

The demography of fine roots in response to patches of water and nitrogen

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SUMMARY

Fine root demography was quantified in response to patches of increased water and nitrogen availability in a natural, second-growth, mixed hardwood forest in northern Michigan, USA. As expected, the addition of water and water plus nitrogen resulted in a significant overall increase in the production of new fine roots. New root production was much greater in response to water plus nitrogen when compared with water alone, and the duration of new root production was related to the length of resource addition in the water plus nitrogen treatments; the average difference in new root length between the 20 vs. 40 d additions of water plus nitrogen amounted to almost 600%. Roots produced in response to the additions of water and water plus nitrogen lived longer than roots in the control treatments. Thus, additions of water and water plus nitrogen influenced both the proliferation of new roots and their longevity, with both proliferation and longevity related to the type and duration of resource supply. Results suggest that root longevity and mortality may be plastic in response to changes in soil resource availability, as is well known for root proliferation.

Key words: Root, demography, production, mortality, turnover, nitrogen, water.

INTRODUCTION

To forage effectively in a heterogeneous environment, plant morphological plasticity must enable parts of the same plant encountering different conditions to grow in different ways (Hutchings, 1988). As an example, plant root systems often proliferate in enriched microsites (Wiersum, 1958; Drew, Saker & Ashley, 1973; Crick & Grime, 1987; Eissenstat & Caldwell, 1988; Grime *et al.*, 1991). Under natural conditions such morphological plasticity presumably facilitates the placement of roots in areas of the soil from which resource acquisition would be relatively high. Jackson & Caldwell (1989) have linked the rapid proliferation of new roots in nutrient-rich soil patches to the greater competitive ability of *Agropyron desertorum* (Fisch. ex Link) Schult. relative to its unresponsive neighbour, *Agropyron spicatum* (Pursh) Scribn. In their experimental bunchgrass system, the timing of root proliferation was important as well as the ability to exhibit morphological plasticity.

Several studies have also shown that plants can alter rates of nutrient uptake when a localized supply of nutrients is experimentally elevated (Russell &

Sanderson, 1967; Anghinoni & Barber, 1980; Jackson, Manwaring & Caldwell, 1990; Jackson & Caldwell, 1991). Although the relative importance of altered root morphology (length, root hairs, etc.) vs. uptake kinetics may still be debatable (Caldwell, Dudley & Lilieholm, 1992), it seems clear that many plant species are capable of rapidly adjusting both their morphology and physiology in order to acquire limiting essential resources that become available in a localized patch of soil.

Less obvious are the effects of soil resource availability on fine root longevity. For example, there are biomass data from forest ecosystems both supporting (Keyes & Grier, 1981; Alexander & Fairly, 1983; Vogt, Grier & Vogt, 1986) and refuting (Aber *et al.*, 1985; Nadelhoffer, Aber & Melillo, 1985) the hypothesis that roots live longer in more fertile soils. Theoretical (Sibley & Grime, 1986) and physiological (Chapin, 1980) arguments have been made that longer root lifespans should be expected of plants growing in low-resource environments, but no one has directly measured the response of fine root lifespan to soil resource supply.

Morphological plasticity (i.e. the ability to exploit soil resources through fine root proliferation)

represents a substantial carbon cost to the plant (Grime, Crick & Rincon, 1986), as does maintaining living roots once they are differentiated (Peng *et al.*, 1993). Clearly, a better understanding of fine root demography (production, longevity and mortality) is necessary to fully quantify the effects of soil resources on below-ground carbon costs and patterns of allocation. The purpose of this paper is to report the results of an experiment designed to quantify how fine root demography responded to patches of increased water and nitrogen availability in a natural, second-growth, mixed hardwood forest in northern lower Michigan, USA.

METHODS

The experiment was conducted at the University of Michigan Biological Station (UMBS) Soil Biotron near Pellston, Michigan (45° 34' N latitude, 84° 40' W longitude). The Soil Biotron is a soil observation chamber 2.5 m × 2.2 m × 31 m in size constructed in 1986 in a second-growth mixed hardwood forest. It contains thirty-four 1.2 m × 1.2 m window bays, and each bay contains 16 removable 28 cm × 31 cm glass windows in a 4 × 4 array. During construction, sieved soil from each soil horizon was carefully repacked into the 1 m space between the windows and the native soil horizon. The root systems of the surrounding and newly established vegetation were then allowed to recolonize the soil naturally. Fogel & Lussenhop (1991) provide a detailed description of the Biotron and its construction.

