

# Root dynamics of southern Ohio oak–hickory forests: influences of prescribed fire and landscape position

William J. Dress and Ralph E.J. Boerner

**Abstract:** This study compares standing root biomass from sequential root cores and new root production in ingrowth cores in three watersheds: an unburned control watershed, a watershed burned once in 1996, and a watershed burned for three consecutive years (1996–1998). Based on root cores collected on six sampling dates from April through November 1998, maximum standing live root biomass occurred approximately 1 month earlier in the growing season in the site burned three times, presumably because of increased soil temperature after the fires. Standing live fine root biomass was significantly lower in the site burned three times in three of the six sampling dates (April, June, and November) and when averaged over the whole growing season. Most of this effect was due to lesser root biomass in the most mesic landscape position. New root production was measured during three ingrowth core intervals: April to August 1998, August to November 1998, and August 1998 to November 1999. Net production was significantly greater in sample plots in xeric landscape positions during each sampling interval. Overall, differences in standing root biomass were inversely correlated with fire-induced changes in N mineralization and increased soil temperature after burning shifted the phenology of root biomass accumulation earlier in the growing season.

**Résumé :** Cette étude compare la biomasse racinaire à partir de carottes de sol séquentielles et de la production de nouvelles racines dans des carottes de croissance dans trois bassins hydrographiques : un bassin témoin non brûlé, un bassin brûlé une fois en 1996 et un bassin brûlé au cours de trois années consécutives (1996–1998). Sur la base des carottes de sol collectées lors de six dates d'échantillonnage, du mois d'avril au mois de novembre 1998, la biomasse maximale de racines vivantes a été produite approximativement un mois plus tôt dans la saison de croissance dans le site brûlé trois fois, probablement à cause de la température élevée du sol après les feux. La biomasse des racines fines vivantes était significativement plus faible dans le site brûlé trois fois lors de trois des six dates d'échantillonnage (avril, juin et novembre) ainsi que sur la base de la valeur moyenne pour toute la saison. La majeure partie de cet effet est dû à une plus faible biomasse racinaire dans la position la plus mésique du paysage. La production de nouvelles racines dans les carottes de croissance a été mesurée au cours de trois intervalles : des mois d'avril à août 1998, d'août à novembre 1998 et d'août 1998 à novembre 1999. La production nette est significativement plus élevée dans les parcelles-échantillons situées dans la partie xérique du paysage durant chacun des intervalles d'échantillonnage. Globalement, les différences dans la biomasse racinaire sont négativement corrélées avec les changements dans la minéralisation de N causés par le feu et l'augmentation de la température du sol après que le feu a modifié la phénologie de l'accumulation de la biomasse racinaire plus tôt dans la saison de croissance.

[Traduit par la Rédaction]

## Introduction

Long-term monitoring of forest plots in unmanaged stands over the past three decades has demonstrated significant changes in forest composition within the central hardwoods region. The abundances of red oak (*Quercus rubra* L.), white oak (*Quercus alba* L.), and hickory (*Carya* spp.) have declined by 41, 31, and 22%, respectively (Iverson et al. 1997). Over the same interval the abundances of red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), yellow-

poplar (*Liriodendron tulipifera* L.), and black cherry (*Prunus serotina* Ehrh.) have increased by 70, 44, 38, and 129%, respectively (Iverson et al. 1997). These changes are hypothesized to be the result of fire suppression and chronic anthropogenic deposition of N, which averages 15–20 kg·ha<sup>-1</sup>·year<sup>-1</sup> in this region (Morris and Boerner 1998).

Dendrochronological studies indicate that low-intensity surface fires in the spring or fall historically occurred at intervals of 3–5 years in this region prior to the implementation of active fire suppression (Smith and Sutherland 1999). In 1994 a long-term ecosystem management research program was initiated to determine the usefulness of prescribed fire at similar intervals in restoring these oak–hickory forests. Among the goals of this study are to use fire to volatilize anthropogenically deposited N and S, increase light, decrease woody stem density, and to shift community composition from fast-growing maples and yellow-poplars back to slow-growing oaks and hickories.

Landscape features are critical to an understanding of fire

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behavior. Fires are typically more severe on upper slopes and ridgetops than on lower slopes, and more severe on south- and west-facing slopes than north-facing slopes (Camp et al. 1997; Taylor and Skinner 1998). Broadly, these differences can be attributed to soil and forest floor moisture, since north- and east-facing slopes and drainages typically have greater soil moisture (Wolfe et al. 1949). Fire intensity is one of the most important factors determining the overall effect of the fire on ecosystem dynamics, such as N mineralization (Boerner et al. 2000). Therefore, prescribed fires can be expected to affect ecosystem dynamics differently depending upon landscape position.

At the ecosystem level, the ecological effects of fire may be difficult to detect from an examination of aboveground processes only. Although species composition may vary among landscape positions and in response to fire, many aboveground ecosystem processes, such as productivity, do not vary as greatly. Belowground ecosystem processes, such as nutrient availability and soil microclimate, do vary both among landscape positions and in response to fire (Boerner 1982, 1984) and, therefore, may represent better measures of the effects of prescribed fire at the landscape scale.

Root biomass also varies at the landscape scale, particularly in relation to slope position (Keyes and Grier 1981; Comeau and Kimmins 1989; Ehrenfeld et al. 1992; Enoki et al. 1996). Such differences have been ascribed to several ecosystem attributes, including soil depth, moisture, and nutrient availability. Furthermore, root dynamics are a key pathway for energy and nutrient flux in forest ecosystems, because as much as 50% of net primary productivity in hardwood forests has been attributed to fine root production (McClaugherty et al. 1982). Fine roots also contribute >50% of the total litter production and >50% of the N input into the soil (Hendrick and Pregitzer 1993a). Clearly, fine root dynamics are key processes in ecosystem nutrient cycling; thus, an understanding of how prescribed burning affects root dynamics is crucial to understanding how plants respond to the altered soil environment caused by the burning treatments.

