



Survival, growth, and photosynthesis of tree seedlings competing with herbaceous vegetation along a water-light-nitrogen gradient

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Abstract

In herbaceous dominated patches and ecosystems, tree establishment is influenced partly by the ability of woody seedlings to survive and grow in direct competition with herbaceous vegetation. We studied the importance of season long wet and dry spells on the competitive interactions between herbaceous vegetation and oak seedlings along a light and nitrogen gradient in an infertile secondary successional grassland in central North America. We conducted a field experiment in which seedlings of bur oak (*Quercus macrocarpa*) and northern pin oak (*Q. ellipsoidalis*) were exposed to two levels of light (full sun and 80% shade), three levels of nitrogen input (0, 5, 15 g m⁻¹ yr⁻¹), and three levels of water input (low, medium and high). In addition, seedlings were grown with and without the presence of surrounding herbaceous vegetation under both light and all three water levels. Seedling survival, growth, and rate of photosynthesis were significantly affected by competition with herbaceous vegetation and these effects varied along the multiple resource gradient. Overall, seedling survival of both species was significantly greater in wetter and shaded plots and when surrounding herbaceous vegetation was removed and was lower in nitrogen enriched plots. We found that soil water was significantly affected by varying inputs of water, light, and the presence or absence of herbaceous vegetation, and that seedling survival and rate of photosynthesis were highly correlated with available soil water. Our findings show that the impact of season long wet and dry spells on tree seedling success in grasslands can be affected by light and soil nitrogen availability.

Introduction

Although trees are long lived organisms, as seedlings they are quite vulnerable to brief episodes of stress or injury that can be tolerated by large individuals, such as drought, frost heaving of the soil, and herbivory (Buell et al. 1971; Myster & McCarthy 1989; Gill & Marks 1991; Inouye et al. 1994). Numerous studies have implicated the role of water stress as an important cause of woody seedling mortality, including studies conducted in natural and anthropogenic grasslands and savannas (McQuilken 1940; Walker et al. 1981; Knoop & Walker 1985; Archer 1989; Williams & Hobbs 1989; De Steven 1991; Bragg et al. 1993; Myster 1993; Crow et al. 1994; Inouye et al. 1994). In many instances, woody seedling mortality during dry

conditions is believed to be due to competition with herbaceous vegetation for soil water (Walker et al. 1981; Archer 1989; Harrington 1991). Although older seedlings, saplings and adult trees are able to tap water reserves deeper in the soil, and thereby reduce competition with herbaceous vegetation (Callaway et al. 1991), it is hypothesized that establishment of woody plants in herbaceous patches and/or communities is limited, even prevented entirely in some cases, because of competition with herbaceous vegetation for soil water during the young seedling stage (Knoop and Walker 1985; Gordon et al. 1989).

Holmgren et al. (1997) proposed that shade from canopy trees may alternatively facilitate or inhibit success of woody seedlings depending on soil wa-

ter conditions. In dry sites, they argued that shade would increase woody seedling success by reducing water stress while in wet sites shade would inhibit seedlings by increasing competition for light. Zutter et al. (1986) showed that soil water declines with increasing herbaceous biomass. Since herbaceous biomass has been found to increase with increased nitrogen inputs (Tilman 1988), elevated soil nitrogen levels, e.g., through atmospheric deposition, might affect seedling success through changes in soil water levels. Thus, the impact on woody seedling success of season long wet or dry spells may be mediated by local conditions involving shade and soil nitrogen levels.

In the nutrient poor and sandy soils of east central Minnesota, USA, trees encroach into old fields and native savanna openings very slowly (Inouye et al. 1994; Davis et al. 1997). Seedling herbivory by white-tailed deer, *Odocoileus virginianus*, and pocket gophers, *Geomys bursarius*, are responsible for some tree seedling mortality (Inouye et al. 1994), but mortality rates from herbivory are not high enough to account for all observed seedling mortality. Since soil water is known to affect tree seedling performance in other semi-arid environments (Walker et al. 1981; Knoop & Walker 1985; Archer 1989), the dry sandy soils of this region of Minnesota may be contributing to the very slow encroachment of trees into grassland environments. It has also been documented that this region is experiencing substantial atmospheric deposition of anthropogenic nitrogen which is believed to be affecting plant community structure (Wedin & Tilman 1996). It is currently unknown whether this nitrogen deposition is affecting tree seedling establishment in herbaceous dominated communities in this region.

