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Shading and the capture of localized soil nutrients: nutrient contents, carbohydrates, and root uptake kinetics of a perennial tussock grass

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Summary. The ability to exploit spatial and temporal heterogeneity in soil resources can be one factor important to the competitive balance of plants. Competition aboveground may limit selective plant responses to belowground heterogeneity, since mechanisms such as root proliferation and alterations in uptake kinetics are energy-dependent processes. We studied the effect of shading on the ability of the perennial tussock grass *Agropyron desertorum* to take up nutrients from enriched soil microsites in two consecutive growing seasons. Roots of unshaded plants selectively increased phosphate uptake capacity in enriched soil microsites (mean increases of up to 73%), but shading eliminated this response. There were no changes in ammonium uptake capacity for roots in control and enriched patches for either shaded or unshaded plants. The 9-day shade treatments significantly reduced total nonstructural carbohydrate (TNC) concentrations for roots in 1990, but had no apparent effect on root carbohydrates in 1991 despite dramatic reductions in shoot TNC and fructan concentrations. Enrichment of the soil patches resulted in significantly greater phosphate concentrations in roots of both shaded and unshaded plants, with less dramatic differences for nitrogen and no changes in potassium concentrations. In many respects the shaded plants did surprisingly well, at least in terms of apparent nutrient acquisition. The effects of aboveground competition on nutrient demand, energy requirements, and belowground processes are discussed for plants exploiting soil resource heterogeneity.

Key words: *Agropyron* – Carbohydrates – Phosphate and ammonium uptake kinetics – Roots and soil microsites – Shading

Despite numerous studies on the ecophysiology of shading and photosynthesis (e.g. Mooney 1972; Evans et al. 1988), relatively few studies have integrated aboveground responses with the belowground ecology of plants. A number of laboratory and glasshouse experiments have examined the effect of shading on root processes (e.g. Massimino et al. 1981; Corré 1983), but few have attempted to do so in the field. This integration of above- and belowground characteristics is important because plants in the field inevitably respond to multiple interacting factors (Chapin et al. 1987; Aerts et al. 1991) and, for many plants, belowground competition can be more important than competition aboveground (Donald 1958; Remison and Snaydon 1980).

In the Great Basin region of the western United States, snowmelt and spring rainfall provide a transient but important source of water for plants (West 1988). This temporal heterogeneity in water abundance most likely results in a flush of available soil nutrients. Plants possess a suite of potential mechanisms for exploiting spatial and temporal heterogeneity in the soil. These mechanisms include root proliferation (Drew and Saker 1975; Jackson and Caldwell 1989), adjustments in nutrient uptake kinetics (Clarkson 1985; Jackson et al. 1990), changes in the frequency of mycorrhizal infection (St. John et al. 1983; Allen and MacMahon 1985), and root exudates (Jungk and Claassen 1986). All of these processes require energy and could potentially be limited by plant competition or stress.

Competition for light may have important consequences for the carbon balance and large belowground energy requirements of cold-desert species. By blocking light that would otherwise reach the periphery of the tussocks, large perennial shrubs such as sagebrush (*Artemisia tridentata*) can commonly shade bunchgrasses. This shading would be most pronounced early and late in the day at lower sun angles. For the same reason, shading in the Great Basin may also be most important during early Spring and late Fall, when water is usually available and growth can be quite rapid (Caldwell et al. 1981; West 1988).

In this field study, we examined the effect of shading on the carbon and nutrient relations of the perennial bunchgrass *Agropyron desertorum* (Fisch. ex Link) Schult. to

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determine whether carbon limitation might decrease the ability of the plants to exploit nutrient-rich soil patches. Our shade treatment allowed direct sunlight to reach plants for one half to one hour each day, but to filter out much of the remaining PPF. This treatment was designed to approximate the shading a tussock might experience when growing among taller shrubs.

