Oecologia
DOI 10.1007/s00442-007-0733-z

ECOPHYSIOLOGY

Effects of fire alone or combined with thinning on tissue nutrient concentrations and nutrient resorption in *Desmodium nudiflorum*

Jianjun Huang · Ralph E. J. Boerner

Received: 13 October 2006 / Accepted: 16 March 2007
© Springer-Verlag 2007

Abstract This study examined tissue nutrient responses of *Desmodium nudiflorum* to changes in soil total inorganic nitrogen (TIN) and available phosphorus (P) that occurred as the result of the application of alternative forest management strategies, namely (1) prescribed low-intensity fire (B), (2) overstory thinning followed by prescribed fire (T + B), and (3) untreated control C), in two *Quercus*-dominated forests in the State of Ohio, USA. In the fourth growing season after a first fire, TIN was significantly greater in the control plots (9.8 mg/kg) than in the B (5.5 mg/kg) and T + B (6.4 mg/kg) plots. Similarly, available P was greater in the control sites (101 μg/g) than in the B (45 μg/kg) and T + B (65 μg/kg) sites. Leaf phosphorus ([P]) was higher in the plants from control site (1.86 mg/g) than in either the B (1.77 mg/g) or T + B plants (1.73 mg/g). Leaf nitrogen ([N]) and root [N] showed significant site–treatment interactive effects, while stem [N], stem [P], and root [P] did not differ significantly among treatments. During the first growing season after a second fire, leaf [N], stem [N], litter [P] and available soil [P] were consistently lower in plots of the manipulated treatments than in the unmanaged control plot, whereas the B and T + B plots did not differ significantly from each other. N resorption efficiency was positively correlated with the initial foliar [N] in the manipulated (B and T + B) sites, but there was no such relation in the unmanaged control plots. P resorption efficiency was positively correlated with the initial leaf [P] in both the control and manipulated plots. Leaf nutrient status was strongly influenced by soil nutrient availability shortly after fire, but became more influenced by topographic position in the fourth year after fire. Nutrient resorption efficiency was independent of soil nutrient availability. These findings enrich our understanding of the effects of ecosystem restoration treatments on soil nutrient availability, plant nutrient relations, and plant–soil interactions at different temporal scales.

Keywords Fire · Herb · Nitrogen · Nutrient resorption · Phosphorus · Thinning

Communicated by Hormoz BassiriRad.

J. Huang (✉) · R. E. J. Boerner
Department of Evolution, Ecology, and Organismal Biology, Ohio State University, 318 West 12th Avenue, Columbus, OH 43210, USA
e-mail: huang.404@osu.edu

Introduction

Dormant season fire and alteration of the woody plant assemblage have been used in many ecosystems for forest management and restoration. Although such management activities typically focus on vegetation and vertebrate animals, prescribed fire can also affect soil characteristics in a variety of ways, depending on the intensity of the fire, microclimate, and time interval between fires. In deciduous forests of eastern North America, fire usually decreases long-term soil nutrient availability through volatilization, leaching, and vigorous plant uptake, whereas over the short term, the availability of many nutrients (especially nitrogen, N) may increase, usually as a result of stimulating N mineralization (Raison 1979; Boerner 1982). In the strongly dissected and complex landscapes of the Appalachian Mountains of eastern North America, the interactions of fire behavior and landscape structure produce complex patterns of short-term fire effects and may not, therefore, be

predictable on an a priori basis in all cases (Boerner et al. 2000).

Consistent with the short-term effect of fire on soil nutrient availability being somewhat site-specific, empirical studies have provided conflicting results on the effects of fire on plant tissue nutrient concentrations after a fire (Christensen 1977; Boerner 1986; Reich et al. 1990; Kruger and Reich 1997; Adams and Rieske 2003). Dormant season treatments usually do not affect herbaceous perennial plants until those plants emerge the following spring and are exposed to the changes in resource availability caused by the dormant season treatments. Plants are assumed to respond to the altered light and soil conditions by altering tissue nutrient concentrations and nutrient resorption efficiency; however, inconsistent results among studies make it impossible to draw a general conclusion on how tissue nutrient concentrations change in the aftermath of fire.

