ECOSYSTEMS ECOLOGY

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Controls of fine root dynamics across a gradient of gap sizes in a pine woodland

Abstract Controls of fine dynamics were investigated in a *Pinus palustris* Mill. (longleaf pine) woodland subjected to two understory vegetation treatments (control versus removed) and four overstory treatments (no gap control, and canopy gaps of three sizes with constant total gap area per stand). Fine root (<2 mm diameter) dynamics were measured over 11 months using ingrowth cores (all treatments) and minirhizotrons (understory removed in no gap control and large gap treatments only). At the fine (microsite) spatial scale, pine and non-pine root mass production responded negatively to each other ($P=0.033$). Each life form was significantly ($P\leq0.028$) related to nearby overstory density, and pine root production compensated for reductions in non-pine roots if understory vegetation was removed. Soil moisture and NO_3 mineralization rate were negatively related to pine root mass production (ingrowth cores; $P<0.001$ and $P=0.052$) and positively related to pine root length production, mortality and turnover (minirhizotrons; P from <0.001 to 0.078). Temperature variance was negatively related to pine root lifespan ($P<0.001$) and positively related to pine root turnover ($P=0.003$). At the ecosystem scale, pattern of overstory disturbance (gap size and number) had no significant effect on non-pine, pine, or total root production. However, the presence of gaps (versus the no-gap control) increased non-pine root mass production (ANOVA, $P=0.055$) in natural understory conditions, and reduced pine root mass production ($P=0.035$) where the understory was removed. Ecosystem-wide pine root length production, mortality and turnover were positively related to weekly soil temperature ($P\leq0.02$). In natural systems, fine root dynamics are highly variable and strongly affected by biotic factors. Roots quickly close belowground gaps because one life form (pine or non-pine) compensates for the absence of the other. When understory vegetation is removed, however, pine roots respond to the local abiotic environment, particularly moisture and NO_3.

Introduction

Although fine roots contribute 50% or more toward total forest net primary productivity (Vogt et al. 1986) and control many ecosystem and community processes, they are one of the most difficult components of forest ecosystems to measure and to predict (Clark et al. 2001). Studies of root growth are hampered by high spatial and temporal variability, which results in noisy data, and by the fact that numerous abiotic and biotic factors influence roots. An additional problem relates to the spatial scale of observation. For example, at submeter scales, production may appear positively correlated with soil nutrient availability (Jackson and Caldwell 1989; Campbell et al. 1991; Pregitzer et al. 1993; Robinson 1994; Mou et al. 1995), whereas at the scale of whole ecosystems, production may appear to decline (in absolute terms or as a proportion of total stand production) when mean nutrient availability increases (Nadelhoffer 2000).

Measuring root responses to different types and spatial patterns of ecosystem disturbance may be one way to: (1) increase signal to noise in root data; (2) determine independent effects of abiotic and biotic factors that control fine root dynamics; and (3) deal with influences of scale. Disturbances kill roots, but some plants may be more affected than others, which results in a shift in the balance between competing root systems. If enough roots are lost, belowground gaps are formed with reduced

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resource uptake and altered soil conditions that may influence subsequent root growth (McGuire et al., 2001).

In forests, belowground gaps are relatively short-lived and their influences on root responses depend on gap size (Silver and Vogt 1993; Wilczynski and Pickett 1993; Parsons et al. 1994a; Jones et al. 1996; Schroeer et al. 1999; McGuire et al. 2001). The ephemeral nature of gaps is related to the overlap of root systems which allows surviving trees to quickly colonize space liberated by the disturbance, and minimizes increases in resource availability within gaps (Parsons et al. 1994b). A threshold canopy gap size can be reached, however, that eliminates live tree roots altogether, thereby increasing availability of soil resources. On the other hand, canopy gaps that equal or exceed this threshold size also increase light in the understory, which can stimulate growth of understory plants present before the disturbance (Schroeer et al. 1999) or in the seedbank (Canham and Marks 1985). Understory vegetation can rapidly capture belowground space released by the loss of the trees. In canopy gaps of intermediate size, where live root systems of overstory trees remain but light in the understory is increased, the distribution of roots between overstory and understory plants may vary due to competition (Coomes and Grubb 2000), and compensatory growth (increased growth of overstory roots in root gaps when the understory is removed and vice versa, e.g. Schoeer et al. 1999).

Because canopy gap size influences the proportional abundance of over- and understory plant roots, stands that differ in size and arrangement of canopy gaps might also differ in mean stand-level fine root responses. For example, in two stands with similar total gap area but different mean gap size, understory plant roots may be less abundant in the stand with smaller mean gap size.

The first objective of this study was to determine which of several abiotic and biotic factors have the strongest influence on fine root growth at the microsite scale in a subtropical pine woodland. We created gaps of different sizes to augment natural variation among soil variables, and thereby increase capacity to tease apart influences of different factors. We hypothesized that: (1) pine and non-pine root growth would be positively related to soil resources, specifically soil moisture and available N, and would respond negatively to soil temperature, which can act as a stressor in subtropical systems; and (2) total growth of pine plus non-pine roots would be nearly constant (reflecting an upper limit set by available resources), although the proportional contribution of each would vary in response to gap size. A second objective of this study was to assess factors influencing mean stand-level responses (i.e., averaged over all microsites). The first factor assessed was the size of gaps, which we tested by varying gap size while holding constant the overall intensity of disturbance. The second factor assessed at the stand level was seasonal climate, which we tested by comparing weekly values of temperature, rainfall and soil moisture against weekly root responses. We hypothesized that: (3) as disturbance pattern changes from single tree to large multi-tree gaps, ecosystem-wide pine root growth

would decline and non-pine root growth would increase; and (4) soil moisture would be a major driver of pine root turnover, reflecting adaptations of pines to climates where growing season drought is common. Our study is part of a larger effort to understand how disturbances influence resources and competition and thus alter the course of tree regeneration and plant succession in *Pinus palustris* woodlands.

Materials and methods

Study site

Research was conducted at the Joseph W. Jones Ecological Research Center at the Ichauway Plantation, a 115-km^2 reserve located in the coastal plain region of southwestern Georgia. The climate is subtropical with mean daily temperatures ranging between 11 and 27°C, and annual precipitation of 132 cm which is distributed evenly throughout the year. Soils at our study site are primarily Orangeburg series, which are fine-loamy, siliceous, thermic typic Paleudults. Prior to study treatments, vegetation was predominantly 70-year-old, second growth *Pinus palustris* Mill. woodland [basal area (BA) approximately 15.5 m^2 ha^{-1}] with an understory dominated by the C4 grass *Aristida beyrichiana* Trin. & Rupr., broad-leaved herbs, and widely spaced clusters of *Quercus* spp. sprouts. For nearly 60 years the forests at our study site have been burned during the spring (March–May) with a return frequency of approximately 1–3 years. The main natural disturbances in this ecosystem are wind-throw and lightning, both resulting in a mix of single-tree and small to large multi-tree gaps (Platt et al. 1988; Palik and Pederson 1996).

