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Kinetic responses of Pseudoroegneria roots to localized soil enrichment

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Abstract

Soil patches on opposite sides of *Pseudoroegneria spicata* plants in the field were treated with either distilled water or a nutrient solution containing N, P, or K. Roots from these enriched and control patches were tested three days later for their capacities of ammonium, phosphate, and potassium uptake. When phosphate was augmented in the enriched patches, rates of phosphate uptake increased significantly, but not rates of ammonium or potassium uptake. When the enriched patches were augmented with nitrogen, uptake capacities of both ammonium and potassium increased significantly (mean increases of up to 88% and 71% for ammonium and potassium, respectively). Potassium augmentation did not lead to increased soil-available K and, correspondingly, did not induce changes in the capacity for uptake of K, N, or P. The potential importance of nutrient uptake kinetics in the exploitation of nutrient-rich soil patches is discussed.

Introduction

Plants growing in soil can encounter heterogeneity in both biotic and abiotic soil characteristics (Charley and West, 1977; Ingham et al., 1985; Snaydon, 1962). Differences in the ability to detect and exploit nutrient-rich soil patches may partly determine the competitive hierarchy among plants (Crick and Grime, 1987; Fitter, 1982; Grime et al., 1986; Robinson and Rorison, 1983a). One example of how such heterogeneity could arise is the local decomposition of organic matter (Eason and Newman, 1990). Mechanisms for exploiting the localized nutrients may include increases in root absorptive surface area (St. John et al., 1983a; b) and changes in nutrient uptake capacity (Jackson et al., 1990).

The nutritional history of a plant has been shown to alter the rate at which a plant takes up nutrients (e.g. Cartwright, 1972; Clarkson et al., 1978; Drew et al., 1984; Humphries, 1951; Jackson et al., 1976). Most of this work has been conducted with plants grown in solution culture and involved changing the nutrient status of the entire plant. For example, a plant deprived of phosphate for a certain period of time usually increases its rate of phosphate uptake compared with a similar plant previously supplied adequately. The increases in uptake for the nutrient-deprived plants are generally selective to the previously withheld ion (Drew and Saker, 1975; Lee, 1982) and temporary, decreasing rapidly after restoration of nutrient supply (Lefebvre and Glass, 1982).

The exploitation of a nutrient-rich soil patch in the field may not, at least in the short term, result in a significant change in the nutrient status of the exploiting plant. Additionally, physiological responses of roots to the enriched patch may be limited to the portion of the root system in contact with the patch. Several studies have examined changes in rates of nutrient uptake

when only a portion of the plant root system was exposed to an increased nutrient environment (e.g., Barta, 1977; Drew and Saker, 1975; De Jager and Posno, 1979). These laboratory studies have generally shown an increase in nutrient uptake for the portion of the root system in the more nutrient-rich environment.

In a previous study we showed that three Great Basin plant species were able to selectively alter their phosphate (P) uptake kinetics in response to localized soil enrichment in the field (Jackson et al., 1990). *Pseudoroegneria spicata* (Pursh) A Löve ssp. *spicata* (syn: *Agropyron spicatum* (Pursh) Scribn. and Smith), a perennial tussock grass native to the Great Basin region of western North America, increased its mean rates of P uptake within three days of soil enrichment. The mean rates of P uptake in roots from enriched soil patches increased up to 80% relative to roots from control patches on opposite sides of the same plants. Each treated soil patch represented less than 2.5% of the total rooted volume of the test plants. Since only small portions of the root systems were in the experimental patches for a short period of time, the treatments may not have resulted in appreciable changes in nutrient status of the plants.

In the current study, we examined whether plants in the field had the ability to alter their rates of nutrient uptake when the major plant nutrients N, P, and K were applied to soil patches individually. Although naturally enriched soil patches would be unlikely to contain high concentrations of single nutrients alone, plants might nevertheless be expected to regulate uptake of these nutrients separately. Three days after treatment with either distilled water or a nutrient solution containing N, P, or K, we tested the roots from the patches for their rates of phosphate, ammonium, and potassium uptake. We examined whether enrichment resulted in increased uptake not only of the nutrient augmented in the enriched soil patches, but also for the two nutrients not augmented in the patches.