Within this context, the specific objectives of this study were (i) to quantify seasonal patterns of root standing biomass and production in an oak-hickory forest ecosystem and (ii) to determine if fire, landscape position, or their interaction, significantly affected root dynamics. Specifically, we hypothesized that root biomass would change inversely with fire-induced or landscape-related variations in N mineralization and that the alterations in soil surface microclimate produced by burning would alter root phenology.

## Study site

The site chosen for this study was Arch Rock, located in Vinton County (39°11'N, 82°22'W) on the unglaciated Allegheny Plateau of southern Ohio. This site is a contiguous block of 80 ha occupied by mixed oak forests that developed following clear-cutting for charcoal production 100–150 years ago. This site is one of four sites being used for the long-term prescribed fire – restoration study (see Sutherland (2001) for a complete description of the study and study sites). For this study we confined our sampling to this one site because of the labor-intensive nature of the sampling.

The parent materials underlying the study site are sandstones and shales of Pennsylvanian age. The soils are silt loams formed

from colluvium and residuum and are predominantly Alfisols (Boerner and Sutherland 2001). The climate of the region is cool, temperate, and continental with mean annual temperature and precipitation of 11.3°C and 1024 mm, respectively (Sutherland and Yaussy 2001). Microclimatic gradients generated by the steep, dissected topography of the region included the tendency for south-, southwest-, and west-facing slopes to be drier and warmer than north-, north-, and east-facing slopes in this region because of differential solar radiation inputs (Wolfe et al. 1949; Hutchins et al. 1976).

Each watershed within Arch Rock was stratified using a geographic information system (GIS) based integrated moisture index (IMI) developed by Iverson et al. (1997) for this region. The IMI stratification was achieved through integration of aspect, hill shade profile, solar radiation potential, flow accumulation, water holding capacity of the soil, and curvature profile of the landscape (Iverson et al. 1997). Each component was weighted and standardized on a 0–100 scale, and three IMI classes were delimited: xeric, intermediate, and mesic. As this metric delimited areas of differing microclimates, it was ideal for representing the topographic scale within each of the watersheds. Within each of the watersheds, three long-term vegetation sample plots of 0.125 ha were established in each of the three IMI classes. The positions of the sample plots were determined from a digital elevation model overlain with an IMI class map in an ARC/INFO environment, and the overall experiment was designed to be a balanced, randomized block design (Sutherland 2001).

Since 1996, one watershed was burned three times (1996, 1997, and 1998), one was burned one time (1996), and one was an unburned control. The surface fires were low to moderate intensity and all occurred in late March – early April. Fire temperatures and behavior are given by Boerner et al. (2000).

## Methods

### Sampling design

Prior studies in these sites have demonstrated a significant effect of the strong topographic gradient described by the IMI on ecological processes (Morris and Boerner 1998, 1999; Decker et al. 1999). Therefore, we stratified our sampling design by IMI. This was accomplished by collecting root cores from areas adjacent to the permanent vegetation plots previously established using the global positioning system (GPS) in known IMI classes. In each burn treatment-by-IMI class combination, we collected five root core samples at random points 4–6 m apart along the elevation contour beginning at a randomly chosen point 5–10 m from the edge of the permanent plot. Previous studies of spatial autocorrelation of soil properties and organisms in these sites (Morris 1999; R.E.J. Boerner, unpublished data) indicate that a distance of 4–6 m between samples is sufficient to ensure spatial independence among samples. Thus, the individual core sample was the experimental unit. A total of 15 cores (3 IMI classes × 5 cores/IMI class) were collected from each burn treatment on each sampling date (early April, mid-May, late June, early August, mid-September, and early November 1998), for a total of 90 cores per burn treatment.

### Field and laboratory methods

To quantify seasonal patterns of standing root biomass (both live and dead), we collected soil cores on each of six sampling dates, approximately 5–6 weeks apart, from early April to mid-November 1998. On the first four sampling dates, cores of 7.5 cm diameter and 15 cm depth were taken and divided into three 5-cm depth increments in the field. On the last two sampling dates, cores of 5 cm diameter and 15 cm depth were taken and divided into 5-cm depth

**Table 1.** Seasonal mean standing fine root mass ( $\text{g/m}^2$  to 15 cm depth) by treatment ( $N = 90$ ; 15 cores on each of six sampling dates), IMI class ( $N = 90$ ), and the treatment  $\times$  IMI class interaction ( $N = 30$ ).

	Live	Dead
<b>Treatment</b>		
Control	939.8 $\pm$ 50.9	315.6 $\pm$ 52.8
Burned one time	805.5 $\pm$ 46.6	243.0 $\pm$ 28.0
Burned three times	764.0 $\pm$ 37.2	230.6 $\pm$ 17.7
<b>IMI class</b>		
Xeric	868.5 $\pm$ 43.5	311.4 $\pm$ 55.0
Intermediate	853.3 $\pm$ 49.9	244.7 $\pm$ 20.3
Mesic	787.5 $\pm$ 40.5	233.2 $\pm$ 21.4
<b>Treatment <math>\times</math> IMI class interactions</b>		
Control $\times$ xeric	1022.9 $\pm$ 87.5	424.9 $\pm$ 145.3
Control $\times$ intermediate	763.7 $\pm$ 98.0	255.7 $\pm$ 42.2
Control $\times$ mesic	1032.9 $\pm$ 70.5	266.2 $\pm$ 46.8
Burned one time $\times$ xeric	805.3 $\pm$ 68.5	272.7 $\pm$ 74.0
Burned one time $\times$ intermediate	959.0 $\pm$ 83.4	258.4 $\pm$ 33.2
Burned one time $\times$ mesic	652.3 $\pm$ 65.3	198.1 $\pm$ 23.3
Burned three times $\times$ xeric	777.4 $\pm$ 61.7	236.3 $\pm$ 24.1
Burned three times $\times$ intermediate	837.2 $\pm$ 75.6	220.3 $\pm$ 29.7
Burned three times $\times$ mesic	677.4 $\pm$ 52.6	235.2 $\pm$ 37.4

increments in the laboratory. Cores were stored at 4°C pending processing.