In order to quantify the effect of shading on the carbon status of the plants, we measured daily timecourses of net photosynthesis for entire shaded and unshaded plants. For a more integrated estimate of carbon status we also measured the total nonstructural carbohydrate (TNC) and fructan contents of root and shoot tissue in each shaded and unshaded plant. We then examined whether shading limited the selective increase in nutrient uptake kinetics found previously for roots in enriched soil patches (Jackson et al. 1990; Jackson and Caldwell 1991). Finally, since demand plays such an important role in regulating nutrient uptake (Glass 1989), we also measured the N, P, and K status of root, stem, and reproductive tissue for each plant.

Methods

The research was conducted at a field site 4 km northeast of Logan, Utah (41°45'N, 111°48'W, 1460 m elev.) during the summers of 1990 and 1991. The average annual precipitation is 468 mm; the 1990 precipitation was below average (380 mm) and 1991 precipitation slightly above average (516 mm). Calcareous soils at the site are loamy-skeletal Typic Haploxerolls formed on alluvial fan material (Southard et al. 1978); pH is approximately 8 and nutrient concentrations in the soil are generally <10 ppm bicarbonate-exchangeable phosphate, <5 ppm extractable NO_3^-, and 100 to 200 ppm extractable K (Jackson and Caldwell 1991). Though growth of plants in calcareous soils of the Great Basin may often be limited by P availability, plants at the site have also been shown to respond to N fertilization (Bilbrough, pers. comm.).

The experiments were conducted in unfertilized, unirrigated monoculture field plots of evenly spaced *Agropyron desertorum* plants established eight years earlier (0.5 m between adjacent individuals). This perennial tussock grass was introduced to North America from Eurasia at the turn of the century (Dillman 1946) and has been widely seeded on several million hectares of rangelands in the Intermountain West. It has vesicular-arbuscular mycorrhizae of the genus *Glomus* (Allen et al. 1989).

Two tussocks per day were randomly selected, one to be shaded and one to remain unshaded. Only one pair of plants was treated per day because time did not permit processing the root samples of more than two plants per day for kinetic analyses. In 1990, seven shaded and seven unshaded plants were used in the experiment; six shaded and six unshaded plants were used in 1991 (with one extra replicate for shoot carbohydrate and nutrient contents). No plants treated in 1990 were selected again in 1991. The 1990 data were collected in the first half of July; 1991 data were obtained in late June and early July. Prior to any treatment, six tillers from each tussock were clipped and frozen in liquid N_2 for nutrient and carbohydrate analyses (1991 experiment only). One of the two randomly selected plants was then shaded for five days with a cone that allowed direct sunlight to reach the plant for 30 min to 1 hr at solar noon each day. The shade cones were made from two layers of Mylar, a layer of shadecloth (50% direct reduction in PPF), and a dark film (3M Scotchtint Windowfilm NR20SMARL) designed to approximate spectral changes as light passes through a plant canopy. The overall reduction in PPF through the cone was 80 to 90%. A whole-plant gas-exchange system designed to track ambient temperature (Gold and Caldwell 1989) measured the decrease in photosynthesis caused by shading for two days of the 1991 season.

After five days of shade or control treatments, pairs of soil patches around each plant were treated by using wicks to place 750 ml of distilled water on one side of a plant and 750 ml of nutrient solution (45 mM NH_4NO_3, 20 mM KH_2PO_4) on the other (Jackson et al. 1990). Each treated patch represented less than 2.5% of the total rooted volume of the test plants. After 4 more days of continued shading or ambient light, samples of the enriched and control soil patches were cored (12-cm diameter, 25-cm depth) and 6 tillers from each plant were again clipped and frozen in liquid N_2 for nutrient and carbohydrate analyses.

