Rapid physiological adjustment of roots to localized soil enrichment

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SOIL microsites rich in available nutrients are an important source of mineral nutrients for plants in many environments[1–5]. Patchiness in nutrient availability below ground is analogous to resource availability in canopy gaps above ground[6]. Although the physiological changes occurring in leaves exposed to sun and shade in canopy gaps are well known[7–9], we do not know any studies that show similar physiological changes in roots in enriched soil patches. Here we present evidence of large and rapid increases in the uptake kinetics of plant roots after creating nutrient-rich soil patches in the field. The mean rate of phosphate uptake at a given external phosphate concentration increased by as much as 80% for roots from enriched soil patches compared with roots of control patches treated with distilled water. The changes took place within days of patch treatment. This degree of plasticity was particularly notable for plants growing in soils of very low available phosphorus. These results showing rapid physiological plasticity of roots in fertile soil microsites have important implications for the theory and modelling of nutrient uptake in all soils.

We performed field experiments with three perennial species common to the Great Basin region of North America: a prominent shrub, *Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle; an introduced tussock grass, *Agropyron desertorum* (Fisch. ex Lonk) Schult.; and a native tussock grass, *Agropyron spicatum* (Pursh) Scribn. and Smith (syn: *Pseudoroegneria spicata* (Pursh) A. Löve ssp. *spicata*[10]). All three species have vesicular-arbuscular mycorrhizae of the genus *Glomus*[15].

The experiments were conducted in monoculture field plots of evenly spaced plants (0.5-m spacing) established 10 years earlier. Soils are Typic Haploxerolls[11], generally contain <6 p.p.m. bicarbonate-exchangeable phosphate[12], and have a solution phosphate concentration of ~1 μM. The average soil pH is ~8.0 (ref. 13), but the solution pH near roots is likely to be considerably more acidic owing to proton efflux from the roots[14].

The first three experiments were conducted in May and June, 1989, with moist soil throughout the rooting zone. The fourth experiment was conducted one month later; the soil was drier and, therefore, water was applied before the experiment. Plants were actively growing during all experiments. We treated pairs of soil patches by placing, by the use of wicks, 750 ml distilled water on one side of a plant and 750 ml nutrient solution (45 mM NH_4NO_3, 20 mM KH_2PO_4) on the other side of the plant. NH_4NO_3 was used in addition to KH_2PO_4 because naturally occurring nutrient-rich patches presumably contain all three main plant nutrients (N, P and K). We removed samples of the soil patches in soil cores (12 cm diameter, 25 cm deep) one week after treatment in the first three experiments and three days after treatment in the fourth experiment.

We sieved the excised roots from each soil patch out of the soil, retained those <0.5 mm in diameter (an approximate upper limit which we chose to confine the analysis to younger, finer roots), and separated them into five random subsamples. The excised-root assays were designed to provide relative comparisons of nutrient uptake; there is some evidence that the rate of uptake of phosphate in excised roots is more representative of intact-root uptake than is the rate of uptake of other ions, such as nitrate or potassium[16]. Both the time dependency and other factors limit the generality of this conclusion, however. We equilibrated subsampled roots in small cheesecloth bags in 0.5 mM $CaCl_2$ solution for 1 h at 20 °C[17], and then placed them for 10 min in 1, 3, 5, 10 or 20 μM solutions of NaH_2PO_4 at 20 °C. The NaH_2PO_4 solutions contained 20–40 μCi l^{-1} ^{32}P-labelled orthophosphoric acid. We used NaH_2PO_4 instead of

