Photosynthetic rates and vegetative production of *Sorghastrum nutans* in response to competition at two strip mines and a railroad prairie

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Abstract

The effect of differing environmental conditions on competition for resources was investigated by a comparison of net photosynthetic rate (P_N) and vegetative production of Indiangrass [*Sorghastrum nutans* (L.) Nash.] at two strip mine sites with differing reclamation histories, and a railroad prairie site where this species occurs naturally. The treatment for a competition experiment consisted of tying back all species of neighboring plants around a target plant, and measuring its P_N and vegetative performance during the growing season. Environmental variables at each site were also measured during the growing season. Soil bulk density and pH were higher at the two mine sites than at the prairie site, and soil texture, nutrients, and water potential were different at each of the three sites. P_N of target plants compared closely among the three sites, and were lowest for plants at the railroad prairie. The competition experiment indicated that lower canopy leaves were most affected by competition for photosynthetically active radiation (PAR) at all sites. Significant differences in P_N of upper canopy leaves were found between treatment and control plants at one of the mine sites. This site had higher soil water potentials and higher soil levels of P and K than the other mine site or the railroad prairie. Target plants at the other mine site experienced a low competition for PAR, likely due to lower soil moisture availability and therefore lower aboveground productivity. The largest differences in P_N and irradiances between upper and lower canopy leaves occurred in target plants with neighbors at the railroad prairie, likely due to inter-specific competition. Vegetative production of the target plants also reflected the environment

Received 7 May 1997, *accepted* 24 July 1997.
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Abbreviations: P_N = net photosynthetic rate; PPFD = photosynthetic photon flux density.
Acknowledgements: This study was supported by the SIUC Office of Research and Development and Administration (Acct. No. 2-11344) to DJG. We thank Paul Gibson for statistical advice, W.C. Ashby for use of his research plots, A. West and S. Coleman for field and laboratory assistance, and B.P. Akers for reviewing the manuscript.

at each site, but did not reflect P_N differences between treatments. *S. nutans* is well adapted to the varying environment at these three sites, and aboveground competition for radiant energy was probably not as limiting for this C_4 grass as belowground competition.

Additional key words: biomass; gas exchange; inflorescence; irradiance; seasonal course; soil texture; tillers.

Introduction

Plant stress has been defined as "external constraints which limit the rate of dry matter production of all or part of the vegetation" (Grime 1979). These "external constraints" can include: soil infertility, nutrients or heavy metal toxicity, competition with other plants, drought, shade, limited space, poor soil structure and/or texture, excess heat or cold, excess water, herbivory, and disease. Plants must adapt to stress from both the environment and competition with other plants for limited resources.

Net photosynthetic rate (P_N) has been measured as an indicator of plant status because gas exchange requires an adequate amount of certain nutrients such as nitrogen, and responds to water and irradiance in the environment. Plants with the C_4 photosynthetic pathway are more efficient under high irradiance, and a higher percentage of C_4 plants occur in areas with higher temperatures, higher irradiances, and lower precipitation (Barnes *et al.* 1983). In general, P_N would be expected to be lower in response to plant competition, and we have shown in a greenhouse experiment that the C_4 grass *Sorghastrum nutans* has reduced P_N under increasing competition regardless of the competitor species (Gibson and Skeel 1996). The C_4 plants, however, produce more dry matter per unit of nitrogen, and therefore tend to be better competitors than C_3 plants in low nitrogen environments that often exist in the field (Brown 1978).

Measuring competition in the field can be challenging because plants compete for many interacting resources that are difficult to separate. The most common method is by vegetation removals where one or more species are removed around a target plant (Gurevitch 1986, Duralia and Reader 1993). Since plants can potentially compete with all other plants around them in their community, diffuse competition experiments are sometimes more appropriate to study the effect on a particular species (Mitchley 1987).

Strip mines are one example of an environment that may be stressful to plant development. The stresses of reclaimed strip mines can include a lack of soil structure, low organic matter, low nutrients, heavy metals, and soil compaction (Thomas and Jansen 1985). Species trials on native prairie plants have evaluated their success in strip mine reclamation (Anderson and Birkenholz 1980, Kuenstler *et al.* 1980, Bonfert and Ashby 1984, Ashby *et al.* 1989). Most of these studies, however, have focused on aboveground yield. Our field study focused on how individual plants respond both morphologically and physiologically, and how competition affects these responses.