Nutrient resorption from senescing leaves is of considerable adaptive significance (Aerts 1990; Boerner 1986; Chapin and Moilanen 1991). The nutrients that are resorbed during senescence are directly available for further plant growth, thus making the plant less dependent on current nutrient uptake (Aerts and Chapin 2000). Forest management activities may result in altered nutrient availability, and hence act as a selective pressure on plant nutrient conservation strategies (e.g., resorption efficiency); however, little is known about the impact of these management treatments on nutrient resorption efficiency (but see Latty et al. 2004).

Studies examining relationship between soil nutrient availability and foliar nutrient resorption have provided mixed results. Some report that N and/or phosphorus (P) resorption efficiency were greater on sites low in nutrient availability (Boerner 1984; Shaver and Mellillo 1984; Aerts and Caluwe 1994), while others report weak or non-existent relationships between nutrient resorption efficiency and soil nutrient availability (Schlesinger et al. 1989; Bowman et al. 1995). In contrast, resorption efficiency was generally assumed to decline with increasing leaf nutrient status, both within and among species (Kobe et al. 2005). If fire were to increase soil nutrient availability and foliar nutrient concentration, and nutrient resorption efficiency was inversely related to soil nutrient availability, we should expect nutrient resorption efficiency to decrease after fire.

Although a considerable body of literature exists on the effects of fire on soil characteristics (reviews by Ice et al. 2004; Boerner 2006) and on plant responses to fire, few studies have employed experimental approaches that permit the simultaneous evaluation of the effects of prescribed fire and overstory thinning on soil nutrient availability, plant tissue nutrient concentrations, nutrient resorption efficiency, and the linkages among them. Thus, the specific objectives of this study were: (1) to examine the effects of prescribed fire alone or combined with thinning on soil nutrient availability and nutrient status in *Desmodium nudiflorum* at several spatial and temporal scales, and (2) to relate plant nutrient concentration and nutrient resorption efficiency with soil total inorganic nitrogen (TIN), available P and topographic position.

Material and methods

Study sites and plant species

This study was carried out in the mixed oak forests of Zaleski State Forest (82°37′W, 39°35′N) and the Raccoon Ecological Management Area (REMA) (82°39′W, 39°20′N) study sites on the unglaciated Allegheny Plateau of southern Ohio, USA. The climate of the region is cool, temperate and continental, with a mean annual temperature of 11.3°C and annual precipitation totaling 1024 mm. The sites are underlain predominantly by sandstones and shales of Pennsylvanian Age. Soils are mostly loams and silt loans that are acidic and well drained (Sutherland and Hutchinson 2003). These sites are typical of oak-dominated stands in the eastern deciduous forest of North America.

Desmodium nudiflorum (L.) DC (Fabaceae), a native perennial legume, was selected because it was abundant in the study areas (frequency was >40%, Hutchinson et al. 2005) and occupied habitats across the light and nutrient gradients produced by the strongly dissected landforms. The aboveground parts senesce during the autumn, and leaves typically do not emerge until May. Dormant season (March–April) low-intensity fire generally has no direct effect on *D. nudiflorum* plants since little or no heat produced by the fires penetrates into the mineral soil to the depth where the overwintering buds and rootstocks are. Mature plants produce a whorl of trifoliate leaves, each 5–10 cm long. Plants usually have one infertile and one or two fertile stems. Adult plants of *D. nudiflorum* range in height from 13 to 30 cm, with a plant dry biomass of approximately 4 g. In the field, flowering starts in early August. Each flower is short-lived, but within an inflorescence, flowers can develop sequentially. Loments form in late August, and two to three seeds are usually produced per loment. Each plant can produce 2–50 seeds. One half of the seeds commonly have under-developed embryos (the embryo is flat and shorter than half of the seed length). A fully developed seed weights approximately 10 mg. Fruit coats are covered with abundant sticky trichomes, which facilitate seed distribution by sticking to animals' fur.

Field methods

The study sites were part of larger Ohio Hills Site of the National Fire and Fire Surrogate Network Study (FFS; http://www.ffs.fed.us). The original experiment design has randomly assigned control (C), burn (B), thin (T), and thin plus burn (T + B) units of 20–30 ha each in three areas of southern Ohio (Tar Hollow State Forest, Zaleski State Forest, and the Raccoon Ecological Management Area) (n = 3 per treatment and n = 12 for the full study). Each treatment unit included the full range of topographic relief. Within each treatment unit, ten permanent 0.1-ha (20×50 m^2) plots were randomly chosen and permanently located by Global positioning system (GPS).