Thus, the purpose of our study was to assess how changes in soil water affect survival, growth, and rate of photosynthesis of tree seedlings and how soil water is affected by competition with herbaceous vegetation along an experimental gradient of water, light and soil nitrogen. We predicted that oak seedling survival, growth, and rates of photosynthesis would be limited by competition with herbaceous vegetation for soil water. We predicted that survival and growth of tree seedlings growing with herbaceous vegetation would decline with increased nitrogen inputs which would favor herbaceous vegetation more than the tree seedlings. Since soil water has been found to be higher under mature tree canopies in old fields (Ko & Reich 1993), we also predicted that tree seedling survival and photosynthesis would be higher in the shade than in full sun under dry conditions, consistent

with the light-water model of facilitation and competition (Holmgren et al. 1997). By manipulating water inputs, measuring soil water levels in the experimental plots, and comparing survival, growth, and rates of photosynthesis of seedlings growing with and without herbaceous vegetation, we also sought to determine if competition between the seedlings and herbaceous vegetation varied predictably with water availability.

Materials and methods

Study area

In spring 1995, an experimental field study was established in an old field at Cedar Creek Natural History Area (CCNHA), Bethel, MN (45°24' N, 93°12' W). CCNHA is situated on the Anoka Sandplain, a glacial outwash area that is characterized by coarse textured soils low in nitrogen (Grigal et al. 1974). Bur oak (*Quercus macrocarpa* Michx.) and northern pin oak (*Quercus ellipsoidalis* E. J. Hill) are the two dominant tree species in the savanna/woodland habitat at CCNHA. See Davis et al. (1998) for more details regarding the study site.

Experimental design and layout

Twenty four plots (8 replicates of three plots) were laid out in three parallel rows running east-west with eight plots per row. A replicate consisted of the three adjacent plots in the respective three rows. That is, replicate one consisted of plot one in rows 1, 2, and 3. Each plot contained a row of eight subplots (1.5 × 1.5 m) separated from one another by a buffer zone of 1.5 m. In total, the experiment contained 192 subplots (3 rows × 8 plots × 8 subplots). Each of the three water levels (dry, medium, wet) was randomly assigned to one of the three plots within each replicate. Four of the eight subplots in each plot were randomly assigned as a shade plot. The four shade and four full sun plots in each plot were then randomly assigned to one of four treatments – ambient soil nitrogen (no added N) with herbaceous vegetation, low N enrichment with herbaceous vegetation, high N enrichment with herbaceous vegetation, and ambient soil N without herbaceous vegetation (competitor absent).

Within each subplot, four two year old seedlings of both bur and pin oaks were transplanted in late April, 1995. See Davis et al. (1998) for more detail on the transplanting. 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.

Treatments

Light

Tree seedling success in herbaceous dominated communities will be influenced by the seedlings' ability to survive and grow in full sunlight vs beneath the shade of parent trees and other woody overstory (Li & Wilson 1998). The shade treatment was imposed using commercial black shade cloth (75 cm height) that reduced incident radiation by approximately 80% (Davis et al. 1998). This shade effect is comparable to understory shade levels beneath canopy trees that surrounded the study field (Davis et al. 1995). 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 1996. They remained in place until the end of the study, September 1996.

Nitrogen

Nitrogen granules (NH_4NO_3) were applied at annual rates of $5 \text{ g m}^{-2} \text{ yr}^{-1}$ of N in low N enriched subplots and $15 \text{ g m}^{-2} \text{ yr}^{-1}$ in high N enriched subplots. Applications were applied to subplots in July and August 1995 and monthly from April through August 1996 in proportion to observed monthly N mineralization rates at Cedar Creek from April to August (Pastor et al. 1987). (Total N application in 1995 was 1.6 g m^{-2} in low N enriched plots and 4.8 g m^{-2} in high N enriched plots). The application area of nitrogen included a 0.75 m buffer zone around the subplots.

Water

The three water treatments were applied during the second summer 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 fact that seedlings exhibited more than 80% survival during the first year of the experiment (prior to the water treatments), indicates that they did not experience a high degree of transplant stress. The purpose of the water treatments was to create three soil water regimes – dry, medium (near ambient), and wet. We strived 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 of full sun control (not weeded, no N addition) plots. Percent volumetric soil water content, θ , was measured using a portable time domain reflectometry system (Topp et al. 1980; Baker 1990; Davis et al. 1998). The 30 cm probes were inserted vertically into the soil surface near the center of the subplots.

Dry conditions were created by pulling a 6 mil plastic tarp ($30 \times 6 \text{ m}$) over plots immediately prior to most rain episodes, and removing it after the rain ended (Davis et al. 1998). The rain tarps were used during the period of June 1 to August 31, 1996. During this time, the study site received 215 mm of rainfall. Dry plots received 85 mm of rainfall.