We have shown that native prairie grasses are physiologically well suited for growth on reclaimed mine spoil (Skeel and Gibson 1996). The objective of the present study was to compare the effects of competition for radiant energy (*i.e.*, above ground diffuse competition) on one of these prairie grasses in the potentially stressful environment of a reclaimed strip mine, with the effects of competition for radiant energy on this species growing in its native habitat.

Materials and methods

Plants: *Sorghastrum nutans* (L.) Nash., or Indiangrass, is a perennial, warm season C_4 grass species, and an important range forage plant (Gould and Shaw 1983). Its physiological performance has been studied extensively in its natural habitat, especially in response to fire and grazing (Hulbert and Wilson 1980, Polley *et al.* 1992, Knapp 1993). When *S. nutans* has been used for mine reclamation it has shown success in terms of cover and biomass (Anderson and Birkenholz 1980, Kuenstler *et al.* 1980, Ashby *et al.* 1989, Corbett *et al.* 1996).

The DeSoto-Hallidayboro railroad prairie is a dry/mesic prairie remnant just north of DeSoto in Jackson County, Illinois (37°51'20"N, 89°13'54"W). It is managed by the Illinois Department of Natural Resources and the Illinois Department of Transportation (West, unpublished). Soils in the area are classified as Bluford and Ava Silt Loams (Herman *et al.* 1975). In March 1993, a prescribed burn was performed on the study area (Fink, unpublishhed). This is a habitat where *S. nutans* has been growing naturally and, therefore, was used as a control to compare with the strip mine sites.

Consolidated Burning Star Mine #5 is in Jackson County, just east of DeSoto Illinois, and was last mined in 1977 (37°58'83"N, 89°17'34"W). During reclamation, the old B and C soil layers were returned and graded, and about 0.41 m of topsoil was replaced (Ashby 1992). In April 1989 a 7.6×15 m trial plot of *S. nutans* cv. Cheyenne was established by first discing the plots, and then broadcasting seed by hand.

Freeman United Coal-Fidelity Mine #11 is in Perry County, 6.5 km west of Du Quoin, Illinois (37°58'83"N, 89°17'34"W). The area was originally mined in the 1950s, and then reopened in 1978. In 1980, the spoil from a boxcut was graded to a 15 % slope, but no topsoil was applied. In March of 1981, as part of a larger species trial, seeds of *S. nutans* from native Illinois populations were obtained from Dr. Peter Schramm, Knox College, Galesburg, Illinois, and sowed in a 500 m^2 plot with a hand seeder at a rate of 0.9 g m^{-2}.

Soils: In a comparison of the three sites (Table 1 in Skeel and Gibson 1996), soil from the railroad prairie site had the lowest soil CEC, whereas soil organic matter content was generally lowest at Burning Star mine. Soils from the mine sites were higher in calcium, magnesium, and manganese than those from the railroad prairie. Samples from Freeman mine and the railroad prairie had lower phosphorus contents than the samples from Burning Star mine. Contents of iron, copper, and zinc were comparable in samples from all three sites.

Soil texture was classified as a clay loam at Burning Star mine, a clay to clay loam at Freeman mine, and a clay loam to loam at the railroad prairie (Table 1 in Skeel and Gibson 1996). Surface soil bulk density and pH was lower at the railroad prairie site than at either of the mine sites.

Plant tissue nutrient content: *S. nutans* plants at Burning Star mine had higher leaf tissue concentrations of N, P, and K than the other two sites (Table 3 in Skeel and Gibson 1996). Plants at Freeman mine had the highest leaf tissue concentration of Ca, and plants at the railroad prairie had the highest leaf tissue concentrations of Mg and Mn. Similar concentrations of B, Zn, Al, Fe, and Cu were found in leaf tissue from at all sites.