Roots from each soil patch were sieved from the soil, retained if <1.0 mm in diameter (to confine the analysis to younger, more active roots), and separated into random subsamples. One subsample was immediately frozen in liquid N_2 for subsequent nutrient and carbohydrate analyses. The remaining root subsamples were equilibrated in a 0.5-mM $CaCl_2$ solution for 1 hr at 20° C and were then immersed for 10 min in radio-labelled solutions of 1, 10, or 20 μM NaH_2PO_4 and 50, 500, or 1000 μM CH_3NH_2HCl. ^{14}C-methylammonium was used as an analog for ammonium because of the lack of a convenient radioisotope for nitrogen (Richie 1987, Chapin et al. 1988). The roots were oven-dried, weighed, and the radioactivity counted by liquid scintillation. Further description can be found in Jackson and Caldwell (1991). Total nonstructural carbohydrates were determined by digesting 50 mg of freeze-dried roots, stems (including leaves), or seedheads with a commercial amylase (0.2% Clarase 40,000 for 24 h at 38° C) (Chatterton et al. 1989). Root TNC concentrations in the 1990 extracts were determined colorimetrically with anthrone as the color reagent (Dimler et al. 1952); TNC and fructans in the 1991 extracts of root, stem, and seedhead tissue were determined colorimetrically using potassium ferricyanide and a Technicon II Auto Analyzer (Chatterton et al. 1987). Fructan accumulation can be important when periods of positive carbon balance are interspersed with periods of negative balance, as occurs in the perennial life cycles of northern temperate grasses (Pollock and Cairns 1991). Total N was determined with a C-N-S analyzer (Carlo Erba Model NA 1500). Total P and K were determined by first digesting the tissue in nitric and perchloric acids. Total K was measured by inductively coupled plasma analysis (Leeman PS1000-UV ICP Emission Spectrophotometer); total P was measured with ascorbic acid/ammonium molybdate as the color reagent.

Root TNC data were first analyzed (SAS, 1985) as a split-plot ANOVA set out in blocks with year as a factor. Because the year term was significant in the analysis, we reanalyzed the root TNC data for 1990 and 1991 as separate two-factor split-plots set out in blocks with shading as the whole-plot factor and nutrient enrichment as the subplot factor. Root fructan, N, P, and K concentrations were each analyzed with a two-factor split-plot ANOVA set out in blocks. Data for nutrient uptake kinetics were analyzed as a split-split-plot ANOVA with year as a factor, shading as the whole-plot factor, nutrient enrichment as the subplot factor, and concentrations of the laboratory solutions as the sub-subplot factor. Stem and seedhead TNC, fructan, and N, P, and K concentrations were analyzed with a repeated-measures ANOVA since both "pre" and "post" shading samples were taken from each shaded and unshaded plant.

Results

Shading had a pronounced effect on carbon gain, reducing net photosynthesis 75% to 95% relative to an unshaded plant (Fig. 1). Since our experiments lasted 9 days, the reduction in available carbon and energy to shaded plants should have been substantial.

For the 1990 and 1991 data, shading significantly limited the selective increase in uptake capacity found for roots of unshaded plants in enriched soil patches ($p<0.05$ for the shade-$\times$-enrichment term, Fig. 2). In 1990, for example, roots of unshaded plants from enriched patches

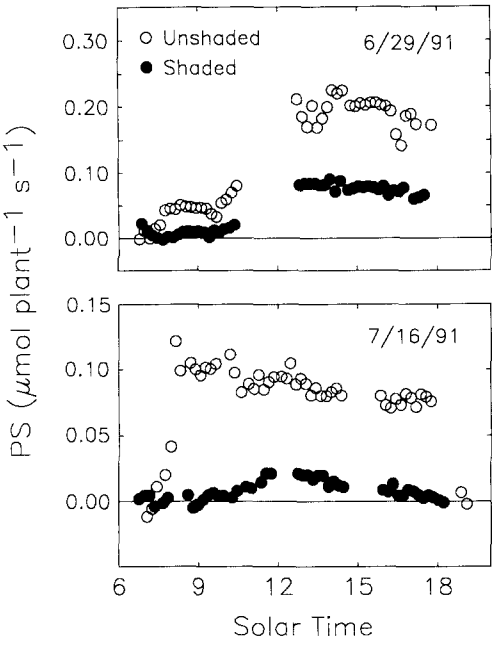

Fig. 1. Net photosynthesis for a pair of shaded and unshaded plants on two days of the 1991 growing season. The data were taken with a whole-plant gas-exchange system that tracks ambient temperature (Gold and Caldwell 1989)

