periods, respectively, at Cedar Creek.

Measurements of soil water content were made in all subplots on 17 July (3 days after the last rain and 5 days since the last watering) and 9 August (4 days after the last rain and 10 days since the last watering). Soil water was measured at a depth of 30 cm using a portable time domain reflectometry system (Topp *et al.* 1980; Baker 1990). (Soil water content for a subplot was calculated as the mean of the soil water measures made on 17 July and 9 August.) Soil water availability is well represented by soil water potential, given similar slope and soil volume. In our study site, soil texture was extremely uniform and the site was flat. Thus soil water content was a good surrogate for soil water potential and soil water availability in our study.

*Removal of herbaceous vegetation*

Subplots designated to be free of herbaceous vegetation (no competition subplots) were treated with a glyphosphate herbicide (Roundup$^{TM}$) prior to implementation of other treatments. These plots were kept free of herbaceous vegetation by periodic hand weeding. The herbicide treatment and hand weeding included a 0.75-m buffer zone around the subplots.

Thus, all seedlings in weeded plots were surrounded by at least a metre of unvegetated soil.

### Herbivores

Known herbivores of oak seedlings, white-tailed deer *Odocoileus virginianus* and pocket gophers *Geomys bursarius* (Inouye *et al.* 1994), were excluded from the study site via fencing (deer) and trapping (gophers). A spray insecticide (Malathion 50™) was applied to the seedlings once during summer 1995 and on three occasions in summer 1996 to reduce insect herbivory.

### DATA COLLECTION AND COMPILATION

#### Seedling biomass and survival

In mid-September 1996, the number of surviving seedlings of each species in each subplot was recorded and the height and basal stem diameter of all surviving seedlings were measured.

Shoot woody biomass (mg) estimates for surviving seedlings were determined using an allometric equation based on height (H, in cm) and basal stem diameter (D, in mm):

$$\text{Log}(\text{biomass}_{Q.\,macrocarpa}) = 0.83196 + 0.94789$$
$$\times \text{Log}(D^2H)\,(r^2 = 0.93\ P < 0.001, n = 27)$$

$$\text{Log}(\text{biomass}_{Q.\,ellipsoidalis}) = 0.88657 + 0.92086$$
$$\times \text{Log}(D^2H)\,(r^2 = 0.97\ P < 0.001, n = 21)$$

Allometric equations were derived from surplus seedlings that had been planted in full sun conditions in the same field as the experiment. Major differences in height:diameter relationships among treatments might indicate the need for separate allometric equations for different treatments. However, no major differences were found when the height:diameter relationship was examined for seedlings in each of the contrasting water and light treatments using separate and same-slope analyses. The number of surviving seedlings of each species and the mean biomass of surviving seedlings of each species were used in subsequent analyses.

#### Biomass of herbaceous vegetation

In order to determine above-ground biomass of herbaceous vegetation in unweeded subplots, a strip of herbaceous vegetation, 10 cm × 1 m, was clipped at ground level along the east side of each subplot in August 1996. The vegetation was dried and weighed. Data were log transformed prior to analysis.

#### Competition intensity

To date, most measurements of CI have been based on plant biomass or growth (Grace 1995). However, in tree seedlings, survival and growth may or may not be closely linked (Walters & Reich 1996), indicating that it may then be important to calculate CI based on survival as well as growth (Berkowitz *et al.* 1995). We calculated CI on the basis of both seedling survival and biomass. Several recent papers (Grace 1993; Reader *et al.* 1994) have pointed out that different conclusions may be reached regarding the relationship between CI and productivity or neighbour biomass depending on whether CI is calculated as the absolute difference (ACI) in plant performance between weeded and unweeded plots (Campbell & Grime 1992) or the relative difference (RCI) (Wilson & Keddy 1986). We calculated CI using both methods, yielding a total of four different calculations of CI for each seedling species: ACI based on biomass ($\text{ACI}_{BM}$), ACI based on survival ($\text{ACI}_{SV}$), RCI based on biomass ($\text{RCI}_{BM}$) and RCI based on survival ($\text{RCI}_{SV}$).

$\text{ACI}_{BM}$ was calculated according to Campbell & Grime (1992):

$$\text{Biomass}_{\text{weeded subplot}} - \text{Biomass}_{\text{unweeded subplot}}$$

and $\text{ACI}_{SV}$ was calculated as:

$$\text{Survival}_{\text{weeded subplot}} - \text{Survival}_{\text{unweeded subplot}}$$

where Survival equals the proportion of seedlings alive at the end of the study.