Wet conditions were created by using an irrigation system of flat sprinkler hoses (Davis et al. 1998). Wet plots received a total amount of water input (precipitation plus irrigation) of 820 mm during the three month period. Medium water conditions were created primarily by exposing plots to ambient rainfall. Plots designated as medium received an additional 13 mm of water during an especially dry period for a total of 228 mm, an amount which fell within the standard deviation of local precipitation for June–August during the past 33 years. The three water application levels produced soil water content (seasonal average in the subplots which were measured weekly) in the dry, medium, and wet levels of approximately 4, 6, and 8%, respectively.

Removal of herbaceous vegetation

Subplots designated to be free of herbaceous vegetation (no competition subplots) were treated with a glyphosphate herbicide (RoundupTM) 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.

Herbivores

Known herbivores of the 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 50TM) 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 survival and growth

In June 1995, six weeks following transplanting and 10 days prior to the implementation of the light and N treatments, seedling shoot height and stem diameter were measured. In mid-September 1996, the number of surviving seedlings of each species in each subplot was recorded and the height and stem diameter of all surviving seedlings were measured.

Shoot woody biomass (mg) estimates for surviving seedlings in June 1995 (beginning of the experiment) and September 1996 (end of experiment) were determined using an allometric equation based on height (H , in cm) and stem diameter (D , in mm):

$$\begin{aligned}\text{Log}(\text{Biomass}_{\text{bur}}) &= 0.83196 + 0.94789 \\ &\text{Log}(D^2 H) \quad (r^2 = 0.934, p < 0.001, n = 27), \\ \text{Log}(\text{Biomass}_{\text{pin}}) &= 0.88657 + 0.92086 \\ &\text{Log}(D^2 H) \quad (r^2 = 0.970, p < 0.001, n = 21).\end{aligned}$$

Allometric equations were derived from surplus seedlings that had been planted in full sun conditions in the same field as the experiment. The height:diameter relationship was examined for seedlings in each of the contrasting water, nitrogen and light treatments using separate and same slope analyses. Major differences in height:diameter relationships among treatments might indicate the need for separate allometric equations for different treatments. However, height:diameter relationships were quite similar in all treatments.

Biomass of herbaceous vegetation

In order to determine above ground biomass of herbaceous vegetation in a subplot, a strip of herbaceous vegetation, 10 cm \times 1 m, was clipped at ground level along the east side of each subplot, excluding weeded subplots, in August 1996. The vegetation was dried and weighed.

Leaf net photosynthesis

To examine the effects of different water and light conditions and competing vegetation on leaf net photosynthesis, we measured oak photosynthesis in both species in dry and wet plots, under both light conditions, in weeded subplots and subplots with herbaceous vegetation and ambient soil N on August 8, 1996, in six of the eight replicates. We measured rates of leaf net photosynthesis on fully expanded, mature

leaves at comparable upper canopy positions. We measured a single leaf from one plant of each oak species in each subplot. Measures were obtained at the light levels of the unshaded (full sun) and shaded treatments. Rates of net CO₂ and water vapor exchange were measured using a portable photosynthesis system (CIRAS-1, PP Systems, Hitchin Herts, UK), operating in an open configuration. Incident irradiances (PPFD, $\mu\text{mol m}^{-2} \text{s}^{-1}$) averaged 1428 (± 31) and 254 (± 6) on August 8 in the unshaded and shaded treatments. Following measurement, a leaf disk was obtained from each leaf to determine rates of net photosynthesis on both a leaf area ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and dry mass ($\text{nmol g}^{-1} \text{s}^{-1}$)

Soil water

In addition to the weekly soil water measurements of full sun, ambient N, unweeded subplots, on July 17 (3 days after the last rain and 5 days since the last watering, and August 9 (4 days after the last rain and 10 days since the last watering), 1996, percent volumetric soil water content, θ , measurements were made in all subplots except low nitrogen enriched treatments. The average of the soil water measurements for both dates was calculated for a subplot and used in subsequent analyses. In addition, soil water potential, Ψ_s , for plots was calculated using θ values and a soil water release curve developed at CCNHA for the soil type of the study field (Grigal et al. 1974).

