Oecologia (1993) 95:61-64

Oecologia

Fine root growth and demographic responses to nutrient patches in four old-field plant species

Katherine L. Gross[1], Andrew Peters[2], Kurt S. Pregitzer[3]

[1] W.K. Kellogg Biological Station and Departments of Botany, Plant Pathology and Zoology, Michigan State University, Hickory Corners, MI 49060, USA
[2] Biology Department, Indiana University, Bloomington, IN 47401, USA
[3] Department of Forestry, Michigan State University, East Lansing, MI 48823, USA

Received: 15 September 1992 / Accepted: 7 April 1993

Abstract. Proliferation of roots in a nutrient patch can occur either as a result of an increase in root length (morphological response) or by a change in root birth or death rates (demographic responses). In this study we attempted to distinguish between these two mechanisms of response to nutrient patches and to compare the responses of four old-field plant species (two annuals, two perennials). For all four species combined, there were significant increases in root numbers and root length in fertilized patches. Root proliferation in fertilized patches was largely due to increased birth (= branching) rates of new roots. However, there was also a significant increase in root death rates in the fertilized patches which reduced the magnitude of the increase in net root numbers. Plots for individual species suggested they differed in the magnitude and timing of root proliferation in fertilized patches due to differences in root birth and death rates. However, because of the limited sample size in this study, there was only a marginally significant difference among species in root birth rates, and no difference in death rates. Further studies are currently underway to better quantify species differences in the demographic mechanism, as well as magnitude, of response to nutrient patches and if this would affect the ability to exploit small-scale heterogeneity in soil resources.

Key words: Root proliferation – Root demography – Nutrient heterogeneity – Root foraging

Several studies have demonstrated that plant roots proliferate in nutrient rich patches (cf. Drew et al. 1973; Drew 1975; Jackson and Caldwell 1989; Campbell and Grime 1989; Friend et al. 1990). Root proliferation can occur as a consequence of two different mechanisms of growth response: morphological (elongation of existing roots) or demographic (an increase in root birth, or branching, rate or decrease in death rate). Studies which measure only net changes in root length, biomass, or numbers fail to detect the demographic response to a nutrient patch which requires following the fates of individual roots. If both root birth and death rates increase in response to a nutrient patch, there may be no observable root proliferation. However, this type of demographic response could produce small, young roots, potentially with high uptake efficiencies, in the patch. Understanding the demographic basis of a response to nutrient patches is also necessary to evaluate the costs and benefits in terms of increased nutrient acquisition and competitive ability (Berendse and Elberse 1990).

In this study, we compared the demographic and morphological responses of fine roots of four plant species (two annuals and two perennials) to patches of enhanced nutrients. The two annuals, *Ambrosia artemisiifolia* and *Chenopodium album,* occur in agricultural and newly abandoned fields where we expected that nutrient distributions are likely to be relatively homogeneous ("fine-grained") as a result of annual plowing and fertilizer application. The two perennials, *Achillea millefolium* and *Bromus inermis,* are common in later successional fields (abandoned for 30–40 years). In late successional fields, differential plant growth and nutrient uptake may produce a more "coarse-grained", spatially heterogeneous distribution of soil nutrients at scales relevant to individual plants (Tilman and Wedin 1991; Jackson and Caldwell 1993; Gross et al 1992b). Thus we expected, a priori, that these species might exhibit different magnitude and/or mechanisms of response to nutrient patches. In previous studies, we have observed that these four species have different patterns of root growth and branching that also could differentially affect their ability to encounter and exploit soil resources (Gross et al. 1992a).