Overstory treatment plots

Within a 100-ha area, twelve 2.5-ha plots were randomly established in fall 1997. Diameter at 1.4 m (dbh) and location (using laser transit) for each tree (dbh≥5 cm) in each plot were measured during summer and fall 1997. Plots were grouped by BA into three blocks (low=mean of 12.8 m^2 ha^{-1}, intermediate=15.8 m^2 ha^{-1} and high=16.3 m^2 ha^{-1}), and then plots within blocks were randomly assigned to one of four overstory treatments (Fig. 1): (1) control (no disturbance); (2) single trees harvested (1.5–2.7 m^2 ha^{-1} removed depending on block) to create a well-dispersed residual stand; (3) trees harvested leaving small ~30-m-diameter gaps (2.4–3.9 m^2 ha^{-1} removed); and (4) trees harvested leaving larger ~50-m-diameter gaps (2.8–3.4 m^2 ha^{-1} removed). The small and large gap treatments produce openings that have been shown to significantly alter light, soil resources and establishment of *P. palustris* seedlings (Grace and Platt 1995; Palik et al. 1997; McGuire et al., 2001). In late fall 1997, stands were harvested by machine, limbs were severed, and stems were carefully removed to minimize disturbance to the soil and understory vegetation. BA immediately after harvests averaged 17.3 m^2 ha^{-1} in control plots, 12.3 m^2 ha^{-1} in the single tree and small gap treatments and 11.9 m^2 ha^{-1} in the large gap treatment. The gap treatments represent a disturbance gradient that varies greatly in pattern but hardly at all in mean, ecosystem-wide intensity. In January 1998, the forest understory was burned to set all plots to the same point in the burn-response cycle.

Understory treatment subplots

Twenty-five 7×4 m subplots were arrayed within each plot to measure plant resources, root responses, and *P. palustris* seedling growth (Fig. 1). To ensure that the subplots covered a range of overstory structure, we first calculated an overstory abundance index for all possible subplot locations that were no less than 15 m
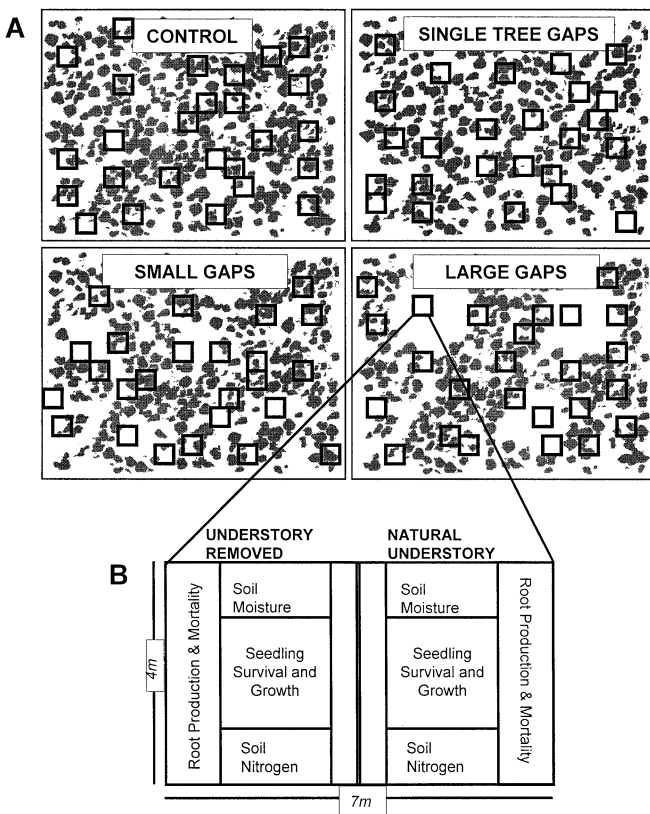
Fig. 1A, B Experimental design to estimate fine root responses to abiotic and biotic factors in a longleaf pine woodland. **A** One of three blocks showing four plots, each with one overstory treatment and 25 subplots used to measure roots and soil environment; *gray blotches* show distribution of pine crowns; **B** one subplot showing split into two quadrats to accommodate two understory treatments

away from the edge of each plot. Using the center of each possible subplot, we used GPS software to construct a 15-m radius, circular area, and to calculate an overstory abundance index as a sum of distance-weighted BA of trees within the circumscribed area. We then divided the range of overstory abundance index values into five smaller ranges of equal width. Within each of the smaller ranges, we randomly selected five subplots yielding 25 subplots per plot.

Each 7×4-m subplot was divided into two 3×4-m quadrats separated by a 1×4-m buffer (Fig. 1). Understory vegetation on one randomly chosen quadrat was left untreated (hereafter referred to as natural). In the other quadrat, understory vegetation was removed by a combination of periodic clipping and application of the herbicide glyphosate (4% active ingredient in water). In February 1998, ten 1-year-old containerized *P. palustris* seedlings were planted in a 2×2-m area within each quadrat. However, because of a severe drought (no measurable rainfall between 5 March and 4 May), seedling growth was low and mortality high (79.5%). Therefore, fine root growth of these seedlings was assumed to be nil. Harvested seedlings showed little lateral growth (<20 cm from the original root plug).

In each plot, six subplots representing the range of overstory abundance index values were used for intensive measurements of root growth, N mineralization, soil temperature, soil moisture, and neighboring overstory density. The remaining 19 subplots per plot were used for additional measures of root growth and neighboring overstory density.

Ingrowth cores

Root production was measured using ingrowth cores. In February 1998, two 15-cm-diameter by 30-cm-deep cores were located arbitrarily around the periphery of each quadrat using two constraints: stump holes (rare) were avoided and cores were at least 15 cm apart from each other. The cores (and minirhizotron tubes described below) were placed without bias with respect to surface debris or vegetation, and therefore we assume random placement. Soil was removed from the cores, sifted to remove roots, and re-placed into the column. In December 1998 (11 months later), a single 7.5-cm-diameter by 30-cm-deep sample core was removed from the center of each ingrowth core. Soil and roots from the two cores per quadrat were combined for a total of 600 samples (12 plots×25 subplots×2 understory treatments×1 composite core). Soil was wet-sieved through a screen with 2×2-mm openings. Live roots <2 mm diameter were separated into pine and non-pine components, dried for 3 days at 60ºC to a constant mass and weighed. All pine root samples, which had variable amounts of embedded sand, were ashed at 400ºC to determine ash-free dry mass. For non-pine roots, which had little or no visible sand attached to them after wet sieving, a random selection of 177 samples was ashed, and a single ash-free dry mass correction value (mean 86.2%, SD=9.3%) was determined. An additional but more limited set of root cores was established in February for a July harvest (5 months later); however, overall root mass in the July harvest was only 29% of the mass in December, and results were fundamentally similar to those from the December harvest; thus, we will not discuss the July sample in this paper.