We used root ingrowth cores to quantify seasonal patterns of new root production. Each ingrowth core was established by first removing a soil core, then refilling that volume with freshly sieved, root-free soil from adjacent to the sampling plot. The ingrowth soil was compacted by hand to a bulk density similar to the original core, and a PVC collar was placed over the top of the core to facilitate later recovery. After a period of time during which roots grew into the ingrowth cores, the cores were recovered with the corer and returned to the laboratory as indicated above. Ingrowth was measured during three time intervals: early April to early August 1998, early August to mid-November 1998, and mid-November 1998 to mid-April 1999.

Roots were recovered from the sequential and ingrowth cores by wet sieving and flotation (Joslin and Henderson 1987). Roots were divided into live fine roots ( $<2$  mm), live coarse roots ( $\geq 2$  mm) (data not shown), and dead fine roots. Classification of roots as live or dead was based on color and mechanical stability. Roots were dried at 70°C to constant mass.

### Data analysis

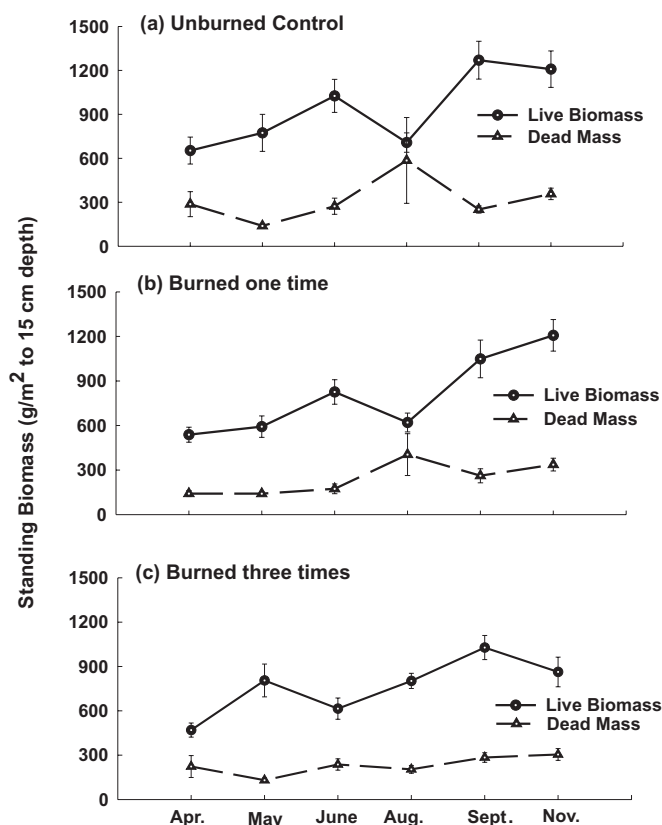
Root biomass recovered from the cores, the change in standing root biomass from one sample date to the next, and new root biomass recovered from the ingrowth cores were all expressed as grams dry root mass per square metre to 15 cm depth. Of the 560 ingrowth cores we examined, three had anomalously low or high biomass and based on Dixon's outlier criteria (Dixon and Massey 1969) at  $\alpha = 0.05$ . We deleted these three observations from the data set. To determine if fire frequency, IMI class, position within the sampling plot, or their interactions affected root biomass, we performed a mixed-model, two-way ANOVA using fire frequency and IMI class as treatment variables (SAS Institute Inc. 1995).

## Results

### Seasonal patterns of standing root biomass

Averaged over the entire growing season, standing live

**Fig. 1.** Seasonal pattern of standing live and dead fine root biomass (mean  $\pm$  SE) from April to November 1998: (a) control, non-burned plot; (b) once-burned plot; (c) thrice-burned plot.



and dead fine root biomass was 17 and 23% greater in the unburned control than in the sites burned one time and three times, respectively (Table 1). Over all treatments, mean standing live and dead fine root biomass was also greater in the xeric and intermediate IMI class plots than in the mesic IMI class plots (Table 1). However, in the control watershed, fine root biomass was lowest in the intermediate IMI class soils, whereas average seasonal live fine root biomass was greatest in the intermediate IMI class soils in the site burned one time and the site burned three times (Table 1).

Standing live fine root biomass in the unburned control increased from approximately  $650 \text{ g/m}^2$  in April to  $>1000 \text{ g/m}^2$  in June (Fig. 1a). Standing live fine root biomass then decreased by approximately 31% between June and August and increased once again to  $>1200 \text{ g/m}^2$  in September (Fig. 1a).

The seasonal pattern of standing live root biomass in the site burned one time paralleled that of the control, with standing biomass at the site burned one time consistently  $100\text{--}200 \text{ g/m}^2$  lower than that of the control (Fig. 1b). In contrast, in the site burned three times the seasonal minimum was in June, 1 month earlier than the observed minima for the control and the site burned one time (Fig. 1c). In the site burned three times, standing live root biomass increased steadily from June through September (Fig. 1c).

In the unburned control, total dead root biomass increased from approximately  $100 \text{ g/m}^2$  in April to  $>500 \text{ g/m}^2$  in August and then decreased into the autumn. The seasonal pat-



**Table 2.** Analysis of variance *p* values for standing root biomass ( $\text{g/m}^2$  to 15 cm depth) in an Ohio oak–hickory forest on each of six sampling dates during 1998.