Materials and methods

Newly germinated seedlings of each species were transplanted into sand-filled 1 L plastic containers (pots) in which two 5 × 5 cm

Correspondence to: K.L. Gross

windows, 3 cm from the soil surface, were cut in opposite sides of the pots. The windows were lined with transparent plastic film with a 1 cm cross-hair grid in the center to allow accurate observations of the fates of individual roots. The windowed pots were placed inside intact pots to exclude light and placed in a wooden frame filled with moist peat to reduce temperature fluctuations. Seedlings were grown in a temperature-controlled (26–30° C) greenhouse with supplemental light to maintain a minimum daylength of 14 h and photosynthetically active photon flux density of 600–1100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ throughout the experiment. Seedlings were planted in mid-July and kept well-watered; they were fertilized twice prior to the patch injection treatment with a weak fertilizer solution [0.3 g/L (= 1/4 tsp/gal) Jobe's All Purpose Plant Food, 20:20:20 N:P:K]. Root growth in the windows was monitored daily and individuals with at least two root segments visible in the windows were selected for the experiment (four to six individuals per species). A minimum of two roots per window was necessary for an accurate assessment of the demographic response. The growth rates of the annuals and perennials differed and as a result the patch injection experiments were done at different times for the annuals and perennials (August 14–29 and October 21–30, respectively).

Nutrient patches were created by injecting 1 mL of concentrated fertilizer solution (3.85 g/L Jobe's) on two consecutive days into the soil behind one randomly selected window in each pot. An equal volume of distilled water was injected in the same manner into the other side of the pot. Injections were made so that the patch was centered on the observation window. Pilot studies using blue dye had shown that this produced an elliptical patch of consistent diameter (2.54 cm ± 0.7 (SE); $n = 10$) and volume (8.7 $cm^3 \pm 0.7$) that occupied approximately 1% of the total soil volume of the pot. Root growth was monitored daily for 7–14 days following injections by video-taping with a Panasonic video camera with a macro 12x zoom lens mounted on a fixed tripod 1 m from the pots. All new roots which appeared in the images following injection were counted as "births"; this was primarily branches from roots visible in the initial images. Roots which disappeared from the images and were not detected again during the monitoring period were counted as deaths.

Analysis

Root growth patterns (births, deaths and length) were obtained using the video image-analysis system "ROOTS" (see Hendrick and Pregitzer 1992). This allowed us to quantify separately the demographic (numerical) and morphological (elongation) responses of these species to the fertilized and control (water only) patches. The video image quality was poor on several dates for a few individuals and the growth responses could not be accurately digitized. These individuals were omitted from the analysis which reduced the sample sizes to 2–4 plants per species (see Fig. 1).

The time series data on root numbers and length were summarized by calculating for each individual window, separate regression coefficients for total number of roots, cumulative number of fine root births and deaths and total root length as a function of time (cf. Gill 1978). The regression coefficient provide an index of differences in the rate, magnitude and direction (increase or decrease) in root numbers or length in response to the experimental treatments. The fit to three models (linear, semi-log and log-log) was compared and overall a linear model gave the best fit; r^2 values ranged from 0.4 to 0.96, except for individuals with no (or low) response to the treatment where r^2 values were near zero. Although initial root numbers differed among individuals and treatments, in all cases, the response was independent of initial root numbers.

To test whether there was an overall response to the fertilized patches, we combined data for all species and tested the differences in slope in the two treatments for root numbers, specific birth and death rate, and length over time with a one-tailed *t*-test (H_o: $b_f - b_c > 0$). We tested for differences among species in the magnitude of response using one-way ANOVA on the differences in slope in the two treatments.

Results and discussion

The analysis examining the response to fertilized patches combining data from all four species showed that in the fertilized patches there were significant increases in root growth rate (in numbers and length) and root birth and death rates (Table 1). The proliferation of roots in the fertilized patches appears mainly to be attributable to an increase in root numbers (e.g. increase branching) rather than increased elongation of existing roots, as there was a highly significant increase in root birth rate ($t = 5.03$, $p < 0.0005$). In all four species, the birth rate of fine roots was 4–5 times greater in the fertilized than control patches (see Fig. 1). Because the death rate of roots also increased in the fertilized patches this reduced the magnitude of the observed increase in total root numbers (Table 1).