Minirhizotrons

In January 1998, polybuterate minirhizotron tubes (5 cm inside diameter×80 cm length) were installed in the control and large gap plots only, and only within the understory control side of the six intensively measured subplots (one tube per subplot for a total of 36 tubes). This sampling strategy provided a focus on response of a single species (*P. palustris*) in the most contrasting set of conditions the study could provide (control versus large gap). Tubes were installed at a 45-degree angle to the soil surface to a minimum of 40 cm vertical depth. The tubes were positioned so that the captured frames were oriented at zero vertical degrees along the top of the tube, and were then anchored to metal stakes with wire and hose clamps to minimize rotation and environment-related heaving. The aboveground portions of tubes were painted and tightly capped to minimize light intrusion.

Minirhizotron sampling was conducted weekly from 2 July 1998 to 7 July 1999, for a total of 55 sampling dates. Forty images along the top of each tube were collected by Hi-8 camcorder (July 1998–February 1999) or by direct digital capture (February–July 1999) using software and a minirhizotron camera system (Bartz ICAP, Bartz Technology Company, Santa Barbara, Calif.). Individual fine roots (0.1–2.0 mm diameter, and exclusive of fungal rhizomorphs) were counted if they were partially or wholly within a reference frame inside of each sample image. If an individual root formed a branch, the branch was counted as a new individual root. Roots were considered "born" on the first date they were seen. Roots were considered dead on the first date that they either disappeared entirely and permanently from the frame, or appeared to be dead due to change in color (to gray or black) and subsequent decomposition. Lifespan was measured for each root that died during the sample period. A root-tracing software package (AR-COS, Graphics Equations Inc, Houston, Tex.) was used to measure the length and diameter of each fine root at each sampling date. The maximum diameter of each fine root and its depth in the soil volume were also recorded. Production was the sum of all increases in fine root length at a single microsite over the duration of the study, including production of new roots and/or the growth of existing roots. Fine root mortality was the sum of all live root length decreases. Mean standing crop for each tube was the average of all weekly measures, and fine root turnover rate was determined

by summing the total production and mortality over a sample period, and dividing that total by the mean fine root standing crop. Two microsites that had no production or mortality were removed from the data set prior to analysis. Further, we determined that two additional microsites were extreme outliers. These stations were located 20 m apart in an area with a significant clay layer, and were often submerged during periods of heavy rainfall for several days. Because these sampling stations had a markedly different soil environment, they too were removed from the data set before analysis.

Environmental measures

Soil moisture was quantified using time domain reflectometry (Topp et al. 1980). A pair of stainless steel rods was buried 30 cm deep in each half of each intensive subplot. Moisture measures were made using a Tektronix-2 A cable tester (Tektronix, Beaverton, Ore.) on 11 dates spanning April through October 1998. On the same dates that moisture was measured, soil temperature at the 5 cm depth was estimated by thermocouple probe (OMEGA Engineering, Stamford, Conn.). Net mineralization of NO_3 and NH_4 were determined using the buried bag technique (Eno 1960). From March to October (total of 255 days), seven collections were made of soil samples buried for 30 days in gas-permeable bags in the top 10 cm of soil. Soil was extracted using 2 M KCl, and NO_3 and NH_4 concentrations were estimated using a Lachat QuikChem 8000 flow-injection analyzer (Lachat Instruments, Milwaukee, Wis.). Differences between initial and final values for the seven sample periods were summed and converted to net N mineralization in kg ha^{-1} 255 days^{-1} in the top 10 cm of soil, assuming a soil bulk density of 1.1 g cm^{-3}, which was derived from 13 bulk density measures made in random locations within the study site (SD=0.09, range 1.07–1.37).

For all 25 subplots within each plot, we estimated nearby overstory density using two methods. First, overstory BA within 20 m of each subplot was calculated using Universal Trans Mercator coordinates and dbh measured for each tree. The 20-m distance was chosen because greater distances were often not possible for subplots near the periphery of the plots, and preliminary analyses showed nearly maximum correlations between pine root mass and overstory BA occurred for distances of approximately 20 m. Second, gap fraction, i.e., total sky not obscured by vegetation, was estimated using hemispherical photographs taken in summer 1998. Photos were scanned to make digital images which were analyzed using Hemiview software version 2.1 (Delta-T Devices, Cambridge, UK). Although gap fraction is normally used to estimate light environment, we used it as a crude measure of leaf area within the neighborhood of each subplot.

Analysis: within-ecosystem scale

All statistical comparisons were performed using Statistical Analysis System (SAS) software, version 8.01 (SAS Institute, Cary, N.C.). To test hypothesis 1, that within-ecosystem scale variation in soil environment will influence root responses, and hypothesis 2, that pine and non-pine roots would exhibit compensatory growth, we regressed (SAS Proc REG) ingrowth core pine, non-pine, and total root production against the following independent variables: soil moisture and temperature (average of 11 measurements), net mineralization of NO_3 and NH_4 (sum of seven measurements), and overstory density (estimated by overstory BA and gap light index). We also included pine root mass as an independent variable for analysis of non-pine root response, and vice versa. Separate analyses were conducted for the natural understory treatment (response variables=pine, non-pine and total roots) and understory-removed treatment (response variable=pine). For variables whose distributions were significantly different from normal, log transformations were used if the transformation resulted in no significant difference from normal. We began our analysis with simple

regressions of each response with each independent variable. Then we used multiple regression to choose a "best" model to predict root mass. Two criteria were used to pick the best model: the largest adjusted R^2 and all parameters significant at =0.1. In the multiple regression, condition number was examined to check for problems with collinearity (Philipi 1993), and residuals were inspected for outliers and systematic errors.

Hypothesis 1 was also tested using minirhizotron data. First, we analyzed fine root lifespans using proportional hazards regression (Cox's proportional hazards model, SAS Proc PHREG). We divided the data into four equal seasons and fit separate models for each, which was a better fit than a single model without seasons (P<0.001 for log-likelihood comparison). We then tested for the influence of soil temperature, net NO_3 mineralization, net NH_4 mineralization, soil moisture, depth of the root in the soil volume, and root diameter on fine root lifespan using simple pairwise, and multiple proportional hazards models with a stepwise selection procedure (inclusion level =0.1). Second, we analyzed the relationship between these same independent variables (except soil depth and root diameter) and minirhizotron derived estimates of production, mortality, standing crop, and turnover using simple and stepwise multiple linear regressions (SAS, Proc REG, inclusion level for stepwise =0.1). To test for depth-related trends in fine root production, mortality, standing crop, and turnover we divided the data into four equal 10 cm depth intervals and compared them using ANOVA (SAS Proc GLM). Due to zero values in depth classes for some tubes, non-transformed data were used for this analysis.