Month	Full model	Burn treatment	IMI class	Interaction
<b>Live roots</b>				
April	<0.002	<0.057	ns	<0.014
May	<0.026	ns	ns	<0.024
June	<0.003	<0.003	ns	<0.046
August	ns	ns	ns	ns
September	ns	ns	ns	ns
November	<0.037	<0.031	<0.042	ns
<b>Dead roots</b>				
April	<0.049	ns	<0.051	ns
May	<0.012	ns	<0.003	ns
June	<0.004	ns	<0.051	<0.002
August	ns	ns	ns	ns
September	ns	ns	ns	ns
November	ns	ns	ns	ns

**Note:** For each sampling date,  $N = 15$  for burn treatment and IMI class comparisons. ns, not significant.

tern of dead root biomass in the control watershed was, for the most part, a mirror image of the seasonal pattern of live root biomass (Fig. 1a). The seasonal pattern of dead root biomass in the site burned one time was similar, save that the August peak in dead root biomass (and the August minimum in live root biomass) was less pronounced (Fig. 1b). In the site burned three times there was a slight, steady increase in dead root biomass through the growing season (Fig. 1c).

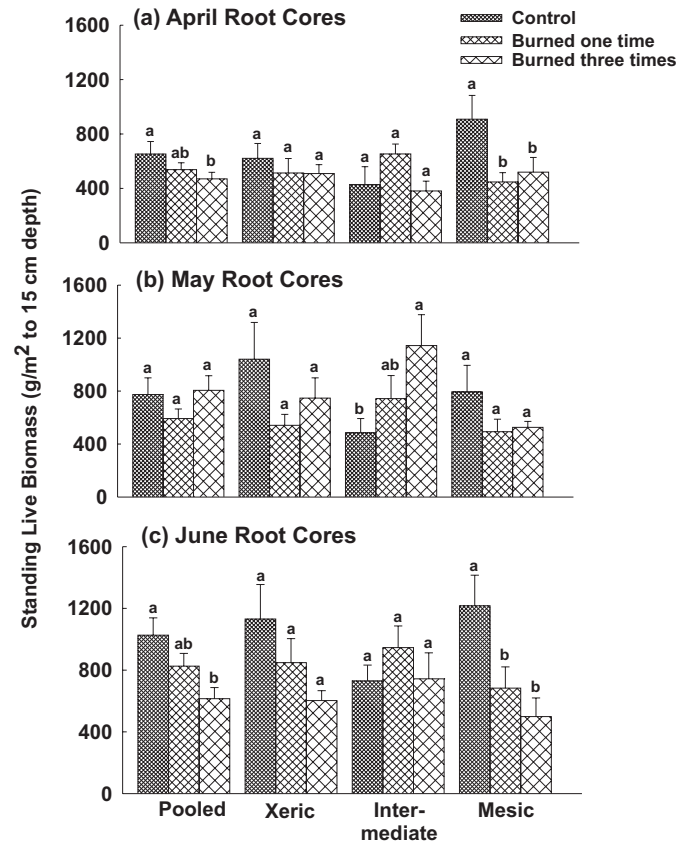
#### Effects of fire and landscape position on root biomass

In April, May, and June there were significant interactive effects of burn treatment and IMI class on standing live root biomass (Table 2). In April there was a marginally significant ( $p < 0.057$ ) effect of fire on standing root biomass, with biomass decreasing in the following order: control ( $653 \pm 92 \text{ g/m}^2$ ) > the site burned one time ( $538 \pm 50 \text{ g/m}^2$ ) > the site burned three times ( $470 \pm 48 \text{ g/m}^2$ ). However, this fire effect was not consistent among IMI classes: standing root biomass was reduced significantly in the burned watersheds in the mesic IMI class plots but not in the xeric or intermediate IMI class plots (Fig. 2a). In May, standing live root biomass increased with increasing fire frequency in soils from the intermediate IMI class (Fig. 2b), but there were no significant variations among burn treatments in soils from the other two IMI classes.

The pattern of variation in standing root biomass in June was similar to that observed in April (Table 2). Overall there was a significant burn effect on standing live root biomass with root biomass decreasing with increasing fire frequency (Fig. 2c). Most of this significant burn effect resulted from the significantly greater biomass in the control than the two burned plots in the mesic IMI class soils (Fig. 2c).

There were no significant effects of either burn treatment or IMI class on standing root biomass during August and September (Table 2). In November, there were significant and independent effects of fire and IMI class on standing root biomass (Table 2). Standing root biomass was significantly lower at the site burned three times ( $863 \pm 100 \text{ g/m}^2$ )

**Fig. 2.** Standing live fine root biomass (mean  $\pm$  SE) for (a) April sequential cores, (b) May sequential cores, and (c) June sequential cores. Means were compared within IMI classes. Histogram bars with the same letter are not significantly different ( $p > 0.05$ ).



than both the control ( $1209 \pm 124 \text{ g/m}^2$ ) and site burned one time ( $1207 \pm 106 \text{ g/m}^2$ ) and greater in the xeric IMI class samples ( $1268 \pm 113 \text{ g/m}^2$ ) than in mesic IMI class samples ( $893 \pm 105 \text{ g/m}^2$ ; data not shown).

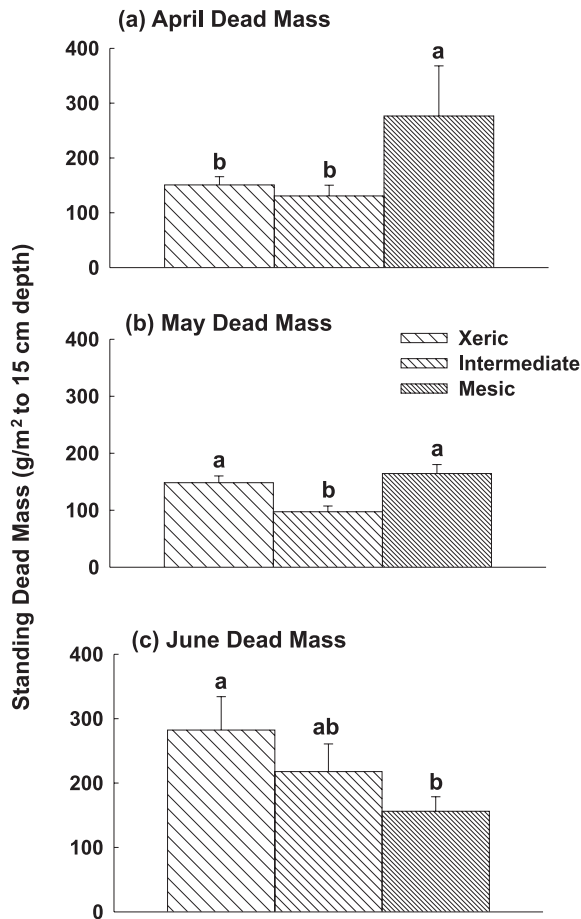
In contrast to live root biomass, where most differences we observed were among burn treatments, most differences in standing dead root mass were among IMI classes (Table 2). In April there was significantly greater dead root mass in the soils from the mesic IMI class plots than in soils from the xeric and intermediate IMI class plots (Fig. 3a). In May, dead root mass was significantly lower in intermediate class samples than in the other two IMI class soils (Fig. 3b). By June, this pattern had changed, such that standing dead root mass decreased with increasing IMI (Fig. 3c).