Examination of the temporal responses of individual species to these treatments suggested that species might differ in the magnitude, mechanism or timing of root proliferation in fertilized patches (Fig. 1). In *Ambrosia artemisiifolia*, for example, there was little net change in root number in either the fertilized or control treatment (Fig. 1A); however, both the birth and death rates of roots increased in the fertilized patches (Fig. 1E) resulting in a high turnover rate of roots in the fertilized patches, but no observable proliferation. In contrast, in *Achillea millefolium*, there were large differences in the net root numbers in fertilized and control patches (Fig. 1C), which appeared to be a consequence of differences in birth rates in fertilized and control patches and not death rates (Fig. 1G).

The ANOVA for species differences however, indicated only a marginally significant difference among species in root birth rate ($p = 0.11$) in fertilized and control patches (Table 2). For both root numbers and birth rate, species differences accounted for over 40% of the observed variation. The small sample sizes (and high level variation among individuals) limited the ability to detect significant species differences in magnitude or mechanism of root proliferation in fertilized patches.

Previous studies of root proliferation in nutrient patches have focused only on changes in total root number, length or biomass in nutrient patches and thus could not detect the changes in root death rate which we observed. As the results for *Ambrosia artemisiifolia* suggest, considering only changes in total root numbers or length

Table 1. Summary of differences in slope between fertilized and control treatments for root growth rate and dynamics combining data for all four species examined. n = total number of pots; sample sizes for each species varied between 2–4 (see Fig. 1). Statistic for the hypothesis Ho: $b_f - b_c > 0$ and probability-level (p) are given for each variable

Variable	*n*	*Mean difference*	*S, E*	*t*	*p*
Numbers/day	12	0.288	0.128	2.24	0.025
Births/day	12	0.413	0.082	5.03	0.0005
Deaths/day	12	0.124	0.065	1.90	0.05
Length (cm)/day	12	0.366	0.192	1.90	0.05