Analysis: whole-ecosystem scale

To test hypothesis 3, that gap size will influence ecosystem-level fine root production, we first estimated plot-wide fine root biomass by averaging ingrowth data from all 25 subplots in each plot. The subplot values, however, were weighted according to the distribution of overstory abundance index values in the plot. These data were analyzed via ANOVA (SAS, Proc GLM) using a 3×4×2 split-plot factorial design with three blocks, four overstory treatments, and two understory treatments split within the overstory treatment. Three *a priori* orthogonal contrasts among overstory treatments were planned: (1) all disturbed plots versus control; (2) single tree versus multi-tree gaps; and (3) small versus large gaps. Because treatments may have been confounded with the blocking by initial BA, we also conducted ANOVA and contrasts ignoring blocks and using initial BA as a covariate. Except where noted, results of the blocking and covariate analyses were qualitatively similar.

To test hypothesis 4, that seasonal weather and soil moisture patterns affect ecosystem-scale root growth, we first summed minirhizotron data across all tubes for each of the weekly sample dates. These data were then analyzed using simple linear regressions (SAS, Proc REG) to determine pairwise relationships between fine root response parameters and three independent variables: weekly mean soil moisture and soil temperature (averaged across all plots and subplots) and weekly rainfall. Multiple regressions with a stepwise selection procedure (inclusion level =0.1) were also used to select the best model for each fine root response. We also examined root response in week x to environmental variables in the 2 previous weeks ($x-1$, $x-2$), and report here the strongest relationships found.

Results

Within-ecosystem scale: ingrowth cores

Understory treatment had a large impact on fine root production within ingrowth cores. In the natural understory quadrats, biotic variables (e.g., presence of roots of another life form) and gap size had strong impacts on root response (Table 1). Pine and non-pine root mass were

Table 1 Regressions relating root mass from ingrowth cores (11 months after they were installed) to soil and plant community attributes in a *Pinus palustris* woodland. In this analysis, slopes are shown only for variables with $P<0.10$. Partial R^2 values indicate variables that were significant ($P<0.10$) in stepwise multiple regression models
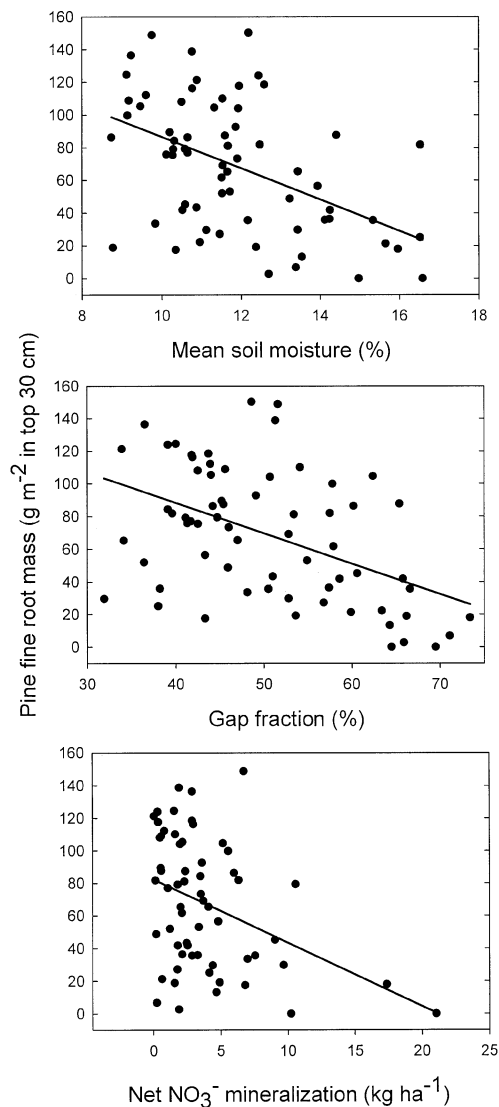
Understory treatment	Root type	Variable	Simple regression			Multiple regression Partial R_2
			Slope	P	R^2	
Natural	Pine	Log(Gap fraction)	–	<0.001	0.173	0.120
		Temperatur variance	–	0.026	0.075	
		Non-pine	–	0.033	0.067	0.074
		Log(NO$_3$)	0	0.306	0.016	
		NH$_4$	0	0.365	0.012	
		BA	0	0.545	0.006	
		Log(Temperature)	0	0.585	0.004	
		Soil moisture	0	0.830	0.001	
	Non-pine	Log(Gap fraction)	+	0.015	0.089	0.089
		Pine	–	0.033	0.067	
		Log(NO$_3$)	0	0.194	0.026	
		BA	0	0.339	0.014	
		Temperature variance	0	0.344	0.014	
		NH$_4$	0	0.504	0.007	
		Log(Temperature)	0	0.592	0.004	
		Soil moisture	0	0.709	0.002	
	Total	Temperature variance	0	0.178	0.028	
		Log(Gap fraction)	0	0.200	0.026	
		NH$_4$	0	0.202	0.025	
		Log(Temperature)	0	0.398	0.011	
		Log(NO$_3$)	0	0.799	0.001	
		BA	0	0.966	0.000	
		Soil moisture	0	0.996	0.000	
Removed	Pine	Soil moisture	–	<0.001	0.227	0.232
		Log(Gap fraction)	–	<0.001	0.199	0.089
		Temperature variance	–	0.007	0.178	
		Basal area	+	0.003	0.130	
		Log(NO$_3$)	–	0.016	0.091	0.065
		NH$_4$	0	0.232	0.023	
		Log(Temperature)	0	0.282	0.018	

Fig. 2 Eleven-month production of pine and non-pine fine roots in *Pinus palustris* woodlands as a function of gap fraction. Root production was estimated using ingrowth cores ($n=279$)
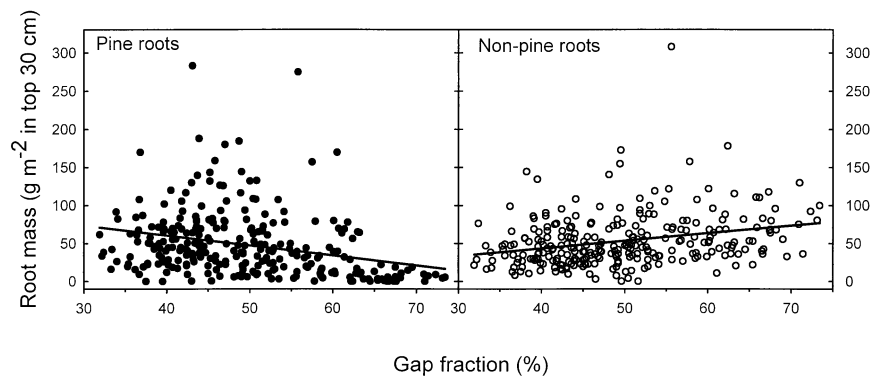
negatively related with each other according to simple linear regressions ($P=0.033$). LogGF, a surrogate for pine tree density within the neighborhood of the quadrat, was negatively related ($P<0.001$) to pine, and positively related ($P=0.015$) to non-pine root mass production (Table 1). Total root mass had no significant relationship with any tested variable. Except for a significant negative association between pine roots and temperature variance ($P=0.026$), abiotic factors were not related to root responses (Table 1). Because temperature variance was not included in the multiple regression model for pine roots (Table 1), but was positively correlated with the log of gap fraction (logGF, $r=0.51$, $P<0.0001$), it is possible that the pine root association with temperature variance is an artifact of pine root response to gaps, although experimental manipulations are needed to test this possibility. Variability in the natural understory treatment was large; R^2 for the significant relationships were between 0.067 and 0.173. The best multiple regression models for the natural understory quadrats returned