Climate: Precipitation at the three sites from May to August 1994 was lower than the 22-year average of 419 mm (Herman *et al.* 1975). The railroad prairie received 340 mm, while Burning Star and Freeman mines received 290 and 275 mm, respectively (Skeel and Gibson 1996). Daily maximum air temperatures were below average in May (20 °C compared with 26 °C), higher than average in June and July (30-35 °C compared with 30 °C), and average in August (30-34 °C). Soil temperatures at the three sites were similar, but Freeman mine had higher values than Burning Star mine and the railroad prairie on 11 of the 17 d.

1994 soil water potentials at the three sites reflected the lower than average seasonal precipitation levels (Fig. 1 in Skeel and Gibson 1996). Differences among sites became most apparent near the end of the season, when Burning Star mine exhibited the highest water potential values, reflecting greater soil moisture, while Freeman mine was generally the driest during this period.

Experimental design: The treatment imposed on the species at each site consisted of removing competition for radiant energy around a 15 cm diameter area of individual plants (genets) from April to September 1994, by holding back the aboveground parts of neighbors of all species with a 1 m^2 piece of vinyl screen material which had a 15 cm diameter circle cut out in the middle. By leaving the neighbor plants whole instead of clipping them, there was less disturbance to the plot and below ground competition was not as affected. The control consisted of not altering any plants in the plot so that the target plant remained shaded by neighboring plants.

Twenty 1 m^2 plots, 10 control and 10 treatment, were established for the species at each site for a total of 60 plots. At the mine sites, plots with *S. nutans* were established in a pairwise random design. At the railroad prairie, paired plots were randomly selected in an area with a significant amount of *S. nutans*. Target plants of similar size were chosen for all plots.

Measurements on target plants: P_N [μmol(CO_2) m^{-2} s^{-1}] was measured with a *LI-COR* 6200 Portable Photosynthesis System (*LI-COR*, Lincoln, NB, USA), which encloses a leaf from the plant non-destructively in a 250 cm^3 chamber. P_N for each target plant was measured on cloud-free days in May, June, July, and early and late August. Measurements were made between 10.00 and 14.00 h. The youngest, healthy, fully expanded leaf near the top of the canopy was chosen, and held parallel to the ground during the measurement. The mean of three successive samples taken within 1 min was retained for subsequent analysis. An additional set of measurements was taken in early August on leaves both near the bottom and near the top of the canopy. Irradiance, PPFD [μmol m^{-2} s^{-1}] was also measured for each P_N sample taken.

Vegetative performance of target plants was compared among sites and between treatments to assess plant responses to stress and competition for radiant energy. In September, flowering tiller height was measured, flowering tillers were counted, and all target plants were clipped at ground level. After the plants were oven dried at 70 °C for 48 h, the total inflorescence and vegetative dry masses were determined separately.

Statistical analysis was performed using *PROC GLM* (*SAS* ver. *6* 1989) with significance set at $p<0.05$. Variables measured once at the end of the growing season such as final dry mass, height, density and biomass of flowering tillers were tested for normality, with non-normal data subsequently transformed to a log 10 scale prior to analysis. Dependent variables were then compared between treatment and control plots, by site, with a one-way ANOVA.

P_N was measured monthly throughout the growing season, but was not measured on the same day for each site. To control for varying climatic conditions between days, leaf temperature and vapor pressure deficit were used as covariates. Gas exchange measurements at leaf temperatures equal to or greater than 42 °C were removed prior to analysis because gas exchange rates of warm season grasses such as *S. nutans* drop sharply at higher temperatures due to photosynthetic enzyme degradation (Knapp 1985). After testing for normality, photosynthetic rates and leaf temperatures were transformed to a square root scale, and vapor pressure deficit was transformed to a log 10 scale. An initial regression was then performed on the dependent variable using the covariates, and the residuals from this regression were compared across time, between treatment and control plots, by site, with a one-way repeated measures ANOVA (Potvin *et al.* 1990).

Irradiance and P_N at top and bottom canopy levels were not statistically compared among sites to avoid pseudoreplication (Hurlbert 1984). After transforming the values to a square root scale, these were compared by site, between top and bottom canopy levels, and between plants with and without neighbors with a two-way ANOVA.