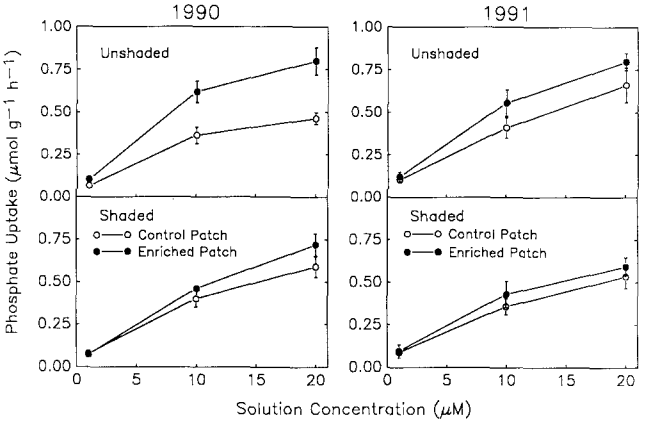

Fig. 2. Rates of phosphate uptake as a function of test solution concentrations for roots of shaded and unshaded plants from enriched and control soil patches (mean ± s.e.m., n = 7 plants per point for 1990, n = 6 plants per point for 1991). Patches on opposite sides of plants were treated with distilled water or nutrient solution and samples of the patches were cored 4 days later. Root mass is expressed on a dry-mass basis

increased their mean uptake capacity by 57%, 71%. and 73% in the three test-solutions, relative to roots of the same plants in control patches (Fig. 2); for shaded plants the mean rates of phosphate uptake were altered by only −8%, 15%, and 22% for roots from enriched patches. The average phosphate uptake capacity for shaded and unshaded plants was also significantly increased by nutrient enrichment ($p < 0.005$ for the enrichment term). The average effect of shading on uptake capacity was not significantly decreased ($p = 0.12$), but the significant shade-×-enrichment interaction makes interpretation of the main

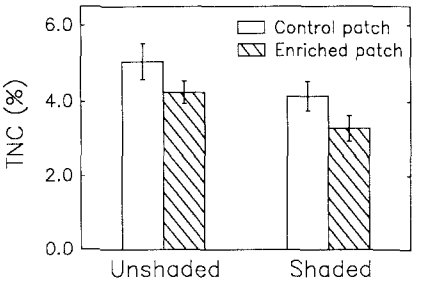

Fig. 3. Percent total nonstructural carbohydrates for roots of shaded and unshaded plants in enriched and control soil patches (mean ± s.e.m., n = 7 plants per bar, 1990 data). Both the 9-day shade treatment and nutrient enrichment substantially lowered TNC concentrations

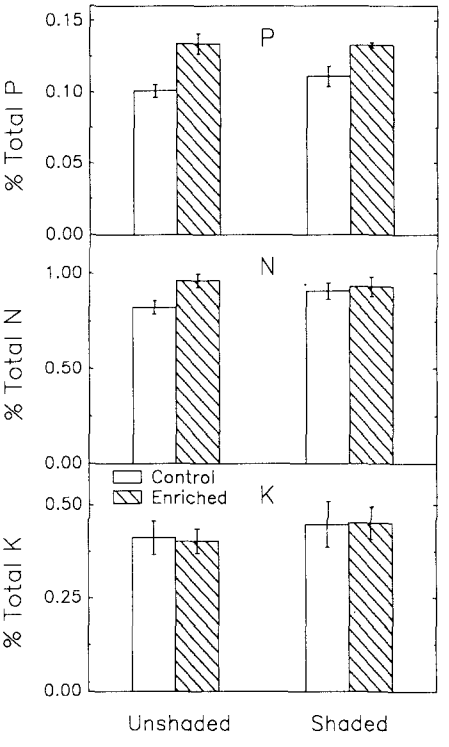

Fig. 4. Total concentrations of N, P, and K in roots from control and enriched soil patches on opposite sides of the same shaded and unshaded plants (mean ± s.e.m., n = 3 plants per bar, 1990 data)

effects difficult. Neither year nor any of the year-interaction terms was significant.