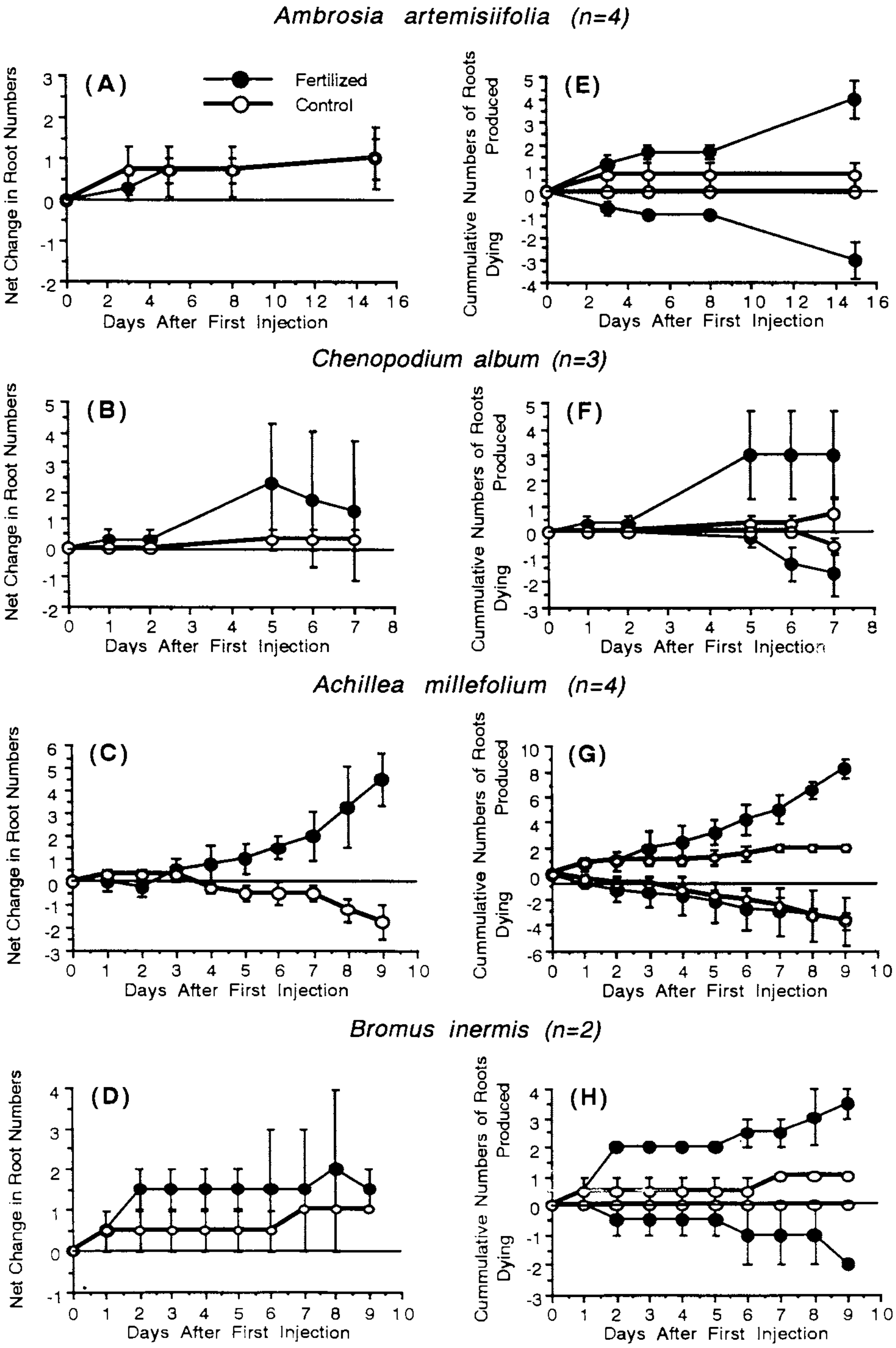

Fig. 1A–H. Temporal patterns of changes in root numbers over time in fertilized *(closed circles)* and water-only control *(open circles)* patches following injection. **(A–D)** Net change in root numbers (from numbers on Day 0). **(E–H)** Cumulative change in numbers of roots produced (=births) and dying (=deaths) following injection. Values are means ± 1 SE

Table 2. Summary of one-way ANOVA for species difference in root growth and dynamics in fertilized patches. Variable tested was the difference in slope for fertilized and unfertilized patches. Degrees of freedom for model and error are 3 and 8, respectively, for all analyses

Variable	*Mean square*	*F*	*p*	R^2
Numbers/day	0.312	2.02	0.19	0.43
Births/day	0.148	2.67	0.11	0.50
Deaths/day	0.037	0.65	0.60	0.20
Length/day	0.604	1.57	0.27	0.37

can be misleading and result in the erroneous conclusion that species fail to respond to a nutrient patch if both root birth and death rates increased in the patch. The higher root turnover (=loss) rates associated with this type of demographic response may be costly, but these costs may be offset by an increase in nutrient acquisition rate (cf. Berendse and Elberse 1990). Jackson and Caldwell (1989) found that there were differences in the magnitude and timing of fine root proliferation in patches of enhanced nutrients among three species of cold-desert perennials. Although individual roots were not followed, the increase in root length was apparently due to an increase in branching of extant roots. In a later study, they demonstrated that roots of both *Agropyron* species have increased P-uptake efficiency after exposure to nutrient rich patches (Jackson et al. 1990). Whether there is a demographic mechanism which can account for increases in uptake efficiency has not been determined.