Pseudoroegneria spicata was used in these experiments. It has vesicular-arbuscular mycorrhizae of the genus Glomus (Allen et al., 1989). Pseudoroegneria was shown not to proliferate roots two weeks after patch enrichment in several experiments, whereas two other species usually initiated root proliferation in as little as one day (Jackson and Caldwell, 1989). Therefore, increases in nutrient uptake capacity observed for Pseudoroegneria should primarily reflect that of roots present in the soil patches prior to treatment.

Methods

This study was conducted in the field at a site 4 km northeast of Logan, Utah (41° 45′ N, 111° 48′ W, 1460 m elev.). Calcareous soils at the site are Typic Haploxerolls formed from alluvial material (Donahue et al., 1983) and their average pH is approximately 8 (Southard et al., 1978). Proton efflux from roots, however, could make the solution pH near roots considerably more acidic (Clarkson, 1985). The soils generally contain $<$ 10 ppm bicarbonate-exchangeable phosphate, $<$ 5 ppm available nitrate, and 100 to 200 ppm available potassium. Further site description is in Caldwell et al. (1981).

The experiments were conducted in monoculture field plots of evenly spaced *Pseudoroegneria spicata* plants (0.5 m between plants) established six years earlier. Pairs of soil patches were treated by using wicks to evenly introduce 750 mL of distilled water on one side of a plant and 750 mL of nutrient solution on the other. The nutrient solutions contained 20 m*M* H_3PO_4, 45 m*M* NH_4NO_3, or 20 m*M* KOH for the P-enrichment, N-enrichment, and K-enrichment experiments, respectively. H_3PO_4 and KOH were chosen so that root responses to phosphate and potassium enrichment would not be confounded by any accompanying nutrient. Calcareous soils at the site are highly buffered and should quickly adjust any imposed pH change. Furthermore, an experiment supplying an extremely dilute HCl solution matching the pH of the H_3PO_4 solution yielded no differences in nutrient uptake rates for roots from treated and control patches ($p > 0.49$). The solution concentrations of N, P, and K are the same individual nutrient concentrations used by Jackson et al. (1990) in N–P–K patches of ammonium nitrate and potassium phosphate.

Samples of the soil patches were obtained by cores (12-cm diameter, 25 cm deep) three days

after treatment. The roots from each soil patch were sieved from the soil, retained if < 1.0 mm in diameter, and separated into random subsamples from individual cores. The root subsamples were equilibrated for 1 hr in small cheesecloth bags in a 0.5 m*M* $CaCl_2$ solution at 20°C. The roots were then immersed in radio-labelled solutions of 1, 10, or 20 μM NaH_2PO_4 or 50, 500, or 1000 μM CH_3NH_4HCl and RbCl; methylammonium and rubidium were used as analogs for ammonium and potassium in the uptake measurements (Chapin et al., 1988; Epstein, 1952; Richie, 1987). Rates of ammonium uptake were studied because of the lack of a convenient radioactive analog for nitrate (e.g. Glass et al., 1985). The lower laboratory concentrations for each ion were chosen to reflect typical soil solution concentrations of N, P, and K (Barber, 1984) and the higher concentrations were designed to represent an enriched soil patch where solution concentrations might be 5 to 10 times higher than bulk soil solution concentrations. The uptake solutions also contained 20 μCi ^{32}P-labeled orthophosphoric acid, 47.5 μCi ^{14}C-labeled methylammonium chloride, or 47.5 μCi ^{86}Rb-labeled rubidium chloride per liter, depending on the solution. All solutions used prior to root drying were well mixed and aerated, adjusted to pH 6.0, and contained 0.5 m*M* $CaCl_2$ to maintain membrane integrity.

After immersing subsampled roots for 10 min in the radioactively labeled solutions, the roots were rinsed three times for at least 2 min in concentrated, unlabeled solutions at 5°C. The rinse solutions were designed to replace any radioisotope adsorbed to the root surfaces. The roots were then oven-dried and weighed. Phosphate-32 was assessed in intact roots by Cerenkov radiation (Läuchli, 1969); methylammonium and rubidium were acid-extracted from roots and the radioactivity was counted in a standard aliquot by liquid scintillation (with corrections for half-life and counting efficiency).