The forest around the Biotron is dominated by *Populus grandidentata* Michx., *Quercus rubra* L., and *Acer rubrum* L. *Fagus grandifolia* Ehrh, *Amelanchier* spp. and *Pteridium aquilinum* Kuhn are dominant in the forest understorey. For a detailed description of the dominant vegetation characteristic of UMBS and the Biotron see Palik & Pregitzer (1992) and Fogel & Lussenhop (1991). Following construction of the Biotron in 1986, *Prunus pensylvanica* L., an early successional pioneer tree species that typically invades after disturbance (Marks, 1974), established along some of its edge.

The soil surrounding the Biotron developed from very well-sorted fluvial glacial sand and it is classified as an Entic Haplorthod (Rubicon series). It is low in organic matter and extractable nitrogen (Zak & Pregitzer, 1990) and, because of its high hydraulic conductivity (> 98% sand), it has a low moisture holding capacity. Second-growth, aspen-dominated forests of northern lower Michigan growing on Rubicon sand are very common, representing more than 400 000 hectares in this area.

In early July 1989, preliminary experiments determined that the volume of water necessary to create a patch of moistened soil 5 cm in diameter on the glass was approximately 60 ml delivered by gravity through capillary tubing. Treatments began

on 21 July 1989 and consisted of: (1) control; (2) 1250 ml of water delivered over 20 d; (3) 2500 ml of water delivered over 40 d; (4) 0.25 g N in 1250 ml of water delivered over 20 d; and, (5) 0.5 g N in 2500 ml of water delivered over 40 d. The N solution (200 mg l⁻¹) was prepared by dissolving NH₄⁺-NO₃⁻ in deionized water. We delivered an average of 62 ml of either water or water plus nitrogen each day. Each treatment was replicated twice and assigned at random to the centre of one of the upper tier of small windows in bays 19, 20, 27 and 28 on the east side of the Biotron. There were no barriers between the treated patches of soil and they were separated by at least 25 cm.

Treatments were delivered by gently inserting a piece of plastic tubing surrounding a metal rod into the soil until the tip of the tubing was visible adjacent to the glass windows. The location of the emitter was then marked on the window. The capillary emitters were attached to Nalgene bottles elevated above the soil surface outside the Biotron. The bottles were first painted black and then white to prevent light penetration and excessive heat. The volume of water delivered to each patch was monitored 3 times daily and the delivery rate was approximately 10 ml h⁻¹ for 6 h daily.

The background moisture levels varied naturally throughout the treatment period as rainfall periodically recharged the sandy soil. For example, the volume water content of the surface meter of soil at 8 different places surrounding the Biotron measured with a neutron probe averaged 48 (± 12.3) kg m⁻³ on 28 July, 1989 and 138 (± 12.7) kg m⁻³ on 15 August 1989. On some days following rainfall the entire soil profile would be saturated to depths greater than 10 cm (treatment depth). At other times, the treatment patches would appear almost dry the morning following treatment. We did not specifically monitor soil matric potential in the patches and adjacent untreated areas, but visual observations suggest that the difference in matric potential between the treated and untreated areas varied substantially due to weather conditions.

We estimate that background N mineralization in this type of soil should average about 2 g N m⁻² y⁻¹ (calculated from Zak & Pregitzer, 1990). Thus, the 20-d water plus N treatment amounted to a patch of elevated N representing about 13% of the amount normally available on an annual basis in a square metre of soil, while the 40-d water plus N treatment amounted to *c.* 25% of the amount of N normally available on an annual basis. Little N mineralization occurs during winter in northern Michigan and peak N availability usually occurs during July and early August (Zak & Pregitzer, 1990), coinciding with patch additions.

The patches were located 10 cm from the surface of the mineral soil at the bottom of the A soil horizon. A grid of 4 × 4 mm numbered squares were

scribed with a fine-tipped permanent marker below the location of each emitter. There were 21 total squares below each emitter arranged in a 7×3 rectangular array. Treatments were randomly assigned to each emitter. The array was centred on the emitter and the upper tier of squares was located 2 cm below it. Each of these 'frames' (21 per replicate) were video-taped at 35X every 2 d from the day before treatment began until 31 October 1989. The video camera was located on a movable tripod and mounted on a X-Y-Z plane table that could precisely control the camera position. The 4×4 mm 'frames' were illuminated with a fiber optic light which was also mounted on the tripod, and images of each frame were systematically recorded on standard VHS video tape. Image quality (colour) was very high and we could resolve root hairs, fungal hyphae and individual sand grains down to about $8.0 \mu\text{m}$. Control patches were monitored and analyzed in the same way as those that were treated.