Data analysis

Our experiment did not consist of a full factorial combination of treatments since the two nitrogen enrichment levels were not applied to weeded plots. Data were separated into two overlapping data subsets to permit separate analyses based on full factorial design. The first subset included all weeded and ambient N subplots with herbaceous vegetation. This data subset was analyzed to determine whether herbaceous vegetation affects soil water, seedling survival, growth, and rate of photosynthesis under different light and water regimes. The second data subset consisted of all subplots with herbaceous vegetation, including those with ambient soil N and those with low and high N enrichment. These data were analyzed to determine the combined effects of different water, light, and soil N regimes on seedling growth and survival, biomass of herbaceous vegetation, and soil water. Analyses of the first data set are hereafter referred to as the 'com-

petition analysis' while analyses of the latter data set are referred to as the 'nitrogen analysis'.

Treatment effects on seedling growth were determined by analyzing treatment effects on final biomass using a split-split-plot ANCOVA, with initial biomass as the covariate (JMP, SAS Inc.). Treatment effects on photosynthesis rates were analyzed using a split-split-plot ANOVA with water as a plot effect, competition and light as subplot effects, and species as a sub-subplot effect. Treatment effects on seedling survival in both experiments were analyzed using logistic regression, with 1995 initial biomass included as a covariate. Treatment effects (competition, nitrogen, light and water) on soil water content, θ , and soil water potential, Ψ_s , were analyzed using a split-plot ANOVA, with water as a plot effect and competition, nitrogen, and light as subplot effects. Treatment effects (light, N and water) on the biomass of herbaceous vegetation were analyzed using a split-plot ANOVA, with water as a plot effect and N and light as subplot effects. Nitrogen and water treatments were defined as quantitative factors in these analyses, based on the amount of N enrichment (0, 5, 15 g m⁻² yr⁻¹) and water (85, 228, 820 mm) applied. *A posteriori* testing of means was conducted using the Newman-Keuls test (Zar 1996). We used simple regression analysis to assess the relationships of seedling survival and rate of photosynthesis with soil water (θ , Ψ_s). We also used simple regression analysis to examine the relationship between seedling survival and herbaceous shoot biomass in subplots. Seedling and herbaceous biomass and soil water potential, Ψ_s , were log transformed and soil water, θ , was arcsine transformed prior to all analyses. Seedling survival data were arcsine transformed prior to regression analyses.

Results

Soil water

The split-plot analyses on percent volumetric soil water content, θ , and soil water potential, Ψ_s , produced comparable results. Throughout our study site, soil texture was extremely uniform and the site was flat. Thus, in this study, θ is a good indicator of Ψ_s and we have presented results for θ . In the competition ANOVA analysis, θ was affected by light ($F = 5.80$, $p = 0.019$) and by a competition \times water interaction ($F = 9.84$, $p = 0.003$). Specifically, θ was usually greater in shaded plots, and although θ was

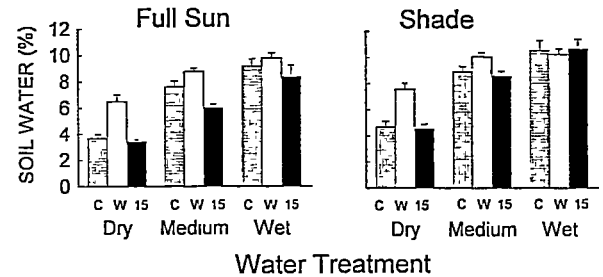


Figure 1. Percent soil water (mean + 1 SE) for treatment combinations of water, light, competition, and nitrogen. C=control subplots (with herbaceous vegetation but no N enrichment); W=weeded subplots (no herbaceous vegetation and no N enrichment); 15=N enriched subplots (with herbaceous vegetation and nitrogen added at a rate of 15 g m⁻² yr⁻¹).

generally greater in plots without herbaceous vegetation, this difference decreased with increasing water input (Figure 1). Thus, herbaceous vegetation had its greatest effect on θ in dry conditions. In the nitrogen ANOVA analysis, θ differed among water treatments ($F = 32.20$, $p < 0.001$, with θ increasing with increasing water input (Figure 1), but θ did not differ among N ($F = 0.98$, $p = 0.325$) or light ($F = 2.39$, $p = 0.127$) treatments.

Herbaceous biomass

Herbaceous biomass differed among nitrogen ($F = 21.25$, $p < 0.001$) and water ($F = 8.13$, $p = 0.025$) treatments, with above ground herbaceous biomass generally increasing with increasing nitrogen and water enrichment (Figure 2). Herbaceous biomass was only marginally different among light treatments ($F = 2.99$, $p = 0.087$, Figure 2). Species composition of the herbaceous vegetation was affected by the nitrogen additions, with grass species (esp. *Poa pratensis*, *Agropyron repens*, and *Bromus inermis*) increasing and forb species declining in cover (unpublished data).