Fig. 3 Relationships between pine fine root production and three soil environmental factors in a *P. palustris* woodland; understory vegetation was removed by herbicide

positive relationship with overstory density (measured by either BA or logGF; $P=0.003$ and $P<0.001$, respectively). However, pine roots also significantly declined as soil moisture ($P<0.001$) temperature variance ($P=0.007$) and net NO_3 mineralization ($P=0.016$) increased (Table 1). The multiple regression model included soil moisture, logGF, and logNO$_3$ mineralization (Table 1); the negative relationship of each variable (untransformed) with pine roots is shown in Fig. 3. Volumetric soil moisture had by far the strongest relationship. Variation in soil moisture accounted for 23% of the variation in pine root mass; the remaining two variables combined (logGF and logNO$_3$) accounted for only an additional 15% of variation.

Within-ecosystem scale: minirhizotrons

Minirhizotron data also revealed significant relationships between the abiotic environment and root response in the reduced understory treatment. Soil moisture and NO_3 mineralization were the two most frequently significant abiotic variables. In the pairwise analyses, each had a strong positive relationship with production and mortality ($P<0.001$), a strong negative relationship with lifespan ($P<0.001$), a positive relationship with turnover ($P=0.078$ and <0.001, respectively), and no apparent influence on standing crop (Table 2). In the stepwise multiple regressions, however, each variable was included in just two models (soil moisture was included in the production and mortality models; NO_3 in the mortality and standing crop models; Table 2). NH_4 mineralization was positively associated with standing crop according to pairwise and multiple regression analysis ($P=0.089$; Table 2). Temperature variance was negatively related to lifespan according to both pairwise and stepwise proportional hazards models ($P<0.001$), and was positively related with root turnover ($P=0.003$) according to pairwise linear regression (Table 2). Mean temperature played no apparent role in regulating root dynamics ($P>0.5$ for all response variables).

Root width and depth in the soil were also significant factors. The proportional hazards model showed that wider and deeper roots lived longer (Table 2). ANOVA indicated that depth influenced mortality and production ($df=3,124$, $P<0.05$); these two responses were greatest in the upper 10 cm of soil (Fig. 4). Standing crop and turnover showed no significant depth-based variability.

Whole ecosystem scale:
effects of over- and understory treatments

As expected, understory removal reduced non-pine root mass within the ingrowth cores and increased pine root mass (Fig. 5). Simple ANOVAs detected a significant positive effect of understory removal on pine roots ($df=1,2$; $P=0.007$), a significant negative effect on non-pine roots ($df=1,2$; $P=0.002$), and a significant negative effect on total roots ($df=1,2$; $P=0.044$). When initial BA

results that were similar to the simple regression results, except that pine root mass was not included as a significant dependent variable in the non-pine root response model. In sum, these results show that in natural understory vegetation, increases in gap size (logGF) reduced pine root mass, but the reduction was about equally offset by increases in non-pine root mass (Fig. 2).

In the areas where the understory was experimentally removed, pine roots within ingrowth cores were more responsive to abiotic soil conditions than when understory vegetation was not removed. Simple linear regressions revealed a greater number of significant relationships, and the relationships were stronger than in the natural understory treatment (Table 1). However, R^2 values were still no greater than 0.23. As seen in the natural understory treatment, pine root biomass had a significant,

Table 2 Regressions relating root responses from minirhizotron tubes to root and soil attributes in a *P. palustris* woodland. Slopes indicate positive or negative relationships between response and independent variables where $P<0.10$. Partial R^2 values indicate variables significant ($P<0.10$) in stepwise multiple regression models. Response and environmental variables were natural log transformed where noted

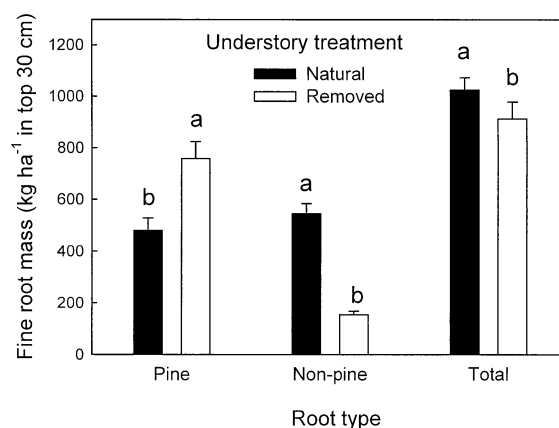| Root response	Variable	Simple regressions			Multiple regression Partial R_2
		Slope	P	R^2	
Lifespan[a]	Root width[b]	+	0.033		
	Soil depth[b]	+	<0.001		
	Temperature variance	−	<0.001		
	Log(Soil moisture)	**−**	<0.001		
	Log(NO_3^-)	−	<0.001		
	Log(NH_4^+)	0	0.104		
	Mean temperature	0	0.521		
Log(Production)	Log(Soil moisture)	+	0.007	0.218	0.218
	Log(NO_3)	+	0.064	0.110	
	Log(NH_4)	0	0.170	0.062	
	Temperature variance	0	0.276	0.039	
	Mean temperature	0	0.771	0.003	
Log(Mortality)	Log(Soil moisture)	+	0.005	0.239	0.239
	Log(NO_3)	**+**	0.028	0.151	0.086
	Temperature variance	0	0.139	0.071	
	Log(NH_4)	0	0.215	0.051	
	Mean temperature	0	0.918	0.000	
Log(Standing crop)	Log(NH_4)	**+**	0.097	0.089	0.089
	Log(Soil moisture)	0	0.170	0.062	
	Temperature variance	0	0.316	0.034	
	Log(NO_3)	0	0.503	0.015	
	Mean temperature	0	0.795	0.002	
Log(Turnover)	Log(NO_3)	+	<0.001	0.367	0.367
	Temperature variance	+	0.003	0.266	
	Log(Soil moisture)	+	0.078	0.100	
	Mean temperature	0	0.541	0.012	
	Log(NH_4)	0	0.659	0.007	