Calculations of RCI were based on a method proposed by Wilson & Keddy (1986) and modified by Markham & Chanway (1996). $\text{RCI}_{BM}$ for a subplot was calculated as:

$$\text{RCI}_{BM} = (\text{Biomass}_{\text{weeded subplot}}$$
$$- \text{Biomass}_{\text{unweeded subplot}})/X$$

where X is either $\text{Biomass}_{\text{weeded subplot}}$ or $\text{Biomass}_{\text{unweeded subplot}}$, whichever is larger.

$\text{RCI}_{SV}$ was calculated in the same way:

$$\text{RCI}_{SV} = (\text{Survival}_{\text{weeded subplot}}$$
$$- \text{Survival}_{\text{unweeded subplot}})/X$$

The RCI calculations produce an index that ranges from 1 to $-1$. Positive numbers indicate the presence of competition with surrounding vegetation, negative numbers indicate facilitation by the surrounding vegetation, and an index of zero indicates that the surrounding vegetation has no effect on biomass or survival of the target plants.

In all calculations of CI, if $\text{Survival}_{\text{unweeded subplot}}$ or $\text{Biomass}_{\text{unweeded subplot}}$ was from a shaded subplot, the datum was compared with the corresponding datum for the weeded subplot that was shaded. If $\text{Survival}_{\text{unweeded subplot}}$ or $\text{Biomass}_{\text{unweeded subplot}}$ was from a full sun subplot, it was compared with the full sun weeded subplot. In all cases, subplot comparisons were within the same plot, i.e. same water treatment.

ESTIMATES OF RESOURCE SUPPLY AND DEMAND

*Gross resource supply*

For tree seedlings in a subplot with herbaceous vegetation, gross resource supply was estimated as the percentage soil water content (arcsine transformed) measured in the weeded subplot with the same light treatment (shaded or unshaded) in the same plot. Technically, gross supply should be measured in subplots without any seedlings either. However, leaf area index (LAI) differences between oak seedlings and herbaceous vegetation on a whole subplot basis indicate our estimates are adequate. Unweeded herbaceous subplots contained herbaceous vegetation with LAI usually between 2 and $3 \, m^2 \, m^{-2}$, whereas oak seedlings usually contributed between 0.05 and $0.1 \, m^2 \, m^{-2}$ LAI. Transpiration rates are similar per unit of leaf area for these oaks and herbs (M. Tjoelker, unpublished data). Thus, oaks used only 2–5% as much water as their competitors. Moreover, a regression analysis of soil water in plots with different numbers of seedlings showed no significant correlation between soil water content and number of seedlings in the subplots in either the dry or wet treatment levels ($P > 0.20$). There was a significant correlation between soil water content and seedling number in the medium water treatments ($P < 0.001$); however, the relationship was a positive one, i.e. subplots with more seedlings had wetter soil. Thus, although seedlings are taking up water, their impact on soil water content in subplots is small.

*Net resource supply*

For tree seedlings in a subplot with herbaceous vegetation, net resource supply was estimated using the soil water content (arcsine transformed) measured for that subplot. Thus, net resource supply represents gross supply minus water taken up by herbaceous vegetation.

In terms of plant available soil water, demand by a competitor is relevant biologically only when the water removed by the competitor is not replaced by additional water and the soil water content is below the saturation point. The extent to which a plant competitor actually reduces soil water content that is biologically relevant can be termed effective resource demand. We calculated effective resource demand by herbaceous vegetation in subplots as the difference in the transformed soil water content between weeded (gross resource supply) and the corresponding unweeded (net resource supply) subplots. In some instances (mostly under the wet treatment), soil water measurements were slightly higher in unweeded than weeded subplots. In these cases, effective resource demand by herbaceous vegetation was deemed to be zero.

DATA ANALYSIS

Water and light effects on competition intensity were analysed using a split-split plot ANOVA with water as a plot effect, light as a subplot effect, and species as a subsubplot effect. Water and light effects on herbaceous biomass were analysed using a split-plot ANOVA with water as a plot effect and light as a subplot effect. Water treatments were defined as quantitative factors in these analyses, based on the amount of water (85, 228, 820 mm) applied.