Seedling survival

Seedling survival differed between species in both the competition ($X^2 = 4.08$, $p = 0.044$) and nitrogen analyses ($X^2 = 4.22$, $p = 0.040$), with bur oak survival exceeding that of pin oak in both cases (Figure 3). In the competition analysis, seedling survival was affected by interactions involving competition with both water ($X^2 = 4.64$, $p = 0.031$) and light ($X^2 = 4.80$, $p = 0.028$). Specifically, although competition often reduced seedling survival, the magnitude of this effect declined (or disappeared) in the

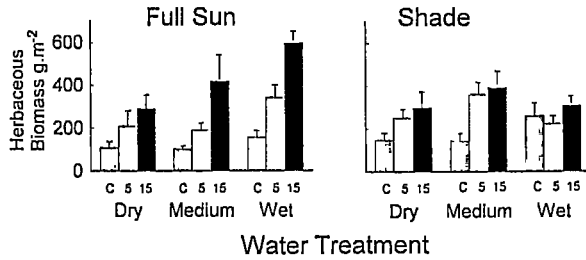


Figure 2. Above ground herbaceous biomass (mean + 1 SE) for treatment combinations of water, light, and nitrogen. C=control subplots (with herbaceous vegetation but no N enrichment); 5=N enriched subplots (with herbaceous vegetation and nitrogen added at a rate of $5 \text{ g m}^{-2} \text{ yr}^{-1}$); 15=N enriched subplots (with herbaceous vegetation and nitrogen added at a rate of $15 \text{ g m}^{-2} \text{ yr}^{-1}$).

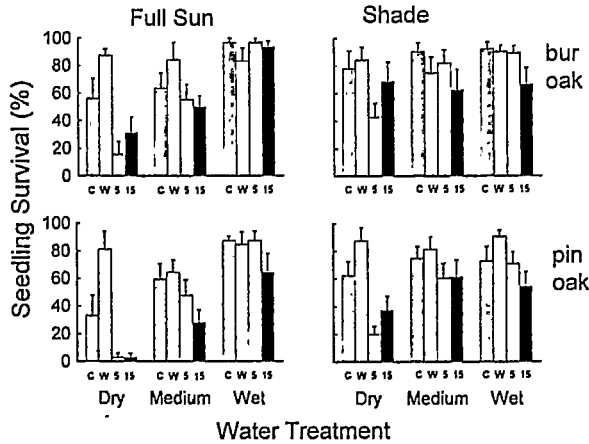


Figure 3. Seedling survival (mean + 1 SE) for bur (*Q. macrocarpa*) and pin (*Q. ellipsoidalis*) oak for treatment combinations of water, light, competition, and nitrogen. C=control subplots (with herbaceous vegetation but no N enrichment); W=weeded subplots (no herbaceous vegetation and no N enrichment); 5=N enriched subplots (with herbaceous vegetation and nitrogen added at a rate of $5 \text{ g m}^{-2} \text{ yr}^{-1}$); 15=N enriched subplots (with herbaceous vegetation and nitrogen added at a rate of $15 \text{ g m}^{-2} \text{ yr}^{-1}$).

shade and with increasing water inputs (Figure 3), indicating that the herbaceous vegetation most likely reduced seedling survival through reduction in soil water. The nitrogen analysis showed that survival was affected by N input ($X^2 = 8.91$, $p = 0.003$) and by a light \times water interaction ($X^2 = 6.12$, $p = 0.013$). Seedling survival was generally lower in nitrogen enriched subplots (Figure 3). This was even true in wet plots, in which soil water was probably not being significantly reduced by increased biomass of herbaceous vegetation due to the high rate of water addition. In the nitrogen enriched wet subplots, the oak seedlings were sometimes buried under the dense herbaceous vegetation. Although light measurements were not taken beneath the herbaceous vegetation in these subplots,

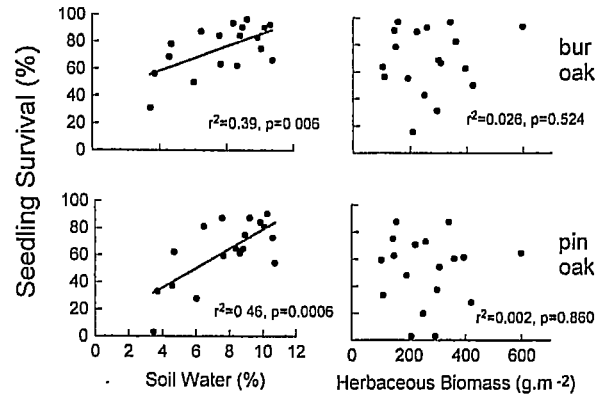


Figure 4. Seedling survival (mean + 1 SE) for bur and pin oak shown as a function of soil water and herbaceous biomass. The regression line is based on untransformed data and is included for illustration purposes. The r and p values are based on analyses of transformed data (arcsine transformation for survival and soil water, log transformation for herbaceous biomass). Seedling survival was also regressed on soil water potential (bur oak: $r = -0.754$, $p = 0.0003$, pin oak: $r = -0.671$, $p = 0.0023$).