Overall, burning affected root biomass early and late in the growing season but not in midseason, with root biomass generally lower in the site burned three times than in the other two treatments. Where there was an effect of IMI class, live standing biomass tended to be greater in soils from the xeric IMI class than intermediate or mesic IMI classes.

#### Seasonal patterns of fine root production

In the unburned control,  $1292 \pm 131 \text{ g}$  of new roots were

**Fig. 3.** Standing dead root biomass (mean  $\pm$  SE) for (a) April sequential cores, (b) May sequential cores, and (c) June sequential cores. Histogram bars with the same letter are not significantly different ( $p > 0.05$ ).



produced between April 1998 and April 1999. Approximately 22% of that total was produced during the first half of the growing season (April–August), 51% during the latter half of the growing season (August–November), and 27% during autumn, winter, and early spring (November–April). We observed similar seasonal patterns of root ingrowth in the two burned plots.

During the April–August ingrowth interval there was no significant effect of burn treatment on new root production, but there was a significant effect of IMI class (Table 3). Root production was greatest in soils from the xeric IMI class and least in soils from the intermediate IMI class (Fig. 4a).

During the August–November interval there were significant and independent effects of burn treatment and IMI class on root production (Table 3). The greatest new root production during this interval occurred in soils from the site burned one time (Fig. 4b). Root production in the site burned one time exceeded that observed in the control and the site burned three times by 13% and 10%, respectively. As was the case for the April–August interval, fine root production was greatest in soils from the xeric IMI class during the August–November interval (Fig. 4b).

During the November–April interval there was once again no significant effect of burning on fine root production. However, there was a significant effect of IMI class and a

significant interaction between burning and IMI class on root production (Table 3). Once again, fine root production was greatest in soils from the xeric IMI class (Fig. 5). In intermediate IMI class soils, fine root production was significantly greater in the site burned one time than in the control and the site burned three times (Fig. 5). In contrast the pattern was reversed in the xeric and mesic IMI class soils, but differences among IMI classes were not significant at  $p < 0.05$  (Fig. 5).

Fine root production was greatest between August and November. It was only during that interval that we observed a significant effect of burn treatment on root production, with production in the site burned one time exceeding that in the control and the site burned three times. Fine root production was consistently greater in the xeric IMI class soils than in the intermediate or mesic IMI class soils.

### Comparison of standing root biomass and production

To gain insight into how root production, mortality, and standing crop were affected by the burn treatments, we compared root production estimated from the ingrowth cores for each time interval to the net difference in the standing crop of dead and live roots over that interval. (To avoid confounding temporal and spatial variations in standing root biomass, net change in standing crop was estimated simply as the difference between the overall mean standing crops at the beginning and end of each interval (Raich and Nadelhoffer 1989).)

During the April–August interval, total root production, as measured by ingrowth, varied little among burn treatments. Of the roots produced during that time interval, approximately two-thirds remained alive to the end of the interval, and one-third died during that time interval in all three treatments (Fig. 6a). Based on comparison of the 95% confidence interval for root production to the change in standing crop over the same time interval, total root production and net live root production both exceeded the net changes in total and live standing crop in the control and the site burned one time but not in the site burned three times (Fig. 6a). In the site burned three times the net change in live root standing crop in sequential cores was similar to the net production of live roots in ingrowth cores, whereas in the control and the site burned one time, net change in live standing crop was only 21–29% of net production (Fig. 6a).

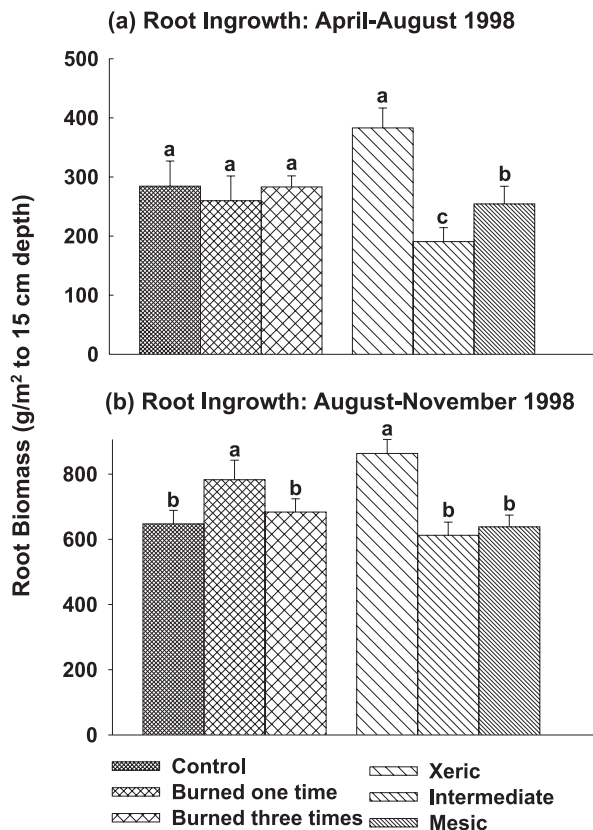
In soils from the site burned three times there was no significant net change in the standing crop of dead roots between April and August, suggesting that rates of mortality and decomposition were similar in this plot during this time period. In contrast, there was considerable net accumulation of dead root biomass in the control and the site burned one time, suggesting that either mortality was greater or decomposition lower (or both) in the control and the site burned one time than the site burned three times (Fig. 6a).