Simple regression analysis was used to evaluate the relationship between competition intensity ($ACI_{BM}$, $ACI_{SV}$, $RCI_{BM}$, $RCI_{SV}$) and net resource supply, the resource supply/demand ratio, and herbaceous biomass. The relationship between competition intensity and herbaceous biomass was also evaluated using a second order polynomial regression.

TESTS OF THE S-D AND C-S-R THEORIES

The S-D theory will be supported if CI is found to be inversely correlated with net resource supply. The C-S-R theory will be supported if CI is found to be positively correlated with neighbour biomass. A finding of no correlation, or a negative correlation, between CI and neighbour biomass will refute the C-S-R theory but will be consistent with the S-D theory.

**Results**

Soil water content was higher in shaded subplots and was affected by a water × weeding interaction (Fig. 2). Specifically, although soil water content in weeded subplots was usually higher than that in unweeded plots, this difference declined with increasing water input (Fig. 2). Owing to very high seedling survival in weeded plots and the method of calculating RCI, analyses of $RCI_{SV}$ and $ACI_{SV}$ produced nearly identical results. [In calculations of RCI, the divisor was the larger survival figure of the two treatments. Since this was usually for weeded subplots and typically equalled 1.0 (no mortality), calculations of $RCI_{SV}$ and $ACI_{SV}$ produced the same or nearly the same values.] Thus, only $RCI_{SV}$ values are given in data, tables and figures.

Competition intensity calculated on the basis of survival was affected by a significant water × light interaction (Table 1). Specifically, in full sun subplots, competition intensity experienced by both *Q. macrocarpa* and *Q. ellipsoidalis* was highest in dry plots and declined with increasing water input (Fig. 3). These findings are in contrast to the prediction of the C-S-R theory that competition intensity should increase as resources become more abundant. In shaded subplots, competition intensity was also highest in dry plots, in contrast to C-S-R theory; however, it was lowest in medium water plots (Fig. 3). There was a trend for *Q. macrocarpa* to experience lower
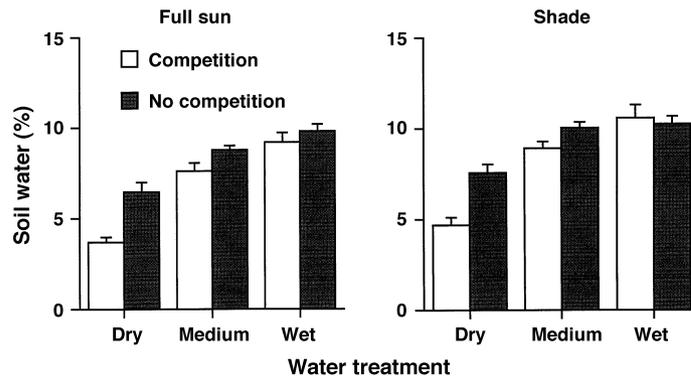
**Fig. 2** Percentage soil water (mean $\pm$ 1 SE) for treatment combinations (water, light, competition).

**Table 1** ANOVA results for the effects of water (W), light (L) and species (S) on relative competition intensity based on survival

| Effect | d.f. | $F$ ratio | $P$ |
|---|---|---|---|
| Main plot | | | |
| W | 1 | 8.72 | 0.021 |
| Error | 7 | 0.73 | 0.646 |
| | | | |
| Subplot | | | |
| L | 1 | 16.12 | 0.005 |
| W × L | 1 | 13.07 | 0.009 |
| Error | 1 | 0.45 | 0.869 |
| | | | |
| Subsubplot | | | |
| S | 1 | 1.16 | 0.286 |
| W × S | 1 | 0.02 | 0.898 |
| L × S | 1 | 0.35 | 0.559 |
| W × L × S | 1 | <0.01 | 0.963 |

competition intensity (based on survival) than *Q. ellipsoidalis* (Fig. 3), although this was not significant at the 0.05 level (Table 1).