In 1990, shading significantly decreased TNC concentrations in roots from both enriched and control patches ($p < 0.05$, Fig. 3); average TNC concentrations in roots of shaded plants were 18% lower than in roots of unshaded plants. Roots in enriched patches of both shaded and unshaded plants had TNC concentrations decreased by 20% compared to roots from control patches treated with distilled water ($p = 0.056$, Fig. 3). These decreased TNC contents of roots from enriched patches presumably reflect carbon used in response to the nutrients in the patches.

Roots from enriched patches had significantly greater P concentrations, for shaded and unshaded plants, than roots from control patches in 1990 ($p < 0.01$, Fig. 4).

Though mean N contents for roots of unshaded plants were 15% larger in enriched patches, there was little difference for roots of shaded plants and neither the shading nor overall enrichment terms was significant ($p > 0.17$ for each, Fig. 4). There were no significant changes in K concentrations for roots of shaded or unshaded plants (Fig. 4).

For the 1991 experiment, we expanded the 1990 methods to include N uptake kinetics and obtained estimates of nutrient, TNC, and fructan concentrations of above and belowground plant parts. Despite the 9-day reduction in photosynthesis for shaded plants (Fig. 1), root TNC and fructan concentrations in 1991 were not significantly decreased by shading (Fig. 5, $p > 0.43$ in each case); there was a significant reduction in TNC concentrations in roots of enriched patches, particularly for the unshaded plants ($p = 0.01$, Fig. 5). The lack of a shading effect on root carbohydrates was quite interesting, since TNC and fructan contents in stem and seedhead tissue of shaded plants were reduced as much as 50% compared with unshaded plants (Fig. 6, $p < 0.05$ for each of four time- × -shade interaction terms).

Surprisingly, no differences in ammonium uptake capacity for shaded and unshaded plants were observed ($p > 0.64$, Fig. 7). There was also no apparent increase in ammonium uptake capacity for roots in enriched soil patches (Fig. 7).

In 1991, P concentrations were again significantly greater for roots from enriched patches compared with roots of the same plants from control patches ($p < 0.05$, Fig. 8). The increases were 31% and 39% for shaded and unshaded plants. Increases in N for roots from enriched patches were 12 and 13% for unshaded and shaded plants; there were no differences in K contents for any treatments (Fig. 8). The overall effect of shading was not significant for root N, P, or K concentrations ($p > 0.25$ for each).

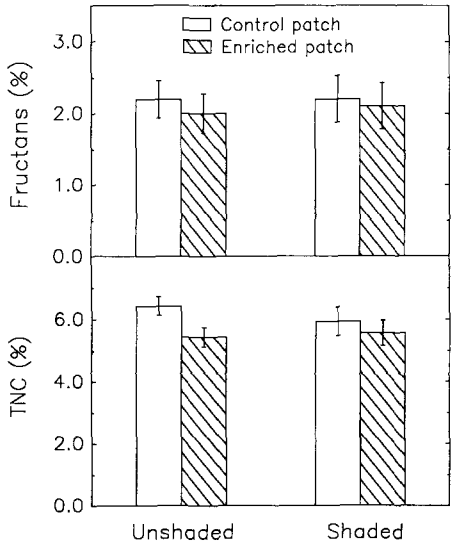

Fig. 5. TNC and fructan concentrations for roots from enriched and control soil patches around each shaded and unshaded plant (mean ± s.e.m., n = 6 plants per bar, 1991 data). Shading had no apparent effect on root carbohydrate status ($p > 0.43$ in each case)