During the August–November interval, the rate and variation among burn treatments in net live and dead root production remained the same but the pattern of variation in the net difference in standing live and dead root biomass was reversed. During this later time interval, the net difference in standing live root biomass in the control and the site burned one time was similar to the rate of net new live root production estimated from the ingrowth cores (Fig. 6b). In contrast,

**Table 3.** Analysis of variance *p* values for new root production ( $\text{g/m}^2$  to 15 cm depth) in an Ohio oak–hickory forest during three ingrowth periods.

Month	Full model	Burn treatment	IMI class	Interaction
<b>Live roots</b>				
April 1998 – August 1998	<0.002	ns	<0.001	ns
August 1998 – November 1998	<0.001	<0.021	<0.026	ns
November 1998 – April 1999	<0.009	ns	<0.001	<0.015
<b>Dead roots</b>				
April 1998 – August 1998	<0.054	ns	<0.007	ns
August 1998 – November 1998	<0.005	<0.039	<0.056	ns
November 1998 – April 1999	<0.008	<0.036	ns	<0.007

**Note:** For each sampling date,  $N = 15$  for burn treatment and IMI class comparisons. ns, not significant.

**Fig. 4.** Root production (mean  $\pm$  SE) into ingrowth cores for (a) April–August 1998 and (b) August–November 1998. Histogram bars with the same letter are not significantly different ( $p > 0.05$ ).

the net difference in standing live root biomass from August to November in the site burned three times was only 9% of net live root production (Fig. 6b). Similarly, there were net decreases in standing dead root biomass during this interval in the control and the site burned one time, and a net increase at the site burned three times; again this pattern was the reverse of what was observed between April and August.

When the rate of new root production and the differences in standing crop were summed over the April–November growing season, the differences among burn treatments were no longer apparent (Fig. 7). In all three treatments, the net differences in live and dead standing crop between April and November were smaller than the total live and dead root production during that period. Although it appeared that the

change in standing crop of dead roots decreased with increasing fire frequency, and that the change in standing crop of live roots was less in the site burned three times than in the other two sites, we could find no way to test these differences statistically without confounding spatial differences and temporal change.

## Discussion

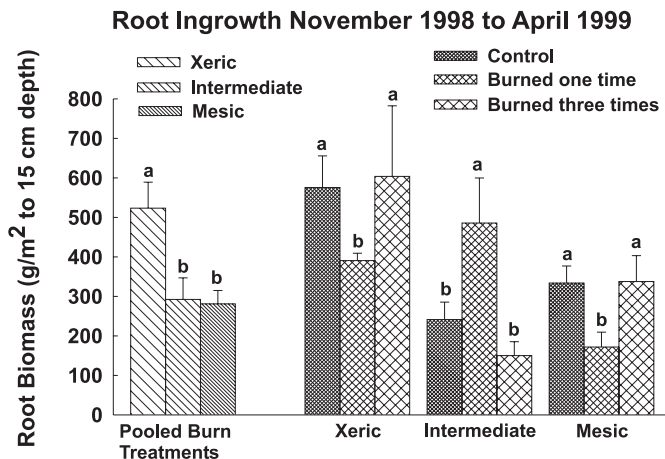
Seasonal average standing live fine root biomass was approximately  $940 \text{ g/m}^2$  in the control compared with  $805 \text{ g/m}^2$  in the site burned one time and  $765 \text{ g/m}^2$  in the site burned three times. These values are approximately two times greater than published values for annual leaf litter fall in similar forests in Ohio ( $330\text{--}500 \text{ g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ; Boerner and Kooser 1989). If fine roots are the belowground counterpart to aboveground leaf biomass (i.e., the biomass that is produced and turns over on a yearly interval), then our data indicate that plants in this system allocate twice the C to belowground structures as to aboveground structures. However, this assumes that all the fine root biomass turns over in 1 year. We defined a fine root as one  $<2 \text{ mm}$  diameter, whereas other studies of root turnover in forests indicate that the size class of roots that turn over on a yearly basis may be somewhat smaller (e.g.,  $<0.3 \text{ mm}$ ; Pregitzer et al. 1997).

One of our objectives was to quantify seasonal patterns of fine root standing biomass and production. We found two major peaks in live standing biomass during the growing season: the first early in the growing season and the second late in the growing season. In the unburned control and the site burned one time the early peak was in June, while in the site burned three times the early peak was in May. In southern Ohio, full canopy closure typically occurs by middle to late May (Wolfe et al. 1949). Thus, the spring peak we observed likely corresponds to the peak in root production prior to canopy closure that has been reported in similar studies (e.g., Coté et al. 1998). Although we did not observe changes in standing biomass until May and June, we feel this may be due to a time lag between initial spring changes in root production and mortality and corresponding changes in the standing pools of live and dead roots.