The data for a given experiment were analyzed with a two-factor split-plot analysis of variance set out in blocks (SAS Institute, 1985). The wholeplot factor was soil treatment and the subplot factor was the nutrient concentration in the laboratory solutions. Since separate analyses for rates of N, P, and K uptake were used within each enrichment experiment, the minimum probability used to denote statistical significance was 0.0167 (a Bonferroni adjustment of 0.05/3).

Soil analyses for available N, P, and K were performed on sets of control and enriched patches from each experiment. Available phosphate and potassium were extracted with 0.5 *M* $NaHCO_3$ (Olsen and Sommers, 1982). Available nitrogen was measured with chromotropic acid primarily as nitrate (Kowalenko and Lowe, 1973; Sims and Jackson, 1971).

Results

Based on previous physiological studies (e.g. Lee 1982) we expected nutrient uptake capacity to increase for roots from enriched soil patches, but only for the nutrient augmented in the enriched patches. In the P-enrichment experiment the mean rates of phosphate uptake were 5 to 26% higher for roots from enriched patches compared to roots from control patches on opposite sides of the same plants (Fig. 1). These increases in phosphate uptake capacity occurred within three days of patch treatment and the effect of phosphate enrichment was significant at $p < 0.01$ (two-factor split-plot analysis of variance set out in blocks). The data are actually quite consistent among plants, especially since the standard errors of Figure 1 include between-plant variability removed in the statistical analysis by blocks. Neither ammonium nor potassium uptake (as measured by uptake capacity of methylammonium and rubidium, respectively) increased significantly in response to enrichment (Fig. 1). Consequently, significant increases in rates of nutrient uptake were limited to the nutrient (P) applied in the enriched patches. The subplot factor of nutrient concentration in the laboratory solutions was highly significant ($p < 0.001$); this result is simply a reflection of higher rates of nutrient uptake at higher solution concentrations.

Results for the N-enrichment experiment were surprisingly different (Fig. 2). While mean rates of ammonium uptake increased between 22 and 88%, mean rates of potassium uptake were also 17 to 71% higher in roots from enriched patches relative to control patches ($p < 0.0167$ for both

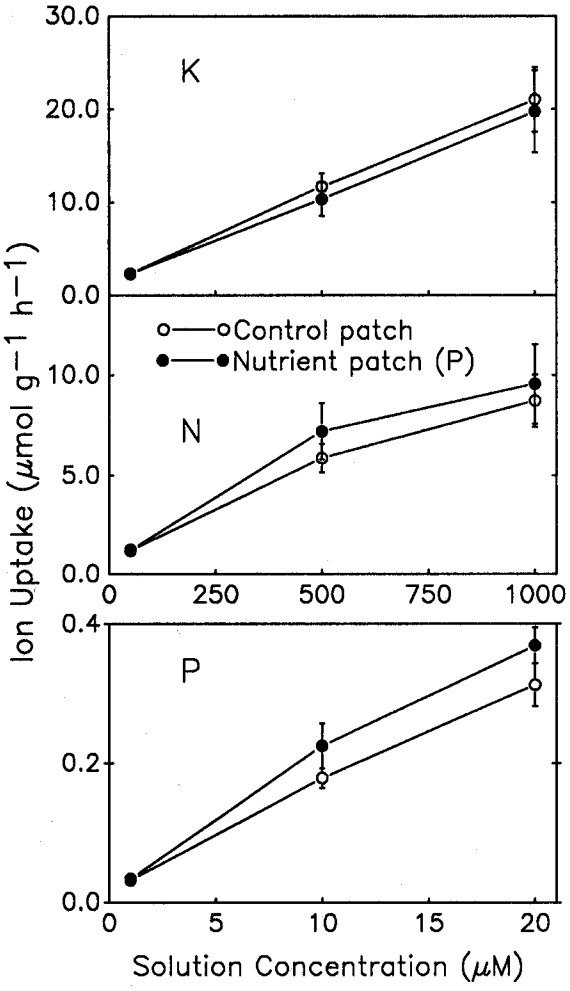

Fig. 1. Rates of potassium, ammonium, and phosphate uptake for the P-enrichment experiment (mean ± s.e.m., $n = 7$). Soil patches on opposite sides of plants were treated with 750 mL of either distilled water (control patches) or 20 m$M H_3PO_4$ (nutrient patches) and samples of the patches were cored 3 days after treatment. Roots from each patch were subsampled and immersed in radioactive phosphate solutions (1, 10, or 20 μM NaH_2PO_4) or radioactive analogs of ammonium and potassium (50, 500, or 1000 μM methylammonium (CH_3NH_4HCl) and rubidium (RbCl), respectively). Root mass was measured on a dry-weight basis. Phosphate enrichment in the field resulted in significant increases in rates of phosphate uptake ($p < 0.01$), but not for rates of ammonium or potassium uptake ($p > 0.26$).