Each treatment unit was also divided into cells of 30×30 m^2, and each cell within each treatment unit was assigned a landscape position metric derived from a Geographic Information System (GIS)-based integrated moisture index (hereafter, IMI) developed by Iverson et al. (1997) for this region. Soil moisture levels are higher where direct solar radiation is minimized, in lower positions on slopes or in depressions, and in soils capable of storing large amounts of water. Therefore, the IMI scores were achieved through integration of elevation, aspect, hill shade profile, solar radiation potential, downslope flow accumulation, soil depth, soil water holding capacity, and surface curvature profile (Iverson et al. 1997).

The T and T + B units were thinned during late fall 2000 and early spring 2001, and the B and T + B units were burned in early April 2001 and again in March 2005. Thinning from below removed an average of 27.9% of the basal area and left an average of 20.9 m^2/ha in residual basal area (D. Yaussy, USDA Forest Service, personal communication). Trees were cut by chainsaw, limbed at the felling site, and removed with rubber-wheeled skidders. Slash was broadcast across the study site to minimize the impact of the additional fine woody debris. No skid trails impacted the permanent sampling plots (Boerner et al. 2006). The low-intensity dormant season spring fires were heterogeneous within and across sites, but flames rarely exceeded 2 m in height. Fire consumed unconsolidated leaf litter and fine woody fuels while leaving the majority of the coarse woody fuels only charred.

For this study, we sampled three treatment units (control, B, T + B) in two of the study sites (Zaleski and REMA). From mid-July to late August 2004, we randomly chose seven to nine plots from the ten permanent plots in each unit. From early June to late July of the 2005 growing season, six plots were randomly chosen from the ten permanent plots in each unit. Within each plot, three to five plants of *D. nudiflorum* were selected using the following criteria: (1) plants were at least 8 m apart to avoid cluster effect, and (2) sampling newly emergent seedlings and individuals with two or more infertile stems was avoided. Each whole plant was carefully excavated and brought to the laboratory. Soil samples were taken at the same time as when the plants were sampled. Samples of approximately 100 g of mineral soil were taken by removing the unconsolidated litter layer (Oi, Oe) and sampling the underlying (fragmentary) Oa and well-developed A horizon with a trowel. Soils were sampled at each corner of the plots in 2004 and sampled near the target plant individuals in 2005. In order to collect fresh litter of *D. nudiflorum*, we bagged the leaves of at least four plants per plot using 2-cm mesh nylon bag from late August to early September in 2005. Litter harvest was coordinated with the peak of leaf drop of this herb in early November.

Nutrient resorption efficiency can be expressed either on a leaf area basis or mass basis. Since senescent leaves of *D. nudiflorum* quickly become folded and shrunken, the leaf area of the senescing leaves would be underestimated. Therefore, in estimating the percentage of N resorbed prior to leaf abscission, N was expressed per unit mass rather than per unit leaf area. Nutrient resorption efficiency from senescing leaves was calculated as:

$$\mathrm{NRE} = [(\mathrm{N_{ufre}} - \mathrm{N_{usen}})/\mathrm{N_{ufre}} \times 100$$

where NRE is nutrient resorption efficiency; $\mathrm{N_{ufre}}$ is the N (or P) concentration of fresh leaves sampled in 2005 summer; $\mathrm{N_{usen}}$ is the N (or P) concentration of leaf litter collected in November 2005.

Laboratory methods

Lamina, stem, rachis, and root were separated and oven-dried at 70°C for 2–3 days and then weighed. The dried lamina, stem (stem and rachis), and root were subsequently ground and digested using H_2SO_4 and H_2O_2. The soil samples were air dried for more than 1 week and passed though a 2-mm sieve. Subsamples of approximately 15 g were extracted in 40 ml of 0.5 *M* K_2SO_4 and then analyzed for NH_4^+ and NO_3^- using microtiter methods (Sims et al. 1995). Total inorganic N was calculated as the sum of NO_3^- and NH_4^+. As NH_4^+ and NO_3^- concentrations in these soils vary in parallel, with NH_4^+ comprising 70–100% of the inorganic N, we chose to represent inorganic N availability as the sum of the two ions. Soil and tissue P concentrations were determined using the stannous chloride method (APHA 1976).