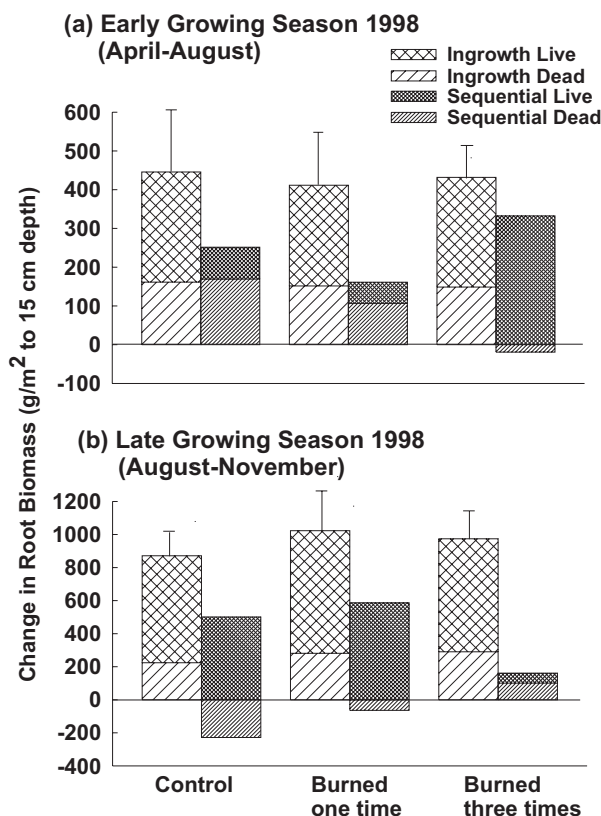
There was a decrease in live root biomass in midsummer following the early season peak in all three treatments studied. Midsummer is often a period of reduced precipitation and increased evapotranspiration in our study area (Wolfe et al. 1949). This decrease in live root biomass was observed in the June sample in the site burned three times and the Au-



**Fig. 5.** Root production (mean  $\pm$  standard error) into ingrowth cores from November 1998 to April 1999. Histogram bars with the same letter are not significantly different ( $p > 0.05$ ).



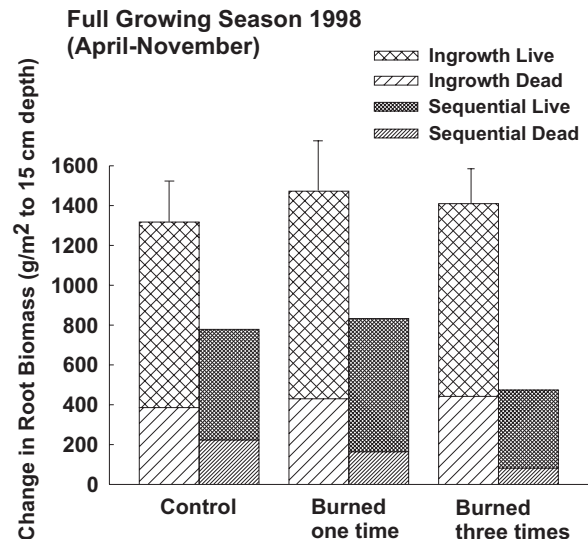
**Fig. 6.** Comparison of live and dead root production into ingrowth cores with the change in live and dead standing fine root biomass over the same interval for (a) April–August 1998 and (b) August–November 1998. Error bars are the 95% confidence interval. No error bars could be calculated for the sequential histograms, since they represent the change in mean standing biomass from April to August 1998.



gust sample in the site burned one time and the control because of a time lag between decreased root production and biomass accumulation.

The increases in root production we observed in the latter part of the growing season may have been due to opportunis-

**Fig. 7.** Comparison of live and dead root production into ingrowth cores with the change in live and dead standing fine root biomass over the same interval from November 1998 to April 1999. Error bars are the 95% confidence interval. No error bars could be calculated for the sequential histograms, since they represent the change in mean standing biomass from April to November 1998.



tic root growth following the return of favorable conditions, such as increased autumn precipitation and decreased evapotranspiration in our region (Kavanagh and Kellman 1992). Côté et al. (1998) and Hendrick and Pregitzer (1996) have also observed two peaks in root production and biomass accumulation in maple-dominated ecosystems.

Burning affected standing root biomass early in the season and in late autumn. In the April, June, and November sampling dates, live fine root biomass was significantly lower in the site burned three times than the control. In contrast, there were no direct effects of burning on dead root biomass.

Most other studies of the effects of prescribed burning on root dynamics have taken place in prairie and grassland ecosystems. Benning and Seastedt (1997) found greater root length in burned prairies in the first year of their study but not the subsequent 3 years. There was also an increase in total root biomass in their burned plots (Benning and Seastedt 1997). They attributed the increase in root length and biomass to a decrease in N availability following burning (Seastedt et al. 1991). Prescribed burning in our oak–hickory dominated ecosystem has resulted in an increase in N mineralization (Boerner et al. 2000), the opposite of what was observed in the prairie. Thus, if there is a strong causal link between N mineralization and root biomass it is logical we should observe a decrease in root biomass when Benning and Seastedt (1997) observed an increase.

Our results become more comparable with results from prairie ecosystems if the landscape position of each plot within each of our treatment watersheds is considered. At Arch Rock, fire intensity was significantly greater in the xeric and intermediate IMI class plots than in the mesic plots (Boerner et al. 2000). These variations in fire intensity resulted in differences among IMI classes in the belowground response to fire. Specifically, Boerner et al. (2000) observed a net, fire-induced increase in N mineralization the mesic

IMI class plots and a significant decrease of similar magnitude in the intermediate IMI class plots but no significant change in the xeric plots (Boerner et al. 2000). In the two burned plots, we observed the greatest live standing root biomass in the soils of the intermediate IMI class plots, the plots in which Boerner et al. (2000) reported the greatest decrease in N mineralization. In the control plots, soils from the xeric and mesic IMI class plots had greater standing live root biomass and lower N mineralization rates than did the intermediate IMI class plots. These data suggest that prescribed burning can alter root biomass in ways that correlated well with changes in nutrient dynamics, particularly N mineralization, just as has been shown for prairie sites in the past (Benning and Seastedt 1997).

An indirect effect of the burning treatments on root dynamics was the shift we observed in the seasonal phenology of root biomass accumulation. The early season peak in root biomass in the site burned three times was in May, 1 month earlier than the peak in root biomass observed in the control and the site burned one time. This pattern was also evident when changes in mean monthly standing biomass were compared with root production estimated from ingrowth cores. During the April to August interval, there was a net accumulation of live roots in soils from the site burned three times that was similar in magnitude to the estimate of new root production from the ingrowth cores. However, the soils from the control and the site burned one time showed no net accumulation of live roots but rather a net accumulation of dead roots over the same interval. This pattern was reversed during the August–November interval; there was a net accumulation of live roots in soils from the control and the site burned one time and no net accumulation of live roots from the site burned three times. Over the entire growing season, there was no apparent difference in net accumulation of live or dead roots among the burn treatments, indicating that the differences observed were simply the result of a temporal shift in belowground productivity.