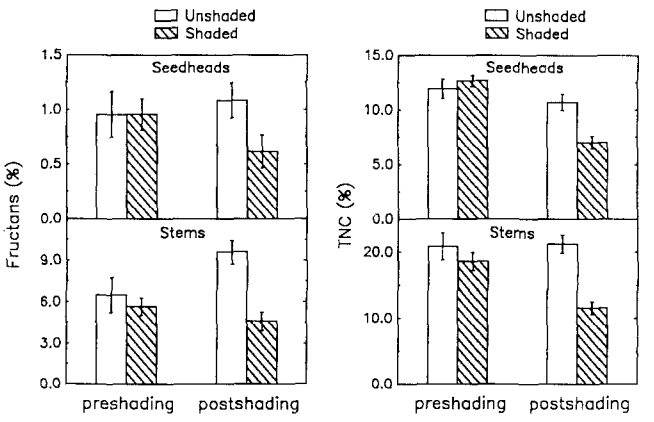

Fig. 6. TNC and fructan concentrations in stem (plus leaf) and seedhead tissue of shaded and unshaded plants at the beginning (preshade) and end (postshade) of the 1991 experiment (mean ± s.e.m., n = 7 plants per bar). No differences between "shaded" and "unshaded" plants were expected prior to shading (preshading); postshading data for the same plants show dramatic declines in TNC and fructan concentrations for the shaded plants

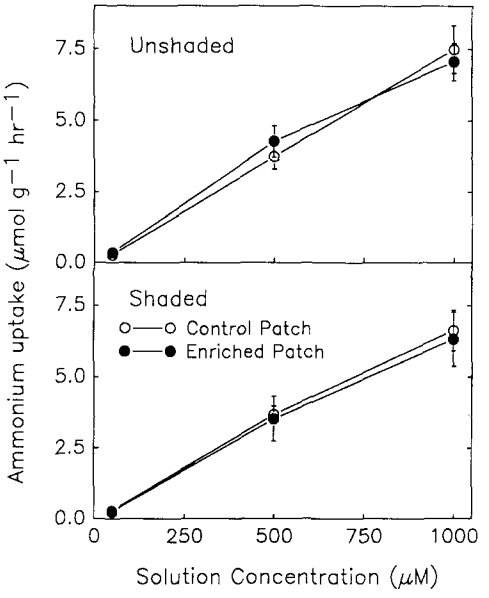

Fig. 7. Rates of ammonium uptake as a function of test solution concentrations for roots of shaded and unshaded plants from enriched and control soil patches (mean ± s.e.m., n = 6 for each point, 1991 data). Root subsamples from each patch were immersed in radioactively-labeled methylammonium solutions for 10 minutes. Root mass was measured on a dry-mass basis

The shade treatment appeared to delay slightly the onset of browning in stem and seedhead tissue, possibly by reducing temperatures and water loss of the shaded plants. There was a significant decrease in stem and seedhead nitrogen (40% decrease in seedhead N) for unshaded plants over the nine days of the experiment ($p < 0.05$ for each shade- × -time interaction term), with no such drop for shaded plants (Fig. 9). A similar phenomenon occurred for P and K in stems and seedheads of unshaded plants (Fig. 9).

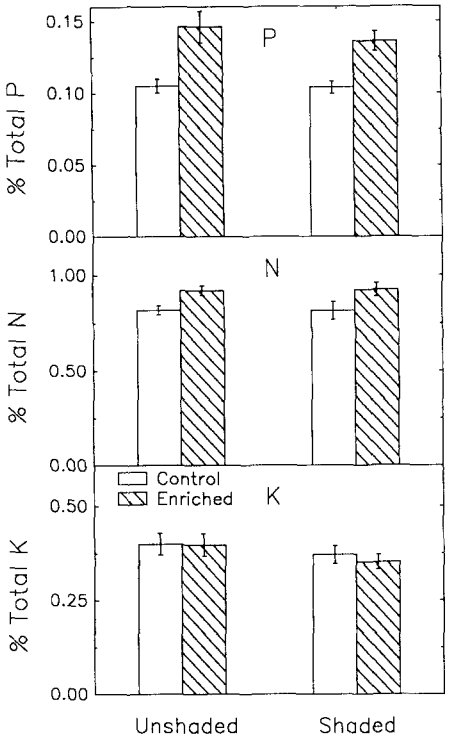

Fig. 8. Total concentrations of N, P, and K in roots from control and enriched soil patches on opposite sides on the same shaded and unshaded plants (mean ± s.e.m., n = 6 plants per bar, 1991 data)