An interactive PC-based software program (ROOTS) developed by K. Pregitzer, W. Enslin and R. Hendrick (Hendrick & Pregitzer, 1992*a, b*; 1993) was used to analyze the root data in the images of each frame. Using ROOTS, we identified, coded and measured the length of all live roots within each treatment replicate (pooled across all 21 frames) that were produced within the first 10 d after treatment started, i.e. a cohort of similarly aged roots. Then, in images from successive dates, the same roots were identified, re-measured and classified as either living or dead based upon their colour, intactness and/or decay and disappearance. We were able to follow the same roots at successive dates by overlaying the tracings and identification codes of each root as it appeared on the previous date onto the image from the next sampling date. The final database for each root was a time series of length measurements and condition codes (live or dead). Further details on the use of ROOTS and the identification and monitoring of cohorts can be found in Hendrick & Pregitzer (1992*a, b*; 1993). In addition to following the fate of cohorts produced in the initial 10 d of the experiment, we also identified, measured and followed the fate of all new roots produced until video monitoring ceased in October 1989.

We tested for treatment effects of fine root longevity by combining all roots into a single cohort for each treatment, and then comparing the survival curves of the cohorts among the treatments. Pairwise comparisons between all treatment combinations were made using a Gehan-Wilcoxon test (Pyke & Thompson, 1986). Tests for treatment effects on root length production and mortality were made on relative data expressed as a proportion of initial root length. Treatment differences were analyzed using orthogonal contrasts in an analysis of variance for a randomized block design.

RESULTS

The addition of water and water plus N to localized patches of soil resulted in a significant overall increase in the production of new fine roots ($P = 0.006$; Fig. 1). Even though the continuous addition of water resulted in a significant increase in the production of new root length, the additional increment relative to the control was not particularly large over 82 d (Fig. 1*a*).

In contrast, the addition of water plus N resulted in a dramatic increase in the production of new root length, and the water plus N treatment stimulated new root production significantly more than water alone ($P = 0.001$; Fig. 1*b*). By October (82 d) there was a 2.4-fold increase in root length in response to the 20-d water plus N addition and an 8.2-fold increase in response to the 40-d treatment (Fig. 1*b*). There was also a dramatic increase in root hair production in response to this treatment that we have not yet been able to quantify. Interestingly, the response to the water treatment was not visible to the naked eye, in stark contrast to the water plus N treatment where the proliferation of new roots was striking to the casual observer.

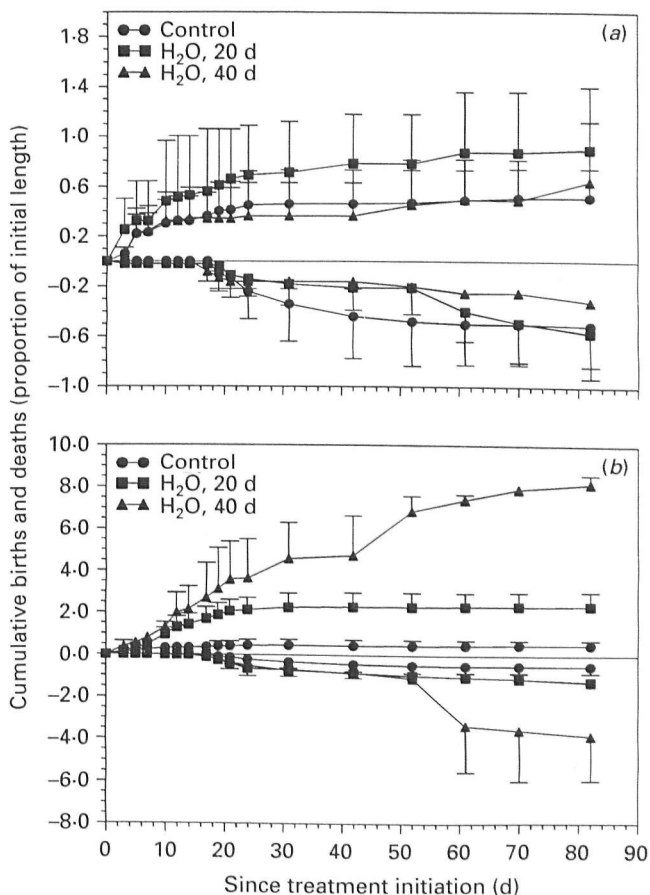


Figure 1. Mean cumulative length production and mortality, as a proportion of the initial length present in each replicate, for the water (*a*) and water+N (*b*) treatments. Control data are shown in each plot for comparison.