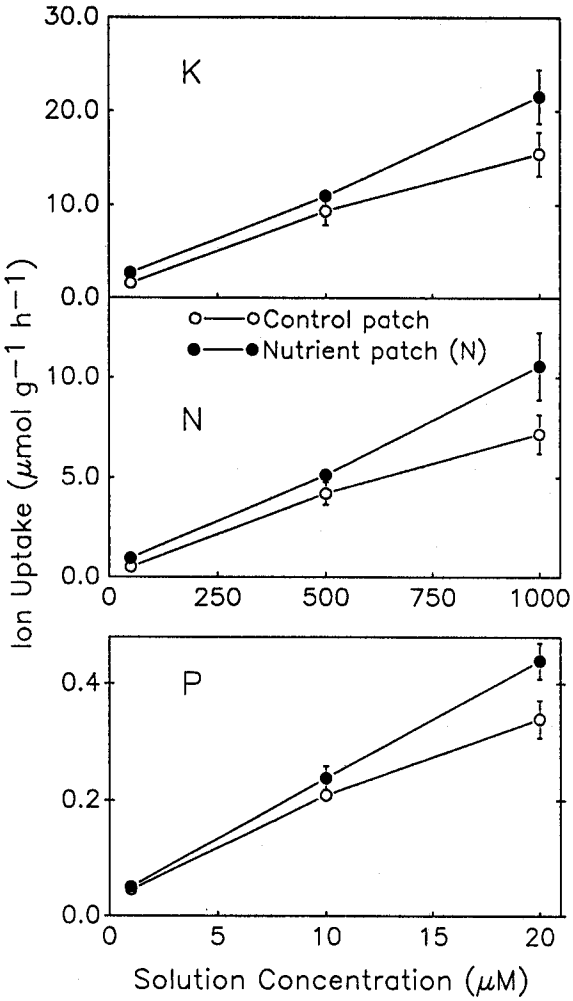

Fig. 2. Rates of potassium, ammonium, and phosphate uptake for the N-enrichment experiment (mean ± s.e.m., $n = 8$). The experimental procedure was the same as outlined in Figure 1, except that the nutrient patches were enriched with NH_4NO_3 instead of H_3PO_4. Nitrogen enrichment in the field resulted in significant increases in rates of both ammonium and potassium uptake ($p < 0.0167$ for each nutrient), but only marginal increases in rates of phosphate uptake ($p = 0.09$).

nutrients, a Bonferroni minimum of 0.05/3). Although rates of uptake for phosphate increased between 11 and 29%, the increase was probably not significant ($p = 0.09$). Increases in nutrient uptake capacity for the experiment were not, therefore, limited to the nitrogen augmented in the enriched patches.

During each of the experiments, we treated additional sets of enriched and control patches and analyzed the soil in the patches for available N, P, and K three days after treatment. Soil nutrient contents for the N- and P-enrichment experiments showed approximately 10-fold enrichment of the element augmented in the ex-