Results

Gas exchange measurements: Maximum P_N was in June and late August at Burning Star mine, in July at Freeman mine, and in May and July at the railroad prairie (Fig. 1). Target plants at Burning Star mine had higher overall P_N than target plants at the other sites, while plants at railroad prairie exhibited the lowest rates throughout the growing season. Significant differences in P_N between plants with and without neighbors were found in early and late August at Burning Star mine [$F(1,19)=10.07$ and 6.42, respectively, $p=0.0053$ and 0.021] , but there were no significant treatment effects in any month at the railroad prairie or Freeman mine. The PPFD was significantly greater around plants without neighbors than around plants with neighbors in June at Burning Star mine [$F(1,19)=10.55$, $p=0.0045$], and in May and early August at the railroad prairie [$F(1,19)=9.95$ and 12.27, respectively, $p=0.0055$ and 0.0025] (Fig. 8 in Skeel 1995). There was no significant treatment effect for PPFD at Freeman mine.

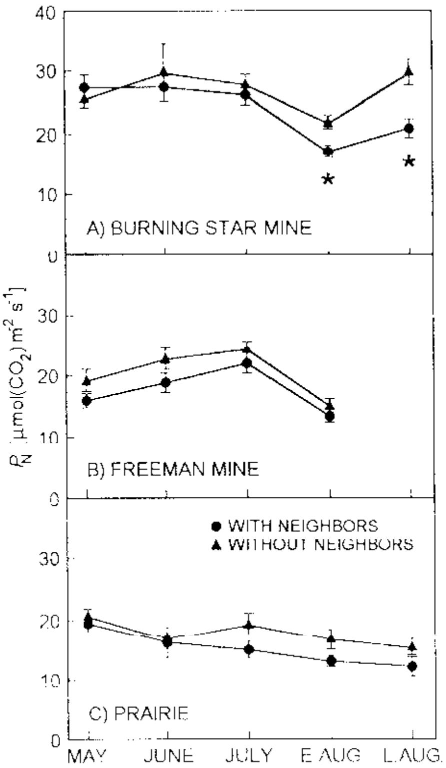

Fig. 1. Monthly mean net photosynmetic rate, P_N [µmol m^{-2} s^{-1}] from May to late August of new, fully expanded leaves on target plants with and without neighbors. * = a significant difference between treatments. Bars = +/- one standard error.

Leaves at the top of the canopy had significantly higher P_N than leaves at the bottom of the canopy for plants with neighbors at Burning Star mine [$F(1,19)=13.16$, $p=0.0023$] (Fig. 2). No significant differences in P_N occurred between top and bottom canopy leaves for plants without neighbors at Burning Star mine. Plants at Freeman mine and the railroad prairie showed significant differences in P_N between top and bottom canopy leaves for plants with and without neighbors [Freeman: $F(1,19)=9.42$, $p=0.0073$; railroad prairie: $F(1,19)=21.18$, $p=0.0003$]. PPFD was significantly higher at the top of the canopy than at the bottom around target plants with neighbors at the railroad prairie and Freeman mine [$F(1,19)=9.40$ and 15.13, respectively, $p(1,19)=0.0074$ and 0.0013], but not around target plants without neighbors (Fig. 2). At Burning Star mine, however, PPFD was not significantly different between the top and bottom of the canopy for plants with or without neighbors. PPFD was significantly higher around plants without neighbors than around plants with neighbors at all three sites [Burning Star mine: $F(1,19)=4.66$, $p=0.0464$; Freeman mine: $F(1,19)=12.71$, $p=0.0026$; railroad prairie: $F(1,19)=24.04$, $p=0.0002$]. Canopy measurements of P_N were significantly higher for plants without neighbors than for plants with neighbors at Burning Star mine [$F(1,19)=15.50$, $p=0.0012$], however, there were no significant neighbor effects on P_N at Freeman mine or the railroad prairie.