Herbaceous above-ground biomass differed among water treatments (Table 2), with highest biomass occurring in wet subplots (Fig. 4). Competition intensity calculated on the basis of biomass ($RCI_{BM}$ and $ACI_{BM}$) was not significantly affected by water or species factors ($P > 0.25$ for both factors and all interactions involving water and species); however, it was marginally affected by light, with competition intensity being higher in full sun plots ($RCI_{BM}$: full sun =

**Table 2** ANOVA results for the effects of water (W) and light (L) on herbaceous biomass. Herbaceous biomass was log transformed prior to analysis

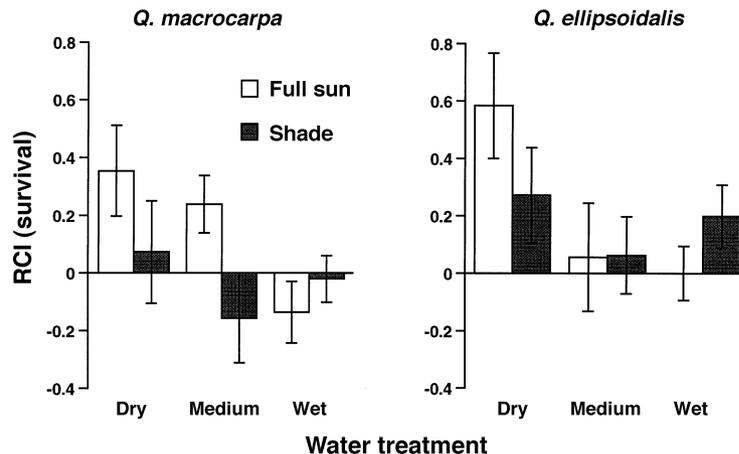| Effect | d.f. | $F$ ratio | $P$ |
|---|---|---|---|
| Main plot | | | |
| W | 1 | 6.59 | 0.037 |
| Error | 7 | 1.19 | 0.336 |
| | | | |
| Subplot | | | |
| L | 1 | 0.55 | 0.465 |
| W × L | 1 | 0.42 | 0.521 |

**Fig. 3** RCI based on survival (mean $\pm$ 1 SE) shown as a function of different water and light combinations for *Quercus macrocarpa* and *Q. ellipsoidalis*.
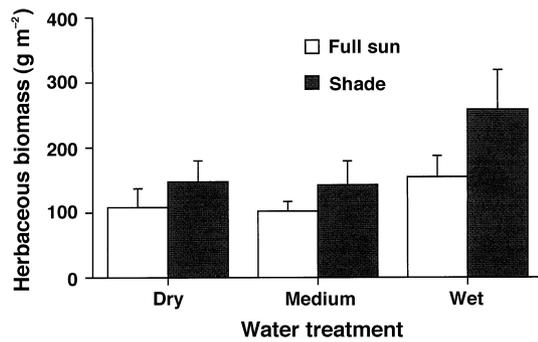
**Fig. 4** Herbaceous biomass (mean $\pm$ 1 SE) shown as a function of different water and light combinations.



**Fig. 6** RCI based on survival shown as a function of herbaceous biomass. A linear regression was not significant, $r^2 = 0.16$, $P > 0.191$. The increase in competition intensity at high herbaceous biomass occurred in shaded subplots in wet conditions. Since water was not limiting in these plots, the increase in competition intensity probably reflects an increase in competition for light.

$0.090 \pm 0.016$, shade $= 0.036 \pm 0.018$, $F = 5.36$, $P = 0.054$; $ACI_{BM}$: full sun $= 0.348 \pm 0.061$, shade $= 0.143 \pm 0.066$, $F = 4.81$, $P = 0.064$).

$RCI_{SV}$ was significantly negatively correlated with net resource supply (Fig. 5). $RCI_{SV}$ was not significantly correlated with herbaceous biomass using a linear regression analysis ($r^2 = 0.168$, $P = 0.191$). A second-order polynomial regression analysis did produce a significant correlation, however, as shown in Fig. 6; the highest level of competition intensity occurred in the subplots with the lowest herbaceous biomass. These results show that when based on survival data, competition intensity increased with a decline in net resource supply, as predicted by the S-D theory. However, competition intensity was not positively correlated with neighbour biomass, and thus the data do not support the C-S-R theory.

Competition intensity based on biomass was not correlated with net resource supply ($RCI_{BM}$: $r^2 = 0.006$, $P = 0.788$; $ACI_{BM}$: $r^2 = 0.008$, $P = 0.781$) or herbaceous biomass ($RCI_{BM}$: $r^2 = 0.123$, $P = 0.261$; $ACI_{BM}$: $r^2 = 0.129$, $P = 0.252$).