The onset of root production in the spring is controlled by soil temperature (Hendrick and Pregitzer 1993a, 1996). During 1999, soil temperature was consistently 1.5–2.0°C higher in the site burned three times compared with the control (L. Iverson, unpublished data). An earlier increase in soil temperature in the site burned three times likely initiates earlier root production and a shift in the seasonal phenology of root biomass.

Past studies conducted in the greenhouse under optimal moisture and nutrient conditions indicate that root growth increases with increased soil temperature (Gregory 1986; McMichael and Quisenberry 1993). Under field conditions, the relationship between soil temperature and root growth is more complex since other factors such as soil moisture can also affect root growth. Both root elongation and the number of growing roots in white oak was related to the interaction between soil temperature and soil moisture that created optimum growing conditions (Teskey and Hinckley 1981). Hendrick and Pregitzer (1993b) found that a southern sugar maple forest in Michigan had more rapid root growth and lower longevity (i.e., faster turnover) than a northern sugar maple forest and these differences were attributed to higher soil temperatures at the southern site. Finally, Fitter et al. (1998, 1999) have reported similar results from a grassland

ecosystem in which soil temperature was increased by 3°C with heat lamps. These studies indicate that soil temperature can influence root production and mortality (i.e., turnover) while not necessarily affecting standing root biomass. Few prior studies have explicitly investigated the effect of temperature changes on the phenology of root production, despite a wide variety of studies of the effect of increased soil temperature on other plant and ecosystem processes, e.g., leaf expansion (Chapin and Shaver 1996; Farnsworth et al. 1995) and reproductive phenology (Price and Waser 1998). The results of our study clearly suggest that soil warming can alter the phenology of fine root production as well as these other plant processes.

Since the site burned one time was burned in 1996 (two years prior to our sampling), comparing this site with the site burned three times (including the month before our sampling began) can help demonstrate how long the effects of the prescribed burns can persist. The seasonal pattern of fine root biomass in the site burned one time was more similar to the control than the site burned three times. This indicates that the 2-year interval between the fire in the site burned one time and the root sampling for this study was sufficient for the soil temperature regime to return to prefire levels. Consistent with this assertion, forest floor sampling done in 1998 failed to find any difference in the mass of leaf litter on the forest floor in the unburned control and the site burned one time (T.F. Hutchinson, unpublished data). Similarly, in the April and June samples, when we observed significantly greater standing live biomass in the control soils than the soils from the site burned three times, root biomass in soils from the intermediate IMI class plots of the site burned one time was not significantly different than observed in the control. Thus, two growing seasons following prescribed fire appear to have been sufficient for root dynamics to return to prefire patterns.

Root production measured from ingrowth cores averaged 1292 g·m<sup>-2</sup>·year<sup>-1</sup> in the unburned control. This level of production was high compared with published data from other forested ecosystems (e.g., 241 g·m<sup>-2</sup>·year<sup>-1</sup> for roots <1 mm diameter in a northern hardwood forest at Hubbard Brook; Fahey and Hughes 1994). Whittaker (1975) estimated that net primary production in temperate deciduous forests averaged 1250 g·m<sup>-2</sup>·year<sup>-1</sup> with a range from 600–2500 g·m<sup>-2</sup>·year<sup>-1</sup>. If fine root production is approximately 50% of NPP, our forests are close to the upper limit described by Whittaker (1975). The large differences in estimates of root production between our Allegheny Plateau sites and the northern hardwood sites at Hubbard Brook may be, at least to some degree, due to differences in soil depth or fertility, growing season length, tree biomass, and climate between these two areas.

One weakness of the ingrowth core method is that these cores provide an optimum growing environment for roots. Simply providing a volume of root-free soil would be expected to increase the amount of root growth into this relatively low competition and low compaction environment (Vogt et al. 1998). Also, the mechanical sieving of the soil is likely to increase the nutrient availability and water holding capacity of the soil (Vogt et al. 1998). While the absolute mass of fine roots from ingrowth cores cannot be used as a precise measure of belowground productivity, we do feel that the ingrowth cores do provide reliable estimates of the



patterns of belowground production for use in determining differences among treatments.

There was greater new root production in the xeric plots than either the intermediate or mesic plots. This was consistent in all three sampling intervals and among burn treatments. Live standing biomass was significantly greater in the xeric IMI class plots only in the November sample. However, there was a trend throughout the season for greater standing live biomass in the xeric and intermediate IMI class soils.

Numerous studies comparing upland and lowland sites have found greater root biomass in xeric sites (pine barrens: Ehrenfeld et al. 1992; lodgepole pine (*Pinus contorta* Dougl. ex Loud.): Comeau and Kimmins 1989; Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco): Keyes and Grier 1981; temperate *Pinus* forests in Japan: Enoki et al. 1996). While it is likely that moisture is important in generating these patterns, it is also probable that nutrient availability plays an important role. In the plots at Arch Rock, pH, N mineralization, Ca:Al ratio,  $\text{NH}_4^+$ , and  $\text{NO}_3^-$  are significantly lower in xeric than mesic plots (Boerner et al. 2000), and other studies have demonstrated close correlations between inorganic N concentration in the soil solution and soil water content (e.g., Yin et al. 1993).

Prescribed burning affected fine root dynamics by increasing early spring soil temperature and altering soil nutrient availability. Increased soil temperature after burning shifted the phenology of root biomass accumulation earlier in the growing season. New root production measured from ingrowth cores was greater in xeric soils than intermediate or mesic soils. The effect of prescribed burning on standing root biomass was dependent on landscape position. In intermediate IMI class plots, where burning decreased N mineralization, standing live biomass was greater in the burned plots. That differences in root biomass can be observed 2 years following a prescribed fire indicates that burning can have at least transient effects on belowground dynamics in forested ecosystems.

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