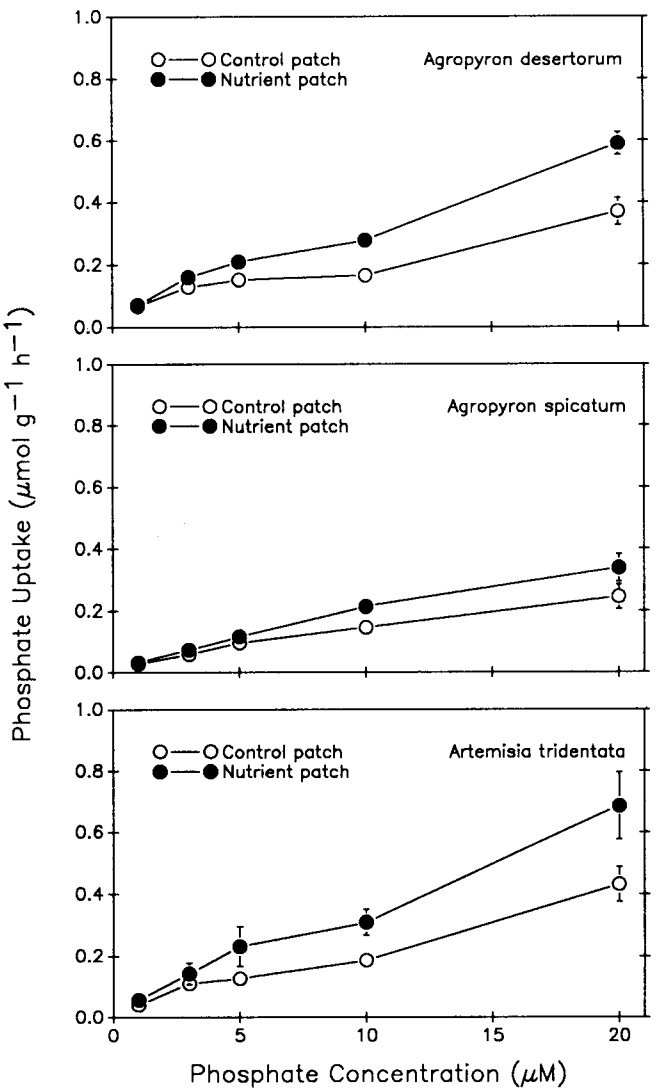

FIG. 1 The rate of phosphate uptake for roots from enriched and control soil patches as a function of the solution phosphate concentration (mean ±s.e.m.; $n=6$ for *Agropyron desertorum*, $n=8$ for *Agropyron spicatum* and *Artemisia tridentata*). Soil patches on opposite sides of plants in monoculture field plots were treated with 750 ml nutrient solution or distilled water. Samples of the soil patches were cored one week after treatment. Roots from each core were subsampled and immersed in radioactive phosphate solutions. The three single-species experiments were conducted at different times and in separate field plots; direct comparison of results among species is therefore inappropriate. The treatment effect was significant at $P<0.05$ for each species (two-factor split-plot analyses of variance set out in blocks).

KH_2PO_4 to eliminate any effect of the important nutrient potassium on root nutrient status in different solution concentrations. (Although no data are available for the species used in our study, there are no significant differences between the uptakes of phosphate when either sodium- or potassium-phosphate solutions are used as phosphate sources for barley roots[18].) We then rinsed the roots three times for at least 2 min in 200 μM unlabelled NaH_2PO_4 solution at 5 °C to replace any adsorbed radioisotope. Roots were dried in an oven, weighed, and counted by liquid scintillation using Cerenkov radiation[19], with corrections for half-life and counting efficiency. All solutions were buffered to pH 6.0, were well mixed and aerated, and contained 0.5 mM $CaCl_2$ (ref. 20).

If plant roots respond physiologically to nutrient-rich soil patches, then increases in uptake capacity for soil nutrients are expected. Indeed, at every solution concentration, we saw striking increases in the mean rate of phosphate uptake per unit root mass—as much as 80% for roots from enriched versus distilled-water patches (Fig. 1). Each of the three species significantly increased its phosphate uptake capacity relative to that of its controls. The mean increases in the rate of phosphate uptake at the five external solution concentrations ranged from 7 to 58% for *Agropyron desertorum*, 16 to 47% for *Agropyron spicatum*, and 30 to 82% for *Artemisia tridentata*. Although the largest percentage increases generally occurred at 10 and 20 μM, increases in the mean rate of uptake at 3 and 5 μM were never less than 20% for any species.

Because we obtained such consistent differences in uptake kinetics one week after soil-patch treatment, we performed a follow-up experiment in which patches were cored three days after establishing enriched and control patches. A single plot planted with *Agropyron spicatum* and *Agropyron desertorum* was used to compare directly the phosphate uptakes of the two tussock grasses. Again, the phosphate uptake rates of roots from enriched and control patches were clearly different (Fig. 2). The mean increases in the rates of phosphate uptake at the experimental solution concentrations ranged from 3 to 14% for *Agropyron desertorum*, and 16 to 46% for *Agropyron spicatum*.