## Discussion

Our results support our S-D theory of competition, which is similar to a theory described by Taylor *et al.*
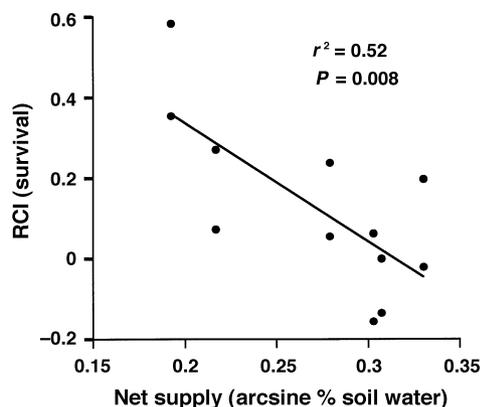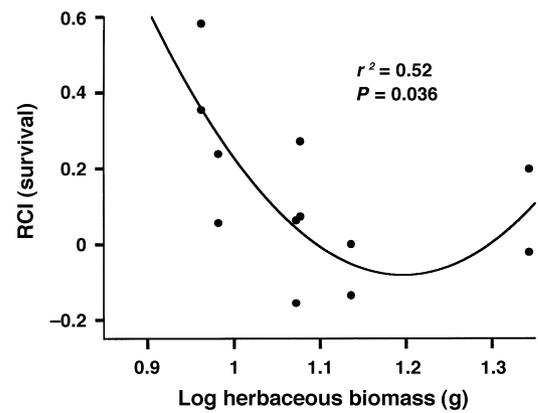
(1990), the latter stating that competition intensity should vary with the ratio of resource supply and demand. In fact, in our study, competition intensity ($RCI_{SV}$) did vary with the ratio of resource (water) supply to demand ($r^2 = 0.30$, $P = 0.065$), but the relationship was not as strong as with net resource supply ($r^2 = 0.52$, $P = 0.008$). We believe that the stronger relationship occurs between competition intensity and net resource supply because plants are most probably responding directly to the actual amount of available resource as opposed to the ratio of supply to demand.

Competition intensity was greatest when herbaceous biomass and soil water content were lowest (under dry conditions), in direct contrast to C-S-R predictions that competition intensity should be positively correlated with resource abundance, habitat productivity and neighbour biomass (Grime 1979; Keddy 1989). A basic difference in the two theories is that the C-S-R theory links competition primarily to community attributes – productivity and neighbour biomass – whereas the S-D theory links competition directly to the balance of resource availability and its use. Grime (1979, 1985) and Keddy (1989) have argued that competition should increase when the competitor increases, e.g. in numbers, biomass, cover or productivity. While focusing on changes in resource demand, this argument ignores variation in resource supply. Ultimately what matters to a species is not a change in the abundance of its competitor, and hence in resource demand, but the extent to which net resource availability is affected by changes in both supply and demand. For example, in full sun subplots, biomass of herbaceous vegetation increased with increasing water input. However, the increased water supply in wet plots more than compensated for any increased demand and thereby resulted in a reduction



**Fig. 5** RCI based on survival shown as a function of net resource supply.

of competition intensity. These results represent the first empirical support for Huston & DeAngelis' (1994) prediction that competition intensity between plants should decline when the plants receive a high supply of new resources.

Our results support Goldberg & Novoplansky's (1997) hypothesis that competition is likely to be an important process in low productive environments if biotic effects on resource levels are important. However, the results do not support a companion hypothesis (Goldberg & Novoplansky 1997) that competitive effects on survival should increase along productivity gradients driven by water. The outpacing of demand by supply along our experimental water gradient probably explains the lack of support for Goldberg and Novoplansky's hypothesis.

Our results show that the effects of light and water on competition intensity are not additive (Fig. 3). In dry and medium water conditions, competition intensity was usually lower in shaded subplots. (In medium water conditions, CI was approximately equal in shaded and full sun subplots for *Q. ellipsoidalis*.) Since soil water content was higher in shaded subplots (Fig. 2), these results support the S-D theory but refute the C-S-R theory, which predicts that competition intensity should increase with increasing resource supply. In wet conditions, CI was also highest where net resource supply was lowest, but in this case the limiting resource was probably light, not water. The high soil water content in both shaded and full sun subplots in wet conditions (Fig. 2) makes it unlikely that soil water was a limiting resource in either light treatment. In wet conditions, herbaceous biomass was greater in shaded than full sun subplots (Fig. 4) and the oak seedlings were often buried under the dense vegetation in these subplots. Thus, the higher competition intensity in wet and shaded subplots (Fig. 3) is likely to be due to competition with herbaceous vegetation for light more than soil water.