it is more likely that the reduced seedling survival observed in the nitrogen enriched wet plots was due to reduced light than reduced soil water. In addition to the nitrogen effect, seedling survival increased with increasing water input in full sun subplots, however water input had less of an effect on survival in shaded subplots (Figure 3). The pattern of survival differences among treatments correlates strongly with the patterns of soil water content, θ , in the same treatments. The same factors that reduced θ also reduced seedling survival. The strong relationship between seedling survival and θ is illustrated by the results of the regression analyses (Figure 4). Survival for both species was significantly ($p < 0.005$) correlated with θ but was not correlated with biomass of its competitor, herbaceous vegetation (Figure 4).

Seedling growth

Shoot growth (final seedling biomass adjusted for initial biomass) of surviving seedlings was affected by water input in both the competition ($F = 9.55$, $p = 0.018$) and nitrogen analyses ($F = 6.71$, $p = 0.036$). As shown in Figure 5, there was a slight, though not entirely consistent, trend for growth to be greater in wet than dry plots. In the competition analysis, growth differed between species ($F = 11.87$, $p < 0.001$), with growth (adjusted biomass) of bur oak seedlings being consistently greater than that for pin oak seedlings. Growth was also affected by a light \times competition interaction ($F = 9.44$, $p = 0.018$).

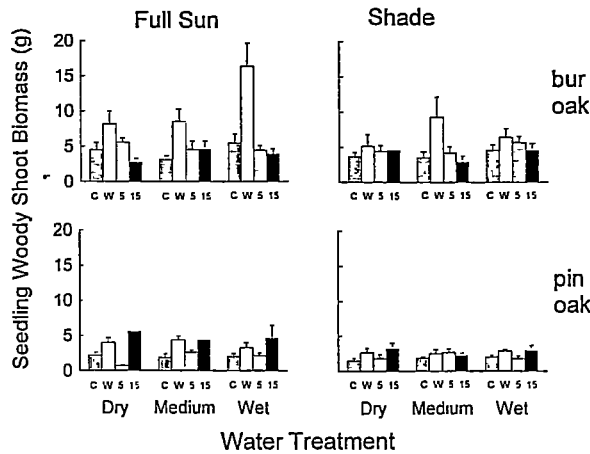


Figure 5. Seedling woody shoot biomass (mean + 1 SE) for bur (*Q. macrocarpa*) and pin (*Q. ellipsoidalis*) oak for treatment combinations of water, light, competition, and nitrogen. C=control subplots (with herbaceous vegetation but no N enrichment); W=weeded subplots (no herbaceous vegetation and no N enrichment); 5=N enriched plots (with herbaceous vegetation and nitrogen added at a rate of $5 \text{ g m}^{-2} \text{ yr}^{-1}$); 15=N enriched plots (with herbaceous vegetation and nitrogen added at a rate of $15 \text{ g m}^{-2} \text{ yr}^{-1}$). Error bars are lacking for pin oak in both nitrogen enriched subplots in the full sun and dry water treatment because only one of the original eight subplots in each of these two treatment combinations contained live pin oak seedlings at the end of the experiment.

Specifically, although growth of seedlings in weeded subplots always exceeded that in subplots with herbaceous vegetation, growth in weeded subplots declined substantially in the shade whereas growth of seedlings growing with herbaceous vegetation did not vary much between shade and full sun conditions (Figure 5). In the nitrogen analysis, seedling growth was affected by an interaction between species and nitrogen ($F = 11.36$, $p < 0.001$). Specifically, pin oak growth usually increased with N enrichment whereas bur oak seedlings did not vary consistently with N enrichment (Figure 5).