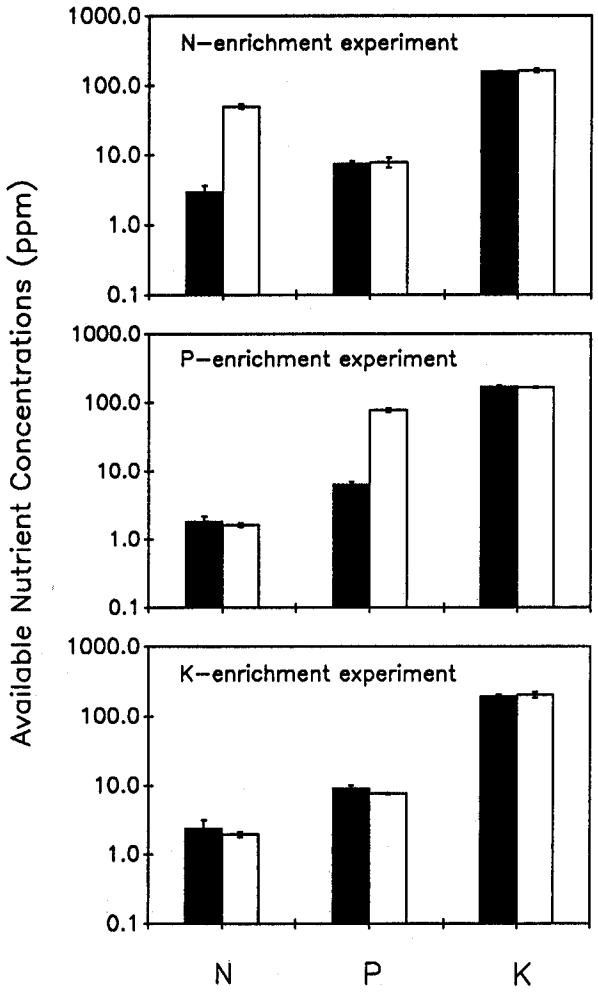

Fig. 3. Available N, P, and K concentrations for control and enriched soil patches of the N-, P-, and K-enrichment experiments (mean ± s.e.m., $n = 4$). Soil patches on opposite sides of plants were treated with 750 mL of either distilled water (closed bars) or nutrient solution (open bars) and samples of the patches were cored 3 days later. Nutrient solutions for the N-, P-, and K-enrichment experiments contained 45 m*M* NH_4NO_3, 20 m*M* H_3PO_4, and 20 m*M* KOH, respectively.

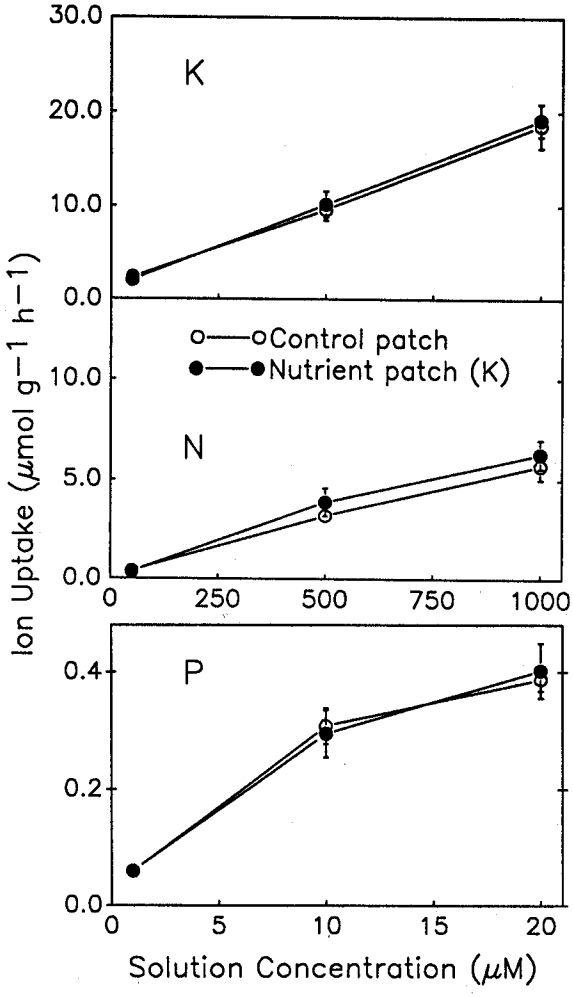

Fig. 4. Rates of potassium, ammonium, and phosphate uptake for the K-enrichment experiment (mean ± s.e.m., $n = 7$). The experimental procedure was the same as outlined in Figure 1, except that the nutrient patches were enriched with KOH instead of H_3PO_4. Potassium enrichment in the field resulted in no significant changes in rates of potassium, ammonium, or phosphate uptake ($p > 0.30$ for each nutrient).

periment, with no differences between control and enriched patches for the two nutrients not augmented (Fig. 3).