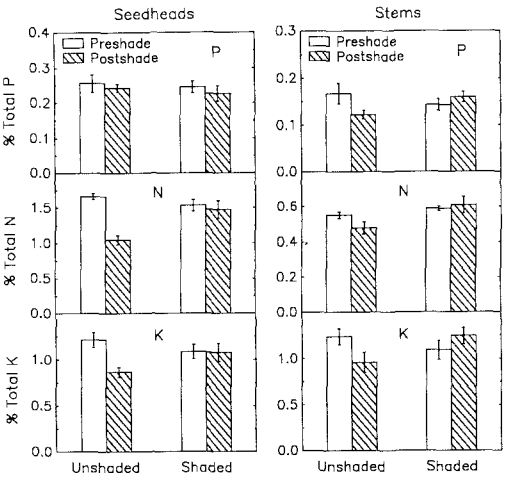

Fig. 9. Total concentrations of N, P, and K in stems (plus leaves) and seedheads of shaded and unshaded plants (mean ± s.e.m., n = 7 plants per bar). Measurements were taken on each plant at the beginning (preshade) and end (postshade) of the 1991 experiment

Discussion

The shading of *Agropyron* tussocks substantially altered above- and belowground plant characteristics. As expected, there were large differences in the carbohydrate status of shaded and unshaded plants. The lack of a change in root carbohydrates for shaded plants in 1991 was surprising, since shoot carbohydrates declined so dramatically. The shaded plants in 1991 were apparently preferentially allocating carbohydrates to their root systems, possibly to maintain the uptake of soil nutrients. In many respects the shaded plants did surprisingly well, obtaining substantial quantities of nutrients from enriched patches despite the 9-day shade treatments. A longer shading treatment, as may likely occur in the field, might have had more pronounced effects.

A decrease in soluble root carbohydrates (as happened in 1990) can affect such belowground processes as root growth and respiration, nutrient uptake, and mycorrhizal infection (Wardlaw 1968, Osman 1971, Peace and Grubb 1982), but these characteristics are not affected to the same degree. Crapo and Ketellapper (1981) showed that a reduction in light had a much greater effect on root growth than on rates of respiration or K uptake. They concluded that maintenance of existing tissues and processes had a higher energy priority than did production of new tissue.

Nutrient demand affects the identity, quantity, and rate of nutrients taken up by plants (Glass 1989). Since our unshaded plants were apparently translocating nutrients out of the shoots as the stems and seedheads began to undergo seasonal browning (Fig. 9), immediate plant demand for N was probably quite low. This low demand in unshaded plants may explain the lack of an increase in NH_4^+ uptake capacity in enriched patches, since a related species was shown to dramatically increase NH_4^+ kinetics in response to the same quantity of NH_4NO_3 (Jackson and Caldwell 1991).

Numerous studies have used techniques similar to those of Donald (1958) to evaluate the relative importance of shoot and root competition. Most of these studies have found root competition to be more important than competition for light (Wilson 1988). Even from our relatively short-term shade treatment one can see the difficulty in separating plant competition in the field into independent above and belowground components. Plant shading can decrease relative growth rates of both roots and shoots, with concomitant changes in demand for nutrients (Glass 1989). Donald (1958) found that the effect of root and shoot competition together, as might be experienced in the field, was multiplicative rather than additive. Many perennial plants might likely experience this interaction between root and shoot competition during at least a portion of their existence.

We believe our current field study is important in examining how light availability can affect the capture of nutrients heterogeneously distributed in the soil. A number of laboratory/glasshouse experiments have shown that a decrease in light generally leads to a scaling down of root processes and a reduction in root/shoot ratio (Hunt and Burnett 1973; Olff et al. 1990; Campbell et al. 1991). Garnier (1991) found that maximum relative growth rates of species correlate well with kinetic parameters of nutrient uptake (specifically V_{max}) and that root specific activity is an important factor for productivity. In our study, shading limited the selective increase in uptake capacity of roots in enriched soil patches. There may also have been reductions in root growth or changes in root morphology, though we were unable to study those factors. Limitations in light availability and its potential effects on root activity

and growth may decrease the ability of plants to exploit spatial and temporal heterogeneity in the soil.

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