[a] Lifespan analyzed by proportional hazards regression, which does not produce R^2 values; all other root responses were analyzed by linear regression
[b] These variables were included in the multiple proportional hazards regression model, each at $P<0.10$
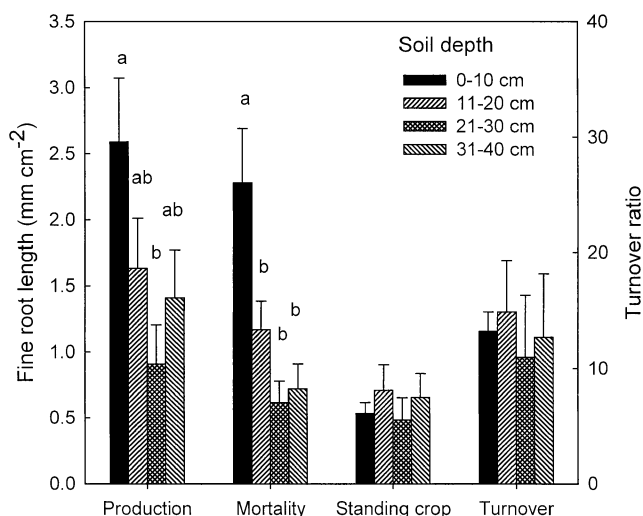
Fig. 4 Mean ecosystem production of fine roots over 11 months in a *P. palustris* woodland, all disturbance treatments combined. $n=12$ plots. *Adjacent bars with different small letters are significantly different* (ANOVA; $P<0.05$)

Fig. 5 Eleven-month fine root production in disturbed ($n=9$ plots) and undisturbed ($n=3$ plots) *P. palustris* woodlands. Data for natural and experimentally removed understory vegetation shown separately. For pine roots, *adjacent bars with different small letters are significantly different* (ANOVA; $P<0.050$). For non-pine roots, the difference between means is at margin of significance ($P=0.055$)

of each plot was used as a covariate (and blocks were ignored), the effects of understory removal remained significant ($P<0.05$) accept for total roots ($df=1,15$; $P=0.163$). In contrast with the understory treatment analysis, overstory treatments had no significant effect

on pine, non-pine or total root mass according to simple ANOVA ($df=3,6$; $P>0.180$).

The more powerful orthogonal contrasts, however, did detect some statistically significant differences among overstory treatments at the ecosystem scale. Yet of the

Table 3 Regressions relating weekly ecosystem-scale root responses (assessed by minirhizotrons) to mean temperature and soil moisture in the same week and rainfall in the previous week in a *P. palustris* woodland. Slopes indicate positive or negative relationships between response and independent variables where $P<0.10$. For all response variables, multiple regression model only included mean temperature as a significant variable ($P<0.10$)

Root response	Independent variable	Slope	P	R^2
Log(Production)	Mean temperature	+	<0.001	0.402
	Rainfall	+	0.023	0.095
	Soil moisture	0	0.366	0.016
Log(Mortality)	Mean temperature	+	0.01	0.171
	Rainfall	0	0.33	0.018
	Soil moisture	0	0.87	0.001
Log(Standing crop) (full year)	Mean temperature	–	0.02	0.106
	Soil moisture	0	0.130	0.044
	Rainfall	0	0.313	0.020
Log(Standing crop) (October 1998–July 1999)	Mean temperature	+	<0.001	0.274
	Soil moisture	0	0.069	0.077
	Rainfall	0	0.194	0.040
Log(Turnover)	Mean temperature	+	<0.001	0.548
	Rainfall	0	0.097	0.052
	Soil moisture	0	0.668	0.004

three contrasts we made, only the comparison between undisturbed and all three disturbance treatments pooled was significant at $\alpha=0.05$. When the understory was removed, mean pine root growth was less in disturbed (mean of 684 kg ha^{-1}, SE=65.5 kg ha^{-1}) than in control plots (mean of 980 kg ha^{-1}, SE=101 kg ha^{-1}). This difference was significant if initial BA was ignored (df=1,6; P=0.035) but was marginally not significant when we used initial BA as a covariate (df=1,7; P=0.062). Non-pine root mass was greater (df=1,6; P=0.055) in disturbed (mean of 504 kg ha^{-1}, SE=53 kg ha^{-1}) than in control plots (mean of 472 kg ha^{-1}, SE=63 kg ha^{-1}) and this became farther from statistically significant when BA was used as a covariate (df=1,7 P=0.158). No significant differences between single tree and gap type disturbances, nor between small and large gap disturbances were detected (P>0.070 for both block and covariate analyses).

Whole ecosystem scale: seasonal and soil depth trends in root response

Weekly soil temperature was positively related to weekly production, mortality, and turnover but negatively related to standing crop (Table 3, Fig. 6). Greatest correlation between temperature and root response occurred for current week observations; temperatures in the previous 1 or 2 weeks were less correlated to weekly root response. We suspected that the effects of temperature could have been an artifact of the low standing stock observed during the first summer of observations (see steep rise in standing crop July–September 1998 in Fig. 6); we therefore re-analyzed both weekly standing crop and turnover after removing the first 11 sampling dates (2 July–11 September 1998). No changes in the response of turnover were observed (data not shown); however, the relationship between temperature and standing crop in this reduced data set was significant and positive (P<0.001, R^2=0.27, Table 3).

Variables other than mean temperature had little or no effect on root demography. Weekly production was
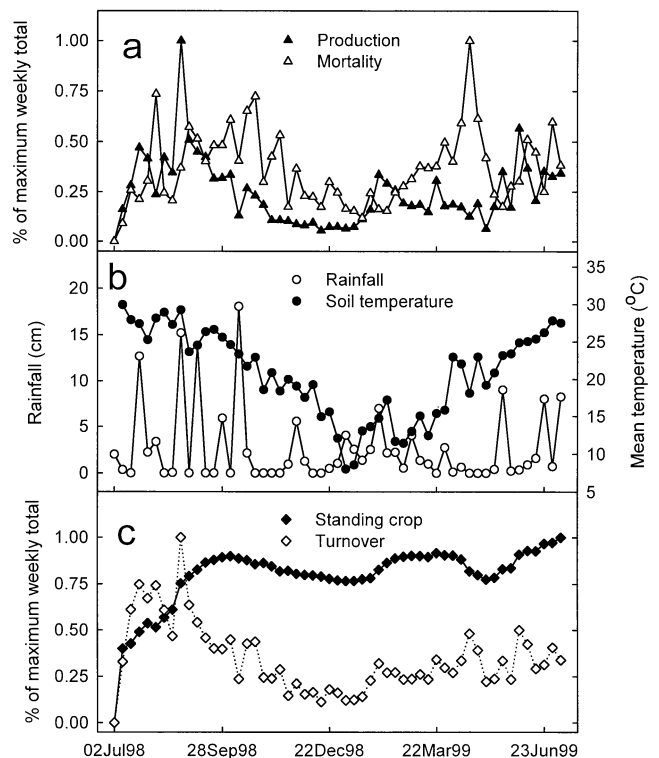
Fig. 6 Weekly patterns of *P. palustris* fine root production and mortality (**a**), rainfall and soil temperature (**b**) and fine root standing crop and turnover (**c**) in a *P. palustris* woodland. Root parameters are based on pooled data from 32 minirhizotron tubes

positively associated with the previous week's rainfall totals (P=0.023); however, rainfall did not significantly affect any other root response. Soil moisture levels were not significantly associated with any of the root responses (P>0.130). All stepwise regression models contained only mean soil temperature.