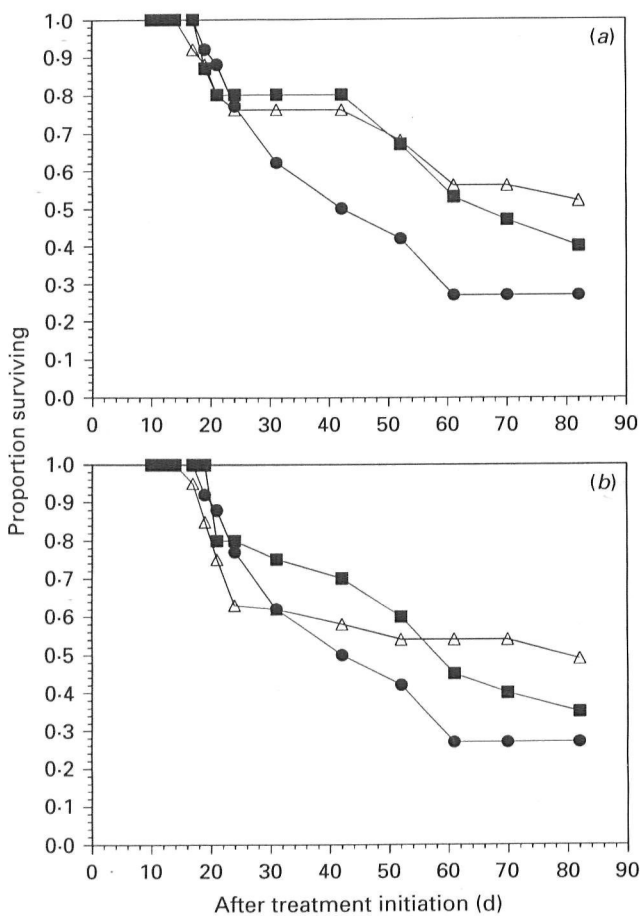


Figure 2. Survivorship curves for new root cohorts (summed across replicates) produced in the first 10 d after the initiation of 40 d (a) and 20 d (b) water and water+N treatments. No new roots had died in any cohort by day 10, at which time total survivorship was defined as 1.0. ●—●, Control; ■—■, H₂O; △—△, N+H₂O.

Production of new roots was significantly greater in the 40-d water plus N treatment compared to the 20-d water plus N treatment ($P = 0.007$; Fig. 1b), but the 20 vs. 40 d contrast for the water treatment was not significant. Note in Figure 1b that as soon as the addition of water plus N ceased at 20 d, the relative increase in new root length also terminated. The same figure clearly shows that as additional water plus N was added to the soil patches in the 40-d treatment, new root length production continued. By the time we stopped measuring the change in root length production in October, there was almost 6 times as much new root length in the 40-d treatment compared with the 20-d treatment (Fig. 1b). Thus, additional water plus N resulted in a significant concomitant increase in new root production.

Roots present at the windows before the initiation of the experiment did not respond to treatment in terms of altered length growth or mortality rate (data not shown). Treatment also had no influence on new root diameter ($P = 0.54$). Thus, the primary morphological response that we detected was an increase in length due to the production of new roots (and root hairs). This sometimes dramatic increase (e.g.

> 8-fold) appeared to be the result of both an increase in the rate of root growth and lateral branching. We occasionally used time-lapse video imaging to observe the growth of putative primary roots of *Prunus pensylvanica*. There was often a remarkable density of root hairs in the water plus N treatment just back from primary root tips, but we never observed any root hairs in the water treatment.

Average new root lifespans during the 82-d period were significantly greater than the control in both the 40-d treatments (water ($P = 0.07$) and water plus N ($P = 0.05$), Fig. 2a). Lifespans in both the 20-d treatments were not significantly different from the control, although this lack of significance was probably due to small sample sizes. The pattern of increased root longevity in response to the 20-d treatments is the same as that in the 40-d treatments (Fig. 2b vs. 2a). By the time we visited the experiment the following spring, most of the roots produced in response to the treatments had disappeared.

DISCUSSION

The increase in root length extension in localized patches of elevated nitrogen availability corroborates the results of similar nutrient addition experiments (Drew & Saker, 1975; 1978), and as demonstrated by Jackson & Caldwell (1989), response to water plus nutrients was rapid. 10 d after enrichment, there was a more than 100% increase in new root length (Fig. 1b). We also clearly demonstrate a differential response depending on treatment. Additions of water plus ammonium-nitrate resulted in a much greater increase in root length production than the additions of water alone (Fig. 1b vs. 1a). Drew (1975) demonstrated that localized supply of nitrate, ammonium and phosphorus stimulated root length production and number of lateral roots while potassium barely stimulated a response. Thus, root length production responds differentially to soil resources, depending on the resources supplied.