Findings from observational studies have shown that oak seedling survival, not surprisingly, is often lower during drought periods (Crow *et al.* 1994; Inouye *et al.* 1994). According to the C-S-R theory, reduced seedling survival under these conditions would best be explained as a direct result of increased physical stress. However, our results show that the increased mortality of tree seedlings during drought conditions may be more likely due to increased competition intensity from herbaceous vegetation and not directly due to the drought itself. For example, although survival in dry full sun subplots with herbaceous vegetation was quite low (33% for *Q. ellipsoidalis*, 56% for *Q. macrocarpa*), survival increased by 145% for *Q. ellipsoidalis* (81% survival) and 57% for *Q. macrocarpa* (88% survival) in weeded subplots. With the elimination of the demand for water from herbaceous vegetation, soil water content in full sun weeded subplots in dry conditions was significantly greater than that in subplots with herbaceous veg-

etation (Fig. 2). Thus, even though seedlings in dry subplots were exposed to extraordinarily dry conditions (water received in dry subplots during June, July and August 1996 was 50% less than that received during the driest summer in the past 33 years), 85% of seedlings (both species) survived when competition with herbaceous vegetation was eliminated.

Our findings are consistent with those of Harrington (1991) who also found that herbaceous vegetation competes vigorously with woody seedlings for soil water during summer months in arid environments. Factors that reduce this competition should increase tree seedling success, while factors that increase competition should reduce seedling success. Factors that may reduce competition intensity from herbaceous vegetation by reducing herbaceous demand for soil water include grazing (Walker *et al.* 1981; McNaughton 1983; Archer *et al.* 1988) and shade (Ko & Reich 1993). However, the non-additive effects of light and water on CI in this study indicate that in wet conditions, shade from mature trees may increase competition intensity, perhaps because light, rather than water, becomes the key limiting resource under these conditions. These results support the light-water model of facilitation and competition proposed by Holmgren *et al.* (1997). According to this model, shade from a canopy species should facilitate growth and survival in seedlings in dry conditions (by reducing drought stress) while the same shade should inhibit seedlings in wet conditions (by increasing competition for light). Although tree canopy shade is likely to benefit seedlings under dry conditions, seedling growth and survival could be inhibited in the shade even under dry conditions if there is a high density of fine roots from the tree located in the near surface soil (Callaway *et al.* 1991).

It is possible that elevated atmospheric $CO_2$ levels may also reduce competition between tree seedlings and herbaceous plants through reduced demand by seedlings and herbaceous vegetation for soil water (the result of lower transpiration rates). This latter possibility has not yet been tested; however, elevated $CO_2$ levels have been proposed as an explanation for the increase in woody plants in grassland environments (Idso 1992; Johnson *et al.* 1993). Finally, an increase in summer precipitation should reduce competition from herbaceous vegetation through the increased supply of available soil water for tree seedlings.

Factors that may increase competition intensity include a decline in summer precipitation (reduced gross supply) and nitrogen fertilization, which would increase demand for soil water as a result of increased biomass of herbaceous vegetation (Tilman 1988). It has been hypothesized that non-native grasses may use water less efficiently than native grasses and hence the exotic species may require increased water uptake (Gordon *et al.* 1989). If this is true, replacement of native with non-native grasses in savannas and grass-

lands may increase water demand, resulting in an increase in competition intensity.

Several studies have failed to find consistent correlations between competition intensity and productivity (see Grace 1995 for a review). Based on the S-D theory and our findings and ideas presented by Taylor *et al.* (1990), we do not believe one should expect any consistent pattern between productivity and competition intensity in a particular environment since there is no a priori reason to expect that changes in productivity or neighbour biomass (i.e. demand) should be predictably correlated with changes in net resource supply. Depending on changes in resource supply rates, changes in productivity or neighbour biomass could be positively, negatively or not correlated with net resource supply. Although positive correlations between neighbour biomass and competition intensity can occur (e.g. when abundance of competitors increase at a site with no or minimal increase in resource supply), these cases are adequately explained by the S-D theory. (In the above example, CI would be expected to increase due to a decline in net resource supply because of static supply and increasing demand.) We believe that many of the inconsistencies and conflicting results that have characterized the recent literature on plant competition will be eliminated in the future if investigators compare changes in competition intensity along a resource gradient with changes in net resource supply instead of with changes in productivity or neighbour biomass.