Discussion

Within-ecosystem scale: unexplained variability

Only a small portion of fine root growth variation could be explained by our measured independent variables, despite our efforts to increase signal by creating canopy gaps and removing understory vegetation. Maximum R^2 among the 61 pairwise and multiple regressions we performed was only 0.386 (multiple regression of pine root ingrowth core response in understory removed), and in all but nine regressions, R^2 was <0.200 (Tables 1, 2). Plots of root growth against independent variables showed considerable scatter (Figs. 2, 3).

High variability in root responses, much of it unexplained by measured variables, implies that roots either respond weakly (if at all) to the range of environmental conditions in our study system, or that root responses are very complex. Complexity is consistent with the idea that multiple factors and their interactions influence roots. The extent of this unexplained variability within natural ecosystems may be underappreciated because many studies to date have compared mean root responses of different ecosystems, often using ANOVA approaches to compare categories (Joslin and Wolfe 1998; Ostertag 2001) which may wash out natural variability at fine spatial scales. Other approaches have used experimental manipulations of small soil volumes to estimate root response (Drew et al. 1973; Jackson and Caldwell 1989; Hodge et al. 1999), which can artificially inflate signal to noise. Recently, some improvement in predicting root responses at the fine scale has been achieved by dividing fine roots into morphological or demographic categories (e.g., based on size, age, date formed, mycorrhizal status, or depth within the soil) before analysis (Hendrick and Pregitzer 1996; Wells and Eissenstat 2001); however, even in these studies, a large amount of root variation remained unexplained. For the time being, it appears that much more work is needed before we can precisely predict root responses to fine-scale spatial variation in the soil environment.

Within-ecosystem scale: abiotic factors

In the natural understory treatment, abiotic factors had little apparent influence. Root production measured by the ingrowth cores had no significant relationship with N mineralization, soil water or soil temperature, although a pairwise relationship with temperature variance was detected (Table 1). These results, coupled with the large variation we observed for root responses, lead us to reject our first hypothesis that fine-scale spatial heterogeneity of soil resources and temperature would result in corresponding variation in fine root dynamics. Further experiments are needed, however, to determine if soil temperature variance is a driver of root responses, or if its relationship with root dynamics is simply a spurious correlation.

When non-pine roots were artificially suppressed, we found some evidence in support of our hypothesis; soil resources and soil temperature had significant, though weak influences on root response. Of the resources measured, soil moisture and net NO_3 mineralization apparently had the strongest influence on roots. Both variables were negatively associated with ingrowth core root mass (Table 1). In minirhizotrons, increases in either resource led to shortened fine root lifespan, and accelerated production, mortality and turnover (Tables 2). Since soil moisture can increase access to NO_3, there is some question about the independent influence of these two variables on roots. However, they were essentially uncorrelated ($r=0.098$, $P=0.414$, $n=72$ quadrats), and thus each may have influenced roots independently of the other.

The responses to soil water detected in our study contrast with some findings in other studies where increases in soil moisture have been shown to reduce root mortality or increase root lifespan (Santantonio and Hermann 1985; Pregitzer et al. 1993; Hendrick and Pregitzer 1996). However, Joslin et al. (2000) found the same trends we did in a temperate hardwood forest: wetter microsites had greater production and mortality and higher rates of fine root turnover. Plant response to soil moisture in our study may have been influenced by periods of severe drought. Little or no rain fell on our sampling sites for two 4-week periods in November and December of 1998, and for 7 weeks from March to May of 1999, producing corresponding decreases in soil moisture (Fig. 6). Microsites with higher average moisture levels were apparently important resource patches, and *P. palustris* root systems showed some plasticity in response to them. More fine roots were produced in wetter microsites, and these roots died faster than in drier microsites. This plasticity of root response may optimize water uptake because younger, finer and more absorptive roots are more efficient at water uptake than older and thicker roots (Eissenstat and Yanai 1997).

Root responses to NO_3 in our study may be related to internal or external factors. Because young roots have increased potential for nutrient uptake (Gross et al. 1993; Eissenstat and Yanai 1997), adjustment of lifespan could be an internal, adaptive mechanism of *P. palustris* to maximize uptake in favorable sites. Alternately, reduced lifespan may result from the increased cost of NO_3 uptake relative to NH_4 (Cannell and Thornley 2000); the latter hypothesis is supported by the apparently low impact of NH_4 on lifespan in our study (Table 1). External controls may operate in the form of root predation if herbivores preferentially graze more NO_3-rich tissues. We did find a significant correlation between the proportion of growing roots that disappeared within 1 week (likely caused by herbivory) and N availability (Stevens et al., 2002).

The lack of response to net NH_4 mineralization is puzzling because NH_4 was not only about as variable as NO_3, it was also the dominant inorganic N source (mean of 8.21 kg ha^{-1} versus 3.08 for NO_3). Aber et al. (1985) found that roots were more responsive to NO_3 than to

NH$_4$, and they attributed this to the greater mobility of NO$_3$, which may permit forests to more easily adjust fine root standing crop to obtain the same level of N. An alternative explanation is that NO$_3$ uptake results in greater fine root mortality due to greater C costs associated with utilization of NO$_3$ versus NH$_4$ (Cannell and Thornley 2000). If this scenario is correct, however, then roots exposed to high concentrations of NO$_3$ would die more frequently, and therefore might stimulate greater production, which is consistent with our minirhizotron but not with our ingrowth core results. The negative relationship found between soil moisture and root growth in the ingrowth cores is also puzzling. The frequent droughts during our study, including the severe one between March and May, may be responsible for this pattern. Roots may be initially stimulated by soil patches rich in water, but once roots have proliferated there, water uptake rates will increase. During droughts, therefore, patches with more roots could have less water.

We can think of two reasons why we detected relationships between abiotic factors in the understory-reduced but not in the control quadrats. First, the understory-reduced quadrats were dominated by roots of a single species, and thus responses to abiotic factors may have been easier to detect than in the multi-species control quadrats, where idiosyncratic responses of individual species may have obscured trends. Second, the reduction of understory created slightly different soil conditions than in control plots, and in particular, a shift in the forms of N produced by mineralization. NO$_3$ and NH$_4$ mineralization were 2.57 and 8.60 kg ha^{-1} in control but 3.63 and 7.80 in the understory reduced treatment.

Within-ecosystem scale: biotic factors

Biotic factors had much stronger influences on root responses than did our measured abiotic factors. Local overstory density and its influence on distribution of life forms in the understory was the prime factor. As expected, where overstory density was low (either naturally or as a result of creating experimental gaps), light stimulated understory vegetation and roots of understory plants (Table 1), and reduced the capacity of pines to expand into space liberated by experimental removal of the understory (Table 1). A more interesting result, consistent with our second hypothesis, was the offset of reduced pine root mass production by an approximately equal increase in non-pine root mass as overstory density declined (Fig. 2). Because of this offset, total root mass (pine plus non-pine) was not related to canopy density in the natural understory treatment (Tables 1). In the understory-removed treatment, pine root growth was accelerated and thereby approximately compensated for the absence of understory roots, a trend that can be seen clearly when means for all ecosystems were plotted (Fig. 5).