Rate of leaf net photosynthesis

Analyses of leaf net photosynthesis based on leaf area and leaf mass produced very similar results, with the same significant interactions terms. Results are presented for the analysis based on leaf mass. Bur and pin oak did not differ in rate of net photosynthesis ($F = 0.04$, $p = 0.845$), but rate of leaf net photosynthesis was affected by a three-way interaction involving light, competition, and water ($F = 23.84$, $p < 0.0001$, Figure 6). Figure 6 shows that net photosynthesis varied little between weeded and fully

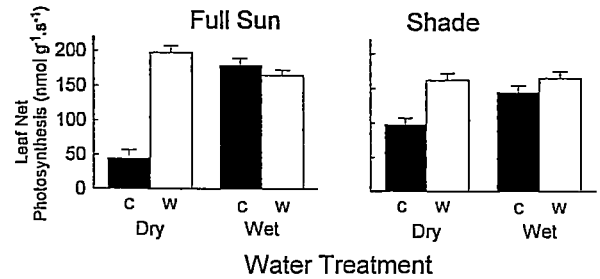


Figure 6. Seedling rates of net photosynthesis (mean + 1 SE) for bur and pin oak for treatment combinations of water, light, and competition. Since analysis showed no species difference, data for the two species were combined in this figure.

vegetated subplots under wet conditions in both light conditions. However, under dry conditions, net photosynthesis was much lower in subplots containing herbaceous vegetation and comparison of means using the Newman-Keuls test showed that this effect was most pronounced in full sun plots (full sun: $q = 18.61$, $p < 0.001$; shade: $q = 7.81$, $p < 0.01$; Figure 6). Net photosynthesis of seedlings growing with herbaceous vegetation in shaded dry conditions was significantly greater than that of seedlings growing with herbaceous vegetation in full sun dry conditions ($q = 5.99$, $p < 0.01$), showing that canopy shade can facilitate success of woody seedlings in dry conditions as predicted by Holmgren et al. (1997). In wet conditions, shade did not promote increased rate of photosynthesis among seedlings growing with herbaceous vegetation ($q = 4.60$, $p = 0.08$), and the trend was for shade under wet conditions to suppress net photosynthesis of seedlings growing with herbaceous vegetation, also consistent with Holmgren et al. (1997). Net photosynthesis was significantly positively correlated with soil water in subplots under both light conditions (full sun: $r^2 = 0.35$, $n = 43$, $p < 0.0001$; shade: $r^2 = 0.36$, $p < 0.0001$, $n = 46$).

Discussion

Our results showed that season long dry or wet periods can significantly affect survival, growth, and rate of photosynthesis of oak seedlings. Survival increased consistently with increasing water input, a finding that is consistent with observational studies that found oak seedling mortality in well drained sites increased during drought years in the upper Midwest (Crow et al. 1994; Inouye et al. 1994). The results also showed that the effects on seedling performance of a dry or wet summer varied under different light

and competition conditions. Although rate of photosynthesis with competitors present increased in the shade under dry conditions, it tended to decline in the shade under wet conditions. These results support the light-water model of facilitation and competition (Holmgren et al. 1997). As predicted, seedling survival declined with N enrichment, and this effect was most pronounced in dry conditions. These results are consistent with Kleiner et al. (1992) who showed that the lowest measures of physiological performance of *Q. rubra* and *Q. prinus* seedlings in a greenhouse experiment occurred under drought and fertilized (N+) conditions.

Both survival and rate of photosynthesis were strongly correlated with soil water content. Data also showed that herbaceous vegetation could substantially reduce soil water, particularly in dry conditions. Moreover, the results showed that survival and rate of photosynthesis were markedly lower in dry subplots when herbaceous vegetation was present, whereas in wet plots, presence of herbaceous vegetation had little effect on survival and rate of photosynthesis. Taken together, these results indicate that in dry conditions, herbaceous vegetation likely reduces seedling success partly through competition for soil water. In a similar field experiment conducted in the semi-arid grasslands of eastern Australia, Harrington (1991) found that survival of shrub seedlings during summer months was positively correlated with water supply and that herbaceous vegetation competed vigorously with the seedlings for this limiting resource.

Comparisons between the two species showed that bur oak survival exceeded that of pin oak under all conditions. This difference is consistent with survival data of naturally growing seedlings of the two species growing in oak woodland/savanna habitat at CCNHA during the same time period as the study (Davis, unpublished data). Our experiment showed that the difference in survival between the two species was greatest under dry and N enriched conditions (Figure 3). These data indicate that the survival advantage of bur oak seedlings relative to that of pin oak seedlings may increase if levels of soil nitrogen continue to increase at the study site due to atmospheric deposition (Wedin & Tilman 1996), and should a drying period develop in the future.