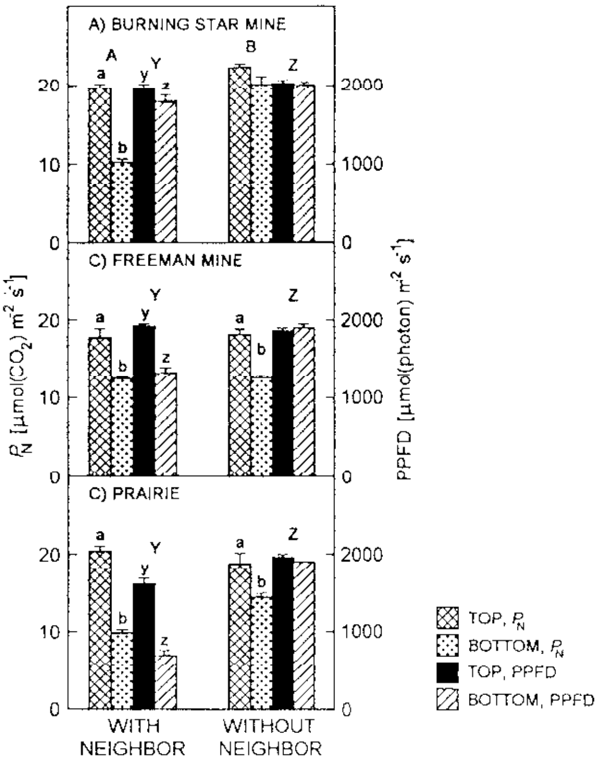

Fig. 2. Net photosynthetic rate, P_N [μmol m^{-2} s^{-1}] and photosynthetic photon flux density, PPFD [μmol m^{-2} s^{-1}] at the top and bottom of the canopy of target plants with and without neighbors in early August. Large letters indicate a significant difference between treatments, small letters indicate a significant difference between top and bottom canopy levels. In both cases, *A* and *B* indicated significant differences in P_N, and *Y* and *Z* indicated significance in PPFD. Bars = +/- one standard error.

Vegetative production: Target plants had higher overall aboveground production at Burning Star mine than at the other two sites (Fig. 3). Plants at the railroad prairie had the lowest production, with the exception of average inflorescence mass, which was lowest in plants at Freeman mine. There were no significant differences in aboveground production between plants with and without neighbors indicating that significant differences in P_N between treatments did not translate into significant differences in production.

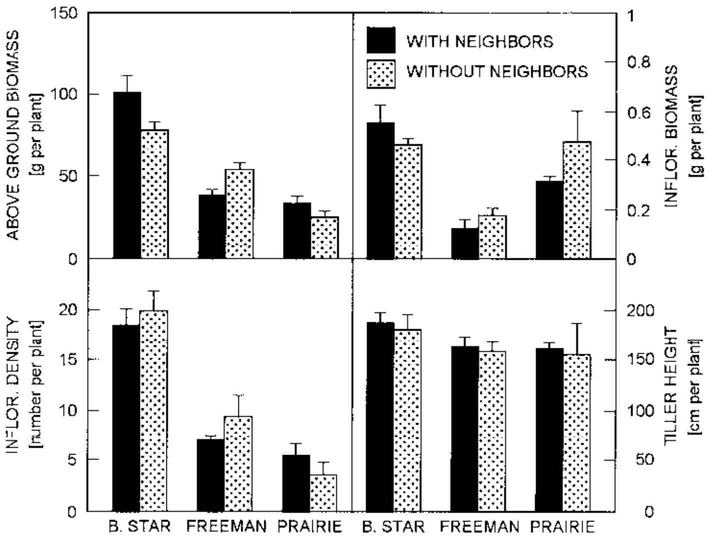

Fig. 3. End of season aboveground production of target plants with and without neighbors at Burning Star mine, Freeman mine, and DeSoto prairie. (*A*) aboveground biomass, (*B*) inflorescence biomass, (*C*) flowering tiller density, (*D*) flowering tiller height. Bars = +/- one standard error.

Discussion

Results of the competition experiment were consistent with differences in the physiological and vegetative performance of the plants at the three sites, and reflected the growth form and life history of *S. nutans*. At Burning Star mine P_N was significantly higher in plants without neighbors compared with plants with neighbors in August during peak standing biomass, indicating that *S. nutans* was reduced by competition with neighboring plants at this site. These results support our greenhouse competition experiment with this species, which showed that increasing the levels of competition with neighbors caused decreasing gas exchange rates, regardless of the neighbor species (Gibson and Skeel 1996). Higher soil nutrient and water potential levels at Burning Star mine compared with the other sites resulted in higher biomass of neighboring plants and, therefore, a high degree of competition. Freeman mine plants had lower contents of nitrogen, potassium, and phosphorus in leaf tissue, and less water was available to the plants compared with the other two sites, which could explain the low competition. This was reflected by no significant differences between treatments for P_N at Freeman mine as compared with Burning Star mine. *S. nutans* had higher P_N and vegetative production at both mine sites than at the railroad prairie site, which supports our previous study (Skeel and Gibson 1996). The plants probably did not experience a large stress at both mine sites, but soil and climatic differences between the three sites had some effect on physiological responses of the plants. Vegetative and flower production also reflected site differences, and was highest at Burning Star mine and usually lowest at the railroad prairie.