In our experiment, the duration and quantity of resource supply also influenced root length proliferation. There was an additional 600% increase in root length production when the water plus nitrogen treatment was extended an additional 20 d (Fig. 1b). Crick & Grime (1987) demonstrated that consistent local enrichment of nutrients resulted in *Agrostis stolonifera* root proliferation while *Scirpus sylvaticus* did not respond. When they altered the duration of nutrient addition, variation in response was high and no consistent pattern was apparent for either species. Their work and ours demonstrates that root length proliferation in response to resource supply is variable and depends on the duration and timing of supply. Thus, the timing, duration, and combination of resources supplied to a microsite can all influence root proliferation. How roots respond to hetero-

genity in resource availability is an important line of investigation that needs greater attention because the availability of essential resources in nature is likely to be variable in both time and space (Crick & Grime 1987, Jackson & Caldwell 1989, Grime *et al.* 1991).

Additions of both water and water plus nitrogen influenced average new root lifespan as well as root proliferation. The 40-d additions of both water and water plus nitrogen extended the lifespan of the roots produced during the first 10 d following treatment initiation (Fig. 2a). This is the first report of the influence of enriched soil microsites on root lifespan, so it is impossible to speculate on the universality of this phenomenon. However, our results do appear to contradict theory (Sibley & Grime, 1986) and empirical evidence (Aber *et al.*, 1985; Nadelhoffer *et al.*, 1985) which suggest that shorter fine root lifespans are associated with high-nutrient soils. Of course, ephemeral resource-rich patches of soil may elicit different demographic responses than soils that are inherently nutrient rich (Grime *et al.*, 1991). In any event, the enriched patches of soil extended the longevity of new fine roots in the 40-d treatments.

The longevity of a root (or part of it) may be inversely related to the duration of resource supply, i.e. root mortality may coincide with patch depletion. Relatively nutrient-deficient roots may need metabolically to recycle more nutrients internally (Gillespie & Deacon, 1988; Lascaris & Deacon, 1991), and this promotes senescence of cortical tissues and perhaps even root mortality. The question of whether or not plants can extend root longevity in response to the magnitude and duration of soil enrichment begs to be answered. Jackson & Caldwell (1989) speculate that plants might be able to regulate the degree of root proliferation in accordance with their demand for nutrients, and our data suggest that root longevity and mortality may also be plastic in response to changes in resource availability in the relatively droughty and nitrogen deficient soil that surrounds the Biotron. Hendrick & Pregitzer (1993) demonstrate that root survival differs among forests that have similar composition but different average soil temperatures. That study and the one reported here strongly suggest that root demography is responsive to changing conditions in the soil. One of the more interesting issues is the possibility that some plants may be able to alter the density of lateral roots and root hairs in direct proportion to nutrient availability and then shed these roots after the patch has been depleted.

Fitter (1985) has pointed out that root system architecture may depend on resource availability and Eissenstat (1991) demonstrated that root length per unit root biomass (or specific root length, SRL) varies by genotype and may be plastic in response to changing levels of resource availability. We had no intention of quantifying the topology or SRL of the roots studied, but it is obvious that the addition of

water plus nitrogen resulted in a proliferation of new lateral roots and root hairs, i.e. certain treatments altered root morphology. We do not know if SRL was altered in response to treatment. To determine accurately the carbon cost of an 800% increase in root length extension (Fig. 1b) it is important to understand if the new roots constructed in response to elevated resource availability have the same or different topology, SRL and degree of mycorrhizal infection.

The age of a root may influence its ability to take up nutrients (Ernst, Romheld & Marschner, 1989; Robinson, Linehan & Caul, 1991). In our case, many new roots which presumably would have a relatively high capacity to acquire nutrients were produced in response to the addition of water plus nitrogen. A synthetic understanding of the ecological significance of root proliferation in enriched patches of soil would require the integration of knowledge about altered morphological plasticity, root demography, mycorrhizal status, and root physiology (including construction and maintenance respiration costs and altered uptake kinetics). Our study lacks resolution because we examined community responses rather than genotypic or species-specific ones, and our sample sizes were small. Some of the response we observed at the community level may have been driven by the response of an individual species. Gross, Peters & Pregitzer (1993) have recently demonstrated that root length proliferation and root demography in nutrient patches vary among species. Regardless of the limitations of this study, it clearly demonstrates that root production and longevity can be responsive to the duration and supply of soil resources.

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