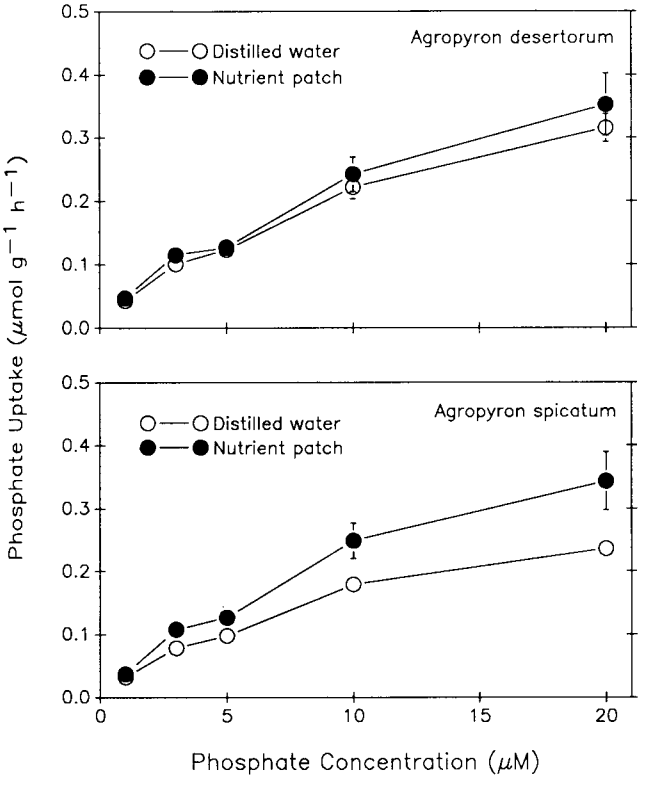

FIG. 2 The rate of phosphate uptake for roots from enriched and control soil patches as a function of the solution phosphate concentration (mean ±s.e.m.; $n=7$). The experimental procedure was the same as outlined for Fig. 1, except that soil patches were cored only 3 days after treatment, no *Artemisia* plants were tested, and results for the *Agropyron* species can be compared directly. The treatment effect was significant at $P<0.05$, but the species term was not significant (three-factor split-plot analysis of variance set out in blocks).

Many factors are important for the uptake of soil nutrients by plant roots. Rooting density and root length are particularly important for the uptake of relatively immobile nutrients, such as phosphate, especially when soil phosphate levels are low and the buffering power of the soil is high[21,22]. Plants growing in relatively nutrient-poor soils often have lower capacities for phosphate uptake than do plants growing in more nutrient-rich soils[23]. Models and sensitivity analysis indicate that phosphate uptake could be more sensitive to changes in root surface area than to changes in kinetic parameters[24]. Nevertheless, increased capacity for uptake of phosphate and other nutrients could contribute to rapid exploitation of the nutrients in the patches. In the relatively high solution concentrations within the patches, an increase in the Michaelis–Menten velocity parameter V_{max} is a likely explanation for the increased rate of phosphate uptake that we observed[25]. This increase in V_{max} would probably be due to an increase in the number of phosphate carriers or pumps per unit weight of root[18,25].

Uptake capacity is greatly influenced by tissue nutrient concentrations and, as a result, plant demand for nutrients[18,26]. Studies of uptake kinetics can be confounded by the inherent variability of plant nutrient demand among individual plants[27]. This should not have confounded our study, because the same plants were exposed to both enriched and control patches.

Plant roots encountering fertile soil patches often branch and proliferate, thereby increasing local rooting density[28]. The species that we studied differ in their relative ability to proliferate roots in nutrient-rich soil patches[29]. *Agropyron desertorum* was shown to begin root proliferation within 1 day of patch enrichment, whereas *Agropyron spicatum* did not proliferate roots within 2 weeks of enrichment in any of the experiments[29]. In the study described here, the excised roots of *Agropyron desertorum* could therefore have consisted of both newly proliferated and existing roots. But, at least for *Agropyron spicatum*, the increases in phosphate uptake capacity occurred in roots present in the patches before treatment.

Plants from relatively nutrient-rich soils are often thought to show more short-term morphological or physiological plasticity than do species in relatively nutrient-poor soils[1,30]. Plants in poorer soils have, nevertheless, demonstrated dramatic growth responses to applied nutrients[31–33]. Also, studies indicate that slower-growing species exploit short-duration unpredictable nutrient pulses more effectively than do faster-growing species[30,34]. Although the three species we studied typically grow in soils in which phosphorus availability is low, they each had the physiological plasticity to rapidly and substantially increase their uptake capacity after phosphate levels in the soil increased. This striking plasticity implies that nutrient uptake capacity could be more important for mineral nutrient capture than is often thought. Explicit modelling of patchiness in soil nutrient availability might show that changes in uptake capacity are important for nutrient capture by plants in many soils. □

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