The biomass and species of neighboring plants at each site likely influenced the degree of inter- and intra-specific competition between target and neighboring plants. Burning Star mine had the highest plant biomass, and a high percentage of neighboring plants were *S. nutans* (Table 3 in Skeel and Gibson 1996). The target plants at Freeman mine also experienced high intra-specific competition, although aboveground biomass at Freeman mine was half that of Burning Star mine, likely due to drier conditions at that site. Target plants at the railroad prairie experienced the highest amount of inter-specific competition, with *Schizachyrium scoparium* (Michx.) Nash., *Rhus copallina* L., *Solidago canadensis* L., and *Helianthus divaricatus* L. as the most abundant competitors. Since the railroad prairie plants were competing with a variety of species, including relatively tall, woody species like *Rhus copallina*, the difference in PPFD between neighbor and control plots, and between the top and bottom of the canopy in control plots was higher at the railroad prairie than in plots from either mine site. This was reflected in a greater difference in photosynthetic rates between the top and bottom of the canopy in the railroad prairie plants.

Plants at Burning Star mine did not show significant differences in gas exchange rates between treatments until August, indicating competition for PAR was not very important until later in the season. Target plants at Freeman mine, however, completed their annual life cycle earlier in the season than target plants at other sites. They had earlier and higher numbers of leaf senescence, and flowered 7-11 d earlier than plants at the other two sites. Gas exchange rates at the top and bottom of the canopy were very similar in early August between plants with and without neighbors at Freeman mine, reflecting the senescence of lower leaves.

Late successional, warm season grasses, such as *S. nutans*, allocate most of their resources to underground parts, and are good competitors for nutrients and water (Tilman 1989, Wedin and Tilman 1990), but poor competitors for PAR. Their biomass is significantly more reduced under limited irradiance than cool season grasses. At the two strip mine environments, PAR was not a limiting resource. In an environment such as Freeman mine, which was drier and therefore had lower aboveground biomass, competition for PAR was less important than at Burning Star mine. At the railroad prairie, PAR was more limiting due to competition with a variety of species having diverse canopy structures. This was reflected in lower aboveground vegetative production, fewer inflorescences, and lower P_N. However, P_N of upper canopy leaves did not significantly differ between treatments, indicating that upper leaves are much less affected by competition for PAR.

Results from this study support findings of other studies on competition with C_4 prairie grass species (Tilman 1989, Wedin and Tilman 1990). Site productivity and soil properties determined the degree of competition for nutrients, water, and PAR, and plants adapted their growth habits and physiological responses to the conditions accordingly. Overall, the degree of competition for PAR was not high for this species at the mine sites because they were not especially PAR limited by neighbors. This was due to the growth habit of this species, or namely, that most of the biomass of prairie grasses is below ground, and was reflected by few significant differences between treatments in gas exchange rates, and a lack of significant differences in vegetative production between plants with and without neighbors. Belowground competition was likely most important later in the season at Burning Star mine, when productivity of *S. nutans* was greatest, while aboveground competition for PAR was more important for *S. nutans* at the railroad prairie where the target species' vegetative and physiological performance was low due to a large competition for space and PAR with neighbor species that had a high canopy coverage. Our previous study of *S. nutans* at these sites (Skeel and Gibson 1996) indicated that plants growing at the railroad prairie were most limited because when grown in a greenhouse pot experiment under more ideal conditions they showed the highest increase in P_N compared with plants from the two mine sites. Plants at Freeman mine were not limited so much by competition, but by environmental conditions at that site, which included lower water availability and lower soil nutrient levels than Burning Star mine.

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