The 1:1 replacement of pine and non-pine roots across the overstory density gradient (Fig. 2), and the compensatory growth of pine roots when non-pine roots were artificially removed (Fig. 5), are intriguing patterns that suggest a resource-controlled carrying capacity for roots, and symmetry of belowground competition between pines and non-pines. A positive relationship between root density and mortality rate (which might lead to a carrying capacity of sorts) was recently demonstrated in apple trees (Wells and Eissenstat 2001), and belowground competition does tend to be symmetric (Wilson 1988). Our data suggest that competitive influence of non-pine roots on pine roots was stronger than vice versa (i.e., see significant non-pine root effect on pine roots but not the reverse pattern in multiple regressions of Table 1). A better understanding of this competitive interaction may be gained if effects of roots on resources and responses of roots to resource levels can be measured (Goldberg 1990). Furthermore, responses should be calculated per unit of surface or length, because pine roots tend to be much thicker than non-pine roots (McGuire et al. 2001). The fact that roots of *P. palustris* can only form ectomycorrhizae, whereas non-pine roots can produce a wide variety of mycorrhizal forms, further complicates comparisons of competitive effects or responses.

Within-ecosystem scale: gaps

The effects of gaps on root response were rather large, and a threshold gap size where pine root growth decreased dramatically was detected. For non-pine roots, predicted non-pine root mass increased from approximately 40 to 75 g m^{-2} over the range of gap fractions measured (32–73%). Pine root mass declined linearly as gap fraction increased; however, when gap fraction reached approximately 65%, pine root density dropped quickly to nearly zero (Fig. 2). This linear decline followed by a steep drop in pine root mass reflects known distribution of roots around trees, and influences of canopy gaps. For most trees, coarse root density declines exponentially from the stem base, whereas fine root density declines linearly (Fayle 1965; Atkinson 1980; Persson 1980; Jones and Raynal 1986). Several studies have shown a threshold gap size where canopy tree root density drops off rapidly. Our threshold gap size (65% gap fraction) occurred mainly in the centers of the largest gaps (slightly less than 25 m radius or approximately 2,000 m^2). Parsons et al. (1994a) found a threshold response in pine ectomycorrhizal root tip density, but for a much smaller gap size (260 m^2) in a 90- to 95-yr-old *Pinus contorta* ssp. *latifolia* (Engelm. ex Wats.) forest in Wyoming. McGuire et al. (2001) found steep declines in pine fine root length at distances from gap edge as small as 9 m during the first year after gaps were created in a *P. palustris* forest. Interestingly, our threshold for pine root mass to drop to near zero (65% gap fraction) corresponds well with a threshold level of light in canopy gaps where planted *P. palustris* seedlings began to show substantial response to light increases (Palik et al. 1997).

Our findings add to a growing literature showing that root gaps in forests and woodlands are less distinct and more ephemeral than canopy gaps (Silver and Vogt 1993; Wilczynski and Pickett 1993; Parsons et al. 1994a; Jones et al. 1996; Schroeer et al. 1999; McGuire et al. 2001). Gaps close quickly because root systems of both the overstory and understory plants are highly plastic and capable of rapid response to disturbance.

Ecosystem-scale

Of the overstory treatments tested, only disturbance in general, i.e., ignoring mean gap size, had significant effects. No changes in total ecosystem root response were detected when the total disturbed area was held constant but gap size was varied. Furthermore, when we ignored blocking and used initial plot BA as a covariate in our analyses, the significant contrasts became marginally non-significant. Therefore we reject our third hypothesis and conclude that for the range of gap sizes we tested, pattern of disturbance had no effect on ecosystem-wide fine root response. This is in contrast with other aspects of our broader study. Battaglia (2001) found that ecosystem-wide light in the understory was 20% greater in the large gap than in the single tree treatment. We also found pattern of disturbance effects on *P. palustris* seedlings planted in January 1999 and re-measured in November 2000; those in the large gap treatment had 13.0 mm groundline diameters and a survival rate of 36.0%, while those in the single tree treatment grew less (10.4 mm diameter) but had greater survival (49.2%).

For pine roots, effects of creating gaps were only detected where the understory was removed (684 kg ha^{-1} in gaps versus 980 kg ha^{-1} in control plots). This interaction between overstory and understory treatments is best interpreted as less capacity for compensatory growth of pine roots (i.e., to fill in gaps left by removal of understory vegetation) where pine density is lower. Thus, we conclude that the disturbance we applied (15.2–21.2% reduction in BA) stimulated non-pine root growth and reduced the capacity for compensatory growth of pine roots at the whole-ecosystem scale.

Our fourth hypothesis, that soil moisture would be a major driver of root turnover at the ecosystem level, was not supported. Instead, we found that mean soil temperature had the strongest impact of the environmental factors examined, explaining 11–55% of variation in root responses (Table 3). All stand-level root processes were stimulated as weekly mean temperature increased. These findings contrast with our results at the within-ecosystem scale, where we saw no variation in root response between microsites that could be attributed to differences in mean temperature.

The stand-level results we observed are consistent with literature results, which show that growth, mortality, and root density increase as soils warm (Kasper and Bland 1992; Hendrick and Pregitzer 1996; McMichael and Burke 1998). Low productivity and standing crop in cold months were followed by high production and standing crop during warmer months (Fig. 6), a seasonal trend that is common in temperate forests (Deans 1979; McClaugherty et al. 1982; Hendrick and Pregitzer 1992, 1993, 1996; Fahey and Hughes 1994). During the growing season, competition between roots and shoots for photosynthate can lead to a pattern of reduced root growth while shoots are expanding (Eissenstat and Van Rees 1994; Pregitzer et al. 2000). We are unable to determine if this occurred in our system; however, the fact that root production was much more variable than temperature during the growing season (Fig. 6) is suggestive.

Results of our study do not suffer from several pitfalls common in the literature. Comparisons within and across studies can be confounded if study locations include not only changes in experimental factors of interest, e.g., soil nutrients, but also changes in species composition, differences in methods to measure roots, and artificial treatments that may expose plants to conditions outside of their normal range of acclimation or adaptation (Ostertag 2001). In our study, we compared root responses to disturbances that mimic natural disturbance patterns, and the species pool was similar across all plots. We can be criticized, however, for the small patches (3x4 m) used to experimentally reduce understory vegetation. This fine scale of disturbance introduces uncertainty into our comparisons at the whole-ecosystem scale.

Despite these potential pitfalls, however, our work showed clearly that: (1) fine root response in our system is quite variable; (2) biotic factors, such as intra-specific competition (carrying capacity) and competition between life forms, influence root growth at the local scale; (3) the presence of an understory facilitates rapid response to gaps such that belowground gaps are quite ephemeral; and consequently, (4) gap size and arrangement has little effect on total fine root growth at the ecosystem scale, at least within the limit of gap size tested in this study.

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