### References

Archer, S., Scifres, C. & Bassham, C.R. (1988) Autogenic succession in a subtropical savanna, conversion of grassland to thorn woodland. *Ecological Monographs*, **58**, 111–127.

Baker, J.M. (1990) Measurement of soil water content. *Remote Sensing Reviews*, **5**, 263–279.

Belsky, A.J. (1994) Influences of trees on savanna productivity, tests of shade, nutrients, and tree-grass competition. *Ecology*, **75**, 922–932.

Berkowitz, A.R., Canham, C.D. & Kelly, V.R. (1995) Competition vs. facilitation of tree seedling growth and survival in early successional communities. *Ecology*, **76**, 1156–1168.

Breshears, D.D., Myers, O.B., Johnson, S.R., Meyer, C.W. & Martens, S.N. (1997) Differential use of spatially heterogeneous soil moisture by two semiarid woody species: *Pinus edulis* and *Juniperus monosperma*. *Journal of Ecology*, **85**, 289–299.

Callaway, R.M., Nadkarni, N.M. & Mahall, B.E. (1991) Facilitation and interference of *Quercus douglasii* on understory productivity in central California. *Ecology*, **72**, 1484–1499.

Campbell, B.D. & Grime, J.P. (1992) An experimental test of plant strategy theory. *Ecology*, **73**, 15–19.

Crow, T.R., Johnson, W.C. & Adkisson, C.S. (1994) Fire and recruitment of *Quercus* in a postagricultural field. *American Midland Naturalist*, **131**, 84–97.

Davis, M.A., Ritchie, B., Graff, N. & Gregg, K. (1995) An experimental study of the effects of shade, conspecific crowding, pocket gophers and surrounding vegetation on survivorship, growth and reproduction in *Penstemon grandiflorus*. *American Midland Naturalist*, **134**, 237–243.

Goldberg, D. & Novoplansky, A. (1997) On the relative importance of competition in unproductive environments. *Journal of Ecology*, **85**, 409–418.

Gordon, D.R., Welker, J.M., Menke, J.W. & Rice, K.J. (1989) Competition for soil water between annual plants and blue oak (*Quercus douglasii*) seedlings. *Oecologia*, **79**, 533–541.

Grace, J.B. (1993) The effects of habitat productivity on competition intensity. *Trends in Ecology and Evolution*, **8**, 229–230.

Grace, J.B. (1995) On the measurement of plant competition intensity. *Ecology*, **76**, 305–308.

Greenslade, P.J.M. (1983) Adversity selection and the habitat template. *American Naturalist*, **122**, 352–365.

Grigal, D.F., Chamberlain, L.M., Finney, H.R., Wroblewki, D.V. & Gross, E.R. (1974) *Soils of the Cedar Creek Natural History Area*. Miscellaneous Report 123. University of Minnesota Agricultural Experiment Station, St Paul, Minnesota.

Grime, J.P. (1973) Competitive exclusion in herbaceous vegetation. *Nature*, **242**, 344–347.

Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. Wiley, New York.

Grime, J.P. (1985) Towards a functional description of vegetation. *The Population Structure of Vegetation* (ed. J. White), pp. 501–514. Junk, Dordrecht, the Netherlands.

Grime, J.P. (1988) The C-S-R model of primary plant strategies – origins, implications and tests. *Plant Evolutionary Biology* (eds L. D. Gottlieb & S. K. Jain), pp. 371–393. Chapman and Hall, London.

Grime, J.P. & Hodgson, J.G. (1987) Botanical contributions to contemporary ecological theory. *New Phytologist*, **106**, 283–295.

Grubb, P.J. (1985) Plant populations and vegetation in relation to habitat, disturbance and competition, problems of generalization. *The Population Structure of Vegetation* (ed. J. White), pp. 595–620. Junk, Dordrecht, the Netherlands.

Gurevitch, J. (1986) Competition and the local distribution of the grass *Stipa neomexicana*. *Ecology*, **67**, 46–57.

Harrington, G.N. (1991) Effects of soil moisture on shrub seedling survival in a semi-arid grassland. *Ecology*, **72**, 1138–1149.

Holmgren, M., Scheffer, M. & Huston, M.A. (1997) The

interplay of facilitation and competition in plant communities. *Ecology*, **78**,1966–1975.