Consideration of how the birth, death and length growth rates of roots change in response to nutrient patches can provide insight into both the mechanism, timing, costs and benefits of root proliferation in response to nutrient patches. If nutrient patches in soil are ephemeral, then differences in the rate at which individuals respond to a nutrient patch will influence how effectively they can exploit these patches (Campbell and Grime 1989). Among the four species we studied, the perennials appeared to respond more rapidly to a patch of enhanced nutrients than the annuals. Both *Achillea* and *Bromus* increased root birth rate 2–3 days following the fertilizer injection, whereas *Ambrosia* and *Chenopodium* took 5–7 days to respond to the treatment (see Fig. 1).

The relative costs (in terms of carbon expended on new root growth) and benefits (nutrients acquired) may differ among environments depending on the spatial heterogeneity or predictability of soil nutrients (Sibley and Grime 1986; Campbell et al. 1991). Linking patterns of root growth and dynamics to the ability to exploit small patches of nutrients may provide an important key to understanding determinants of competitive ability in different environments. The results of this study demonstrate the importance of considering the demographic as well as numerical and morphological responses of plant species to patches of enhanced soil nutrients. Further studies are currently underway to determine if there are species differences in the timing, magnitude and mechanism of response to uniform and patchy distributions of soil nutrients than can be related to the scale of spatial heterogeneity of nutrient distributions in successional fields (Gross et al. 1992b).

Acknowledgments. This research was supported by the National Science Foundation (REU Supplement to BSR 8818441 for A. Peters and DEB 9107481). We would like to thank Mark Olson for assistance with the statistical analysis and valuable comments on the manuscript; Lisa Huberty, Deborah Goldberg and two anonymous reviewers also provided valuable comments on the manuscript.

References

Berendse F, Elberse WT (1990) Competition and nutrient availability in heathland and grassland ecosystems. In: Grace JB, Tilman GD (eds) Perspectives on Plant Competition. Academic Press, Inc., San Diego, CA, pp 93–116

Campbell BD, Grime JP (1989) A comparative study of plant responsiveness to the duration of episodes of mineral nutrient enrichment. New Phytol 112:261–267

Campbell BD, Grime JP, Mackey JML (1991) A trade-off between scale and precision in resource foraging. Oecologia 87:532–538

Drew MC (1975) Comparison of the effects of a localized supply of phosphate, nitrate, ammonium and potassium on the growth of the seminal root system, and the shoot, in barley. New Phytol 75:479–490

Drew MC, Saker LR, Ashley TW (1973) Nutrient supply and the growth of the seminal root system in barley. J Exp Bot 24:1189–1202

Friend AL, Eide MR, Hinckley TM (1990) Nitrogen stress alters root proliferation in Douglas-fir seedlings. Can J For Res 20:1524–1529

Gill JL (1978) Design and Analysis of Experiments in the Animal and Medical Sciences. Iowa State University Press, Ames, IA

Gross KL, Maruca D, Pregitzer KS (1992a) Seedling growth and root morphology of plants with different life-histories. New Phytol 120:535–542

Gross KL, Pregitzer KS, Burton A (1992b) Changing scales of spatial heterogeneity in soil nitrogen and plant distributions in successional fields. Bull Ecol Soc Am 73:194

Hendrick RL, Pregitzer KS (1992) The demography of fine roots in a northern hardwood forest. Ecology 73:1094–1104

Jackson RB, Caldwell MM (1989) The timing and degree of root proliferation in fertile-soil microsites of three cold-desert perennials. Oecologia 81:149–153

Jackson RB, Manwaring JH, Caldwell MM (1990) Rapid physiological adjustment of roots to localized soil enrichment. Nature 344:58–60

Jackson RB, Caldwell MM (1993) The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. Ecology 74:612–614

Sibley RM, Grime JP (1986) Strategies of resource capture by plants – evidence for adversity selection. J Theor Biol 118:247–250

Tilman GD, Wedin DA (1991) Plant traits and resource reduction for five grasses growing on a nitrogen gradient. Ecology 72:685–700