Nutrient uptake capacities for the K-enrichment experiment are most appropriately considered in light of the soil-available K in the control and enriched patches of the experiment. Soil analyses indicated no apparent differences between enriched and control patches, including the potassium supposedly augmented in the experiment (Fig. 3). Since the soil analyses were completed after the uptake measurements, we were, however, unaware of the fact that during the experiment the K enrichment was ineffectual. Not surprisingly, no significant changes in rates of ammonium, phosphate, or potassium uptake were evident (Fig. 4).

Discussion

Pseudoroegneria spicata is an important perennial tussock grass common to Great Basin range-

lands of western North America. It was selected for this study because of an apparent inability to proliferate roots quickly in response to localized soil enrichment (Jackson and Caldwell, 1989). There was no evidence in the present experiment of either greater root densities or an increase in the proportion of fine roots in the enriched patches, and the short three-day field treatments made substantial root proliferation unlikely. If the observed increases in uptake capacities were attributable solely to an increase in the proportion of fine roots, then the uptake of all three nutrients should have been affected equally. This did not occur. Thus, the apparent physiological changes were most likely occurring in the roots already present when the patches were created. Clarkson et al. (1978) found that enhanced phosphate uptake induced by P-stress occurred first in the older parts of the seminal axes of barley roots and later in the younger parts. Drew and Saker (1978) found that localized P enrichment resulted in enhanced P uptake before root proliferation took place.

The lower solution concentrations at which we examined phosphate, potassium, and ammonium uptake were chosen to reflect typical soil solution concentrations (Barber, 1984). Because of the scale of the graphs used to present the data (Figs. 1, 2, and 4), it often appears that the greatest relative increases in mean rates of nutrient uptake were found at the highest solution concentrations. This is not always the case, however. In the N-enrichment experiment (Fig. 2) the greatest relative increases in ammonium and potassium uptake (88% and 71%, respectively) actually occurred at the lowest concentration tested for each nutrient (50 μM). Changes in kinetic parameters have the potential, therefore, to be important even at average soil solution concentrations (Lee, 1982).

The apparent lack of soil enrichment in the K-enrichment experiment (Fig. 3) may be due to several factors. The potassium augmented in the patches could have been adsorbed between layers of illitic or zeolitic clays (Dudley, personal communication) or, alternatively, a more concentrated solution might have been required to effect enrichment. Since the background of available potassium in our soil is 15 to 20 times that of phosphate, no root response to successful K enrichment might be expected since the nutrient would be unlikely to limit plant growth. Despite the ineffectual K enrichment, the uptake capacities measured in the experiment demonstrate surprising consistency in roots sampled from numerous plants in the field (Fig. 4). Mean rates of nutrient uptake in enriched and control patches differed almost always less than 10% and never more than 21%.

The increase in potassium uptake for the N-enrichment experiment was notable, since changes in uptake kinetics are often selective to the nutrient with altered availability (Drew and Saker, 1975; Lee, 1982). However, ammonium and potassium have been found to interact in balancing the charge of anions such as nitrate taken up by roots (Bloom and Finazzo, 1986). The stimulation of K uptake in the N-enrichment experiment may, therefore, be partly a result of greater nitrate flux from the field enrichment of NH_4NO_3 (e.g. Vale et al., 1988).

Several models and sensitivity analyses have shown that nutrient uptake may be influenced more by morphological parameters such as root surface area, diameter, and density than by kinetic parameters (e.g. Robinson and Rorison, 1983b; Silberbush and Barber, 1983a,b). This is most likely to be true for diffusion-limited nutrients such as phosphate (Jungk and Claassen, 1986; Nye and Tinker, 1977). Nevertheless, Nielsen and Schjørring (1983) found close agreement between actual and predicted phosphate uptake in the field as predicted solely by kinetic parameters generated from solution-grown barley cultivars. That changes in kinetic parameters have been observed so frequently in nutrient-deprived plants (Drew et al., 1984; Humphries, 1951; Morgan and Jackson, 1988) and within root systems of individual plants (Drew and Saker, 1975; 1978; Jackson et al., 1990) implies that changes in kinetic parameters may be more important for nutrient capture in soil than often believed. The present study and the results of Jackson et al. (1990) provide the first evidence that changes in kinetic parameters actually occur in the field in response to microsite nutrient conditions.

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