Huston, M.A. & DeAngelis, D.L. (1994) Competition and coexistence: the effects of resource transport and supply rates. *American Naturalist*, **144**, 954–977.

Idso, S.B. (1992) Shrubland expansion in the American southwest. *Climate Change*, **22**, 85–86.

Inouye, R.S., Allison, T.D. & Johnson, N.C. (1994) Old field succession on a Minnesota sand plain, effects of deer and other factors on invasion by trees. *Bulletin of the Torrey Botanical Club*, **121**, 266–276.

Joffre, R. & Rambal, S. (1988) Soil water improvement by trees in the rangelands of southern Spain. *Oecologia Plantarum*, **9**, 405–422.

Johnson, H.B., Polley, H.W. & Mayeux, H.S. (1993) Increasing $CO_2$ and plant–plant interactions, effects on natural vegetation. *Vegetatio*, **104–105**, 157–170.

Keddy, P.A. (1989) *Competition*. Chapman and Hall, London.

Knoop, W.T. & Walker, B.H. (1985) Interactions of woody and herbaceous vegetation in a southern African savanna. *Journal of Ecology*, **73**, 235–253.

Ko, L.J. & Reich, P.B. (1993) Oak tree effects on soil and herbaceous vegetation in savannas and pastures in Wisconsin. *American Midland Naturalist*, **130**, 31–42.

MacArthur, R.H. & Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.

McGraw, J.B. & Chapin, F.S. III (1989) Competitive ability and adaptation to fertile and infertile soils in two *Eriophorum* species. *Ecology*, **70**, 736–749.

McNaughton, S.J. (1983) Serengeti grassland ecology, the role of composite environmental factors and contingency in community organization. *Ecological Monographs*, **53**, 291–320.

Markham, J.H. & Chanway, C.P. (1996) Measuring plant neighbor effects. *Functional Ecology*, **10**, 548–549.

Newman, E.I. (1973) Competition and diversity in herbaceous vegetation. *Nature*, **244**, 310.

Reader, R.J. & Best, B.J. (1989) Variation in competition along an environmental gradient, *Hieracium floribundum* in an abandoned pasture. *Journal of Ecology*, **77**, 673–684.

Reader, R.J., Wilson, S.D., Belcher, J.W., Wisheu, P.A.,

Keddy, P.A., Tilman, D., Morris, E.C., Grace, J.B., McGraw, J.B., Olff, H., Turkington, R., Klein, E., Leung, Y., Shipley, B., van Hulst, R., Johansson, M.E., Nilsson, C., Gurevitch, J., Grigulis, K. & Beisner, B.E. (1994) Intensity of plant competition in relation to neighbor biomass, an intercontinental study with *Poa pratensis*. *Ecology*, **75**, 1753–1760.

Scholes, R.J. & Archer, S.R. (1997) Tree–grass interactions in savannas. *Annual Review of Ecology and Systematics*, **28**, 517–544.

Southwood, T.R.E. (1977) Habitat, the template for ecological strategies? *Journal of Animal Ecology*, **46**, 337–365.

Taylor, D.R., Arsine, L.W. & Loehle, C. (1990) On the relationship between r/K selection and environmental carrying capacity, a new habitat template for plant life history strategies. *Oikos*, **58**, 239–250.

Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, New Jersey.

Tilman, D. & Cowan, M.L. (1989) Growth of old field herbs on a nitrogen gradient. *Functional Ecology*, **3**, 425–438.

Topp, G.C., Davis, V.L. & Annan, A.P. (1980) Electromagnetic determination of soil water content measurements in coaxial transmission lines. *Water Resources Research*, **16**, 574–582.

Walker, B.H., Ludwig, D., Holling, C.S. & Peterman, R.M. (1981) Stability of semi-arid savanna grazing systems. *Journal of Ecology*, **69**, 473–498.

Walters, M.B. & Reich, P.B. (1996) Are shade tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. *Ecology*, **77**, 841–853.

Watkinson, A.R. (1982) Factors affecting the density response of *Vulpia fasciculata*. *Journal of Ecology*, **70**, 149–161.

Wilson, S.D. & Keddy, P.A. (1986) Measuring diffuse competition along an environmental gradient, results from a shoreline plant community. *American Naturalist*, **127**, 862–869.

Wovcha, D., Delaney, B. & Nordquist, G. (1995) *Minnesota St Croix River Valley and the Anoka Sandplain*. University of Minnesota Press, Minneapolis, Minnesota.