Pin oak was more consistently affected by changes in soil water and nitrogen resources. The greater sensitivity of pin oak to different water regimes may be due to the particularly rapid root growth of bur oak seedlings which may enable them to access deeper soil

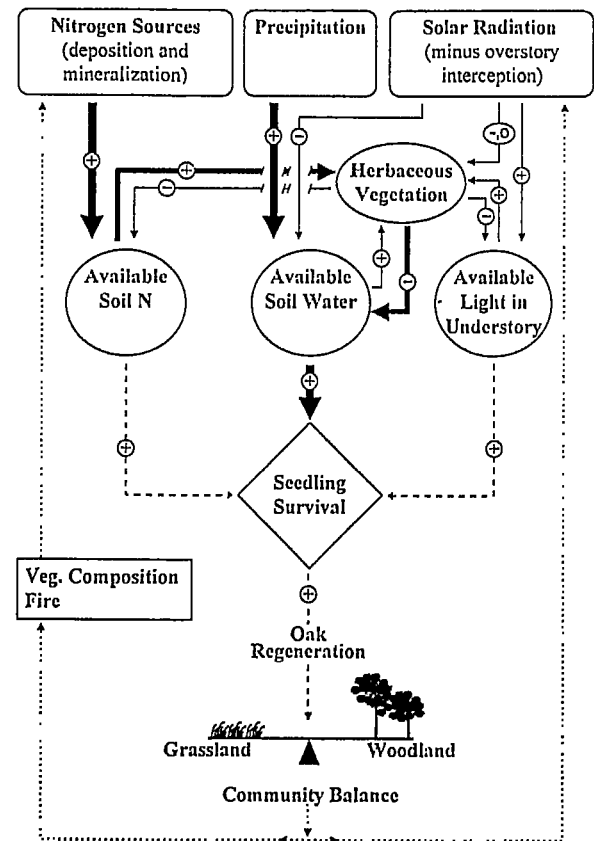


Figure 7. Model showing how nitrogen, water, and light supply are hypothesized to affect oak establishment and regeneration in savannas and herbaceous dominated communities in semi-arid environments. The nature of the proposed relationships between factors is indicated with a plus (positively correlated) or minus (negatively correlated) sign and the hypothesized strength of the relationship is indicated by the width of the arrow. Solid lines indicate relationships documented in this study. Dotted lines indicate relationships documented in other studies. The dashed lines indicate speculated relationships, for which specific data are not available. The figure shows that effects on oak regeneration occur via changes in a self-reinforcing (positive) feedback loop involving seedling survival. See text for elaboration.

water (Weaver & Kramer 1932), thereby making them less sensitive to changes in shallow soil water content.

In summary, our findings indicate that soil water may be playing an important role in defining the competitive dynamics occurring between herbaceous vegetation and oak seedlings in semi-arid environments in accordance with a model illustrated in Figure 7. The model presents our view that changes in nitrogen, light, and water input all affect tree seedling survival by their ultimate effects on soil water, which, in the absence of heavy seedling predation, is the primary determinant of seedling survival in these en-

vironments. The figure shows that effects on oak establishment and regeneration occur via changes in a self-reinforcing (positive) feedback loop involving seedling survival. Our data show that seedling establishment in dry herbaceous communities is likely to be persistently difficult due to competition with herbaceous vegetation for soil water. Once tree invasion begins, possibly during several consecutive wet years, the increase in soil water availability that will result from the shade created by maturing saplings and trees will facilitate more successful seedling establishment, thereby tipping the community away from a grass dominated system and toward one dominated by trees. The figure shows that a decline in precipitation levels should cause the herbaceous dominated community to become more resistant to invasion by oak seedlings, whereas an increase in precipitation should result in increased survival of seedlings. Nitrogen enrichment, e.g., by nitrogen deposition, may reduce oak establishment due to increased growth and biomass of herbaceous vegetation thereby decreasing available water and light for tree seedlings. Other factors that could be incorporated into the model include grazers that primarily eat herbaceous vegetation, and hence would increase soil water (Archer 1989); elevated levels of atmospheric CO₂ which may increase water use efficiency (Idso 1992; Johnson et al. 1993) and hence may increase soil water; and invasion of exotic grasses, which, if they use water less efficiently (Gordon et al. 1989), may decrease soil water.

This model is consistent with previous studies of tree establishment in semi-arid conditions throughout the world that have emphasized the importance of soil water in the interactions between herbaceous vegetation and tree seedlings (Walker et al. 1981; Knoop & Walker 1985; Archer et al. 1988; Williams & Hobbs 1989; Gordon et al. 1989; Skarpe 1990; Harrington 1991; Bragg et al. 1993; Inouye et al. 1994; Scholes and Archer 1997). It extends these studies by demonstrating how these interactions can be affected by changes in the amount of precipitation during the growing season, and, in turn, how the impact of dry and wet summers on tree seedling-grass interactions can be affected by light and soil nitrogen availability.

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