Statistical analysis

All soil and plant variables were averaged for each plot, and plot means were then analyzed as response variables

using mixed-model (PROC MIXED) analysis of variance (ANOVA) (SAS Institute 2001). We considered 2004 as the fourth growing season after the first fire and 2005 as the first growing season after the second fire, and analyzed these independently instead of using repeated measures methods. Sampling site, treatment, and the interaction between these two factors were included as fixed effects. IMI scores were included as covariate. Plots, which represented the experiment units, were considered to be replications. Least square means were used to test for significant treatment differences. In the case where there was a significant treatment-by-site effect, a posteriori least squares mean separation with the Tukey correction was used to test for differences among treatments and years. Pearson correlations were employed to test the relationships between plant nutrient concentration and soil nutrient availability. Plant nutrient resorption efficiency was regressed on soil nutrient availability or initial leaf nutrient concentration by linear and quadratic regression.

Structural equation models were used to link the soil conditions and plant leaf nutrient concentration using AMOS 6.0 software (SPSS, Chicago, Ill.). Site and treatment were included as categorical variables with special care. Previous studies in this area have shown that many of the physiological responses of this herb to burning alone did not differ significantly from those to burning combined with thinning (Huang et al. 2007b). Therefore, the treatments were coded as 0 and 1 for control and fire manipulation (B and T + B), respectively. The maximum likelihood estimation method was used to estimate the goodness of fit.

Results

Treatment effects during the fourth growing season after first burning (2004)

There were significant treatment effects and treatment-by-site interactive effects on leaf [N] and root [N] (Table 1). At REMA, plants in control (C) plots had higher leaf [N] than those inT + B plots; in contrast, there were no such significant differences at Zaleski (Fig. 1a). T + B plants had higher root [N] than B plants at REMA (Fig. 1b). The leaf N:P ratio was similar among the different treatments at both sites; however, it tended to decrease after burning (with or without thinning) at REMA, while it tended to increase after the fire manipulation at Zaleski. The only significant difference was that B plants at Zaleski had a significantly higher N:P ratio than T + B plants at REMA (Fig. 1d). Leaf [P] was consistently higher in C plants than in either B or T + B plants, whereas plants from the latter two treatments did not differ significantly (Fig. 1c).

Soil nutrient pools also exhibited substantial differences among treatments. Soil TIN and available P were consistently higher in control plots than in B or T + B plots (Table 2). Despite significantly reduced soil nutrient availability after treatment, stem [N], stem [P], and root [P] did not differ significantly among treatments (Table 1).

Table 1 Results of ANCOVAs[a] comparing the effects of different silvicultural treatments on soil nutrient availability and plant nutrient concentration

Parameter	Fourth growing season after fire			First growing season after second fire		
	Treatment	Treatment–site interaction	IMI covariate[b]	Treatment	Treatment–site interaction	IMI covariate
Leaf N	4.03*	6.04**	15.25***	27.55***	1.11	0.79
Stem N	0.44	2.57	3.07	4.35*	1.39	1.25
Root N	4.92*	3.47*	2.79	0.16	0.11	0.07
Leaf P	3.34*	1.11	11.88***	21.53***	3.33*	0.39
Stem P	1.29	0.57	1.98	4.06*	4.43*	0.14
Root P	0.82	1.87	1.41	2.50	2.71	2.72
Leaf N:P ratio	0.58	7.14**	0.29	0.47	1.01	0.01
Total inorganic N	6.60**	2.30	10.28**	5.12*	4.02*	3.41
Available P	4.63*	2.78	0.32	7.91**	1.42	2.44
Soil N:P ratio	1.18	1.18	3.96	0.16	1.82	0.16

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

[a] The F values are presented for effects of treatment, treatment–site interaction and the IMI covariate. Plants were sampled in 2004 (fourth growing season after fire) and 2005 (first growing season after second fire)

[b] IMI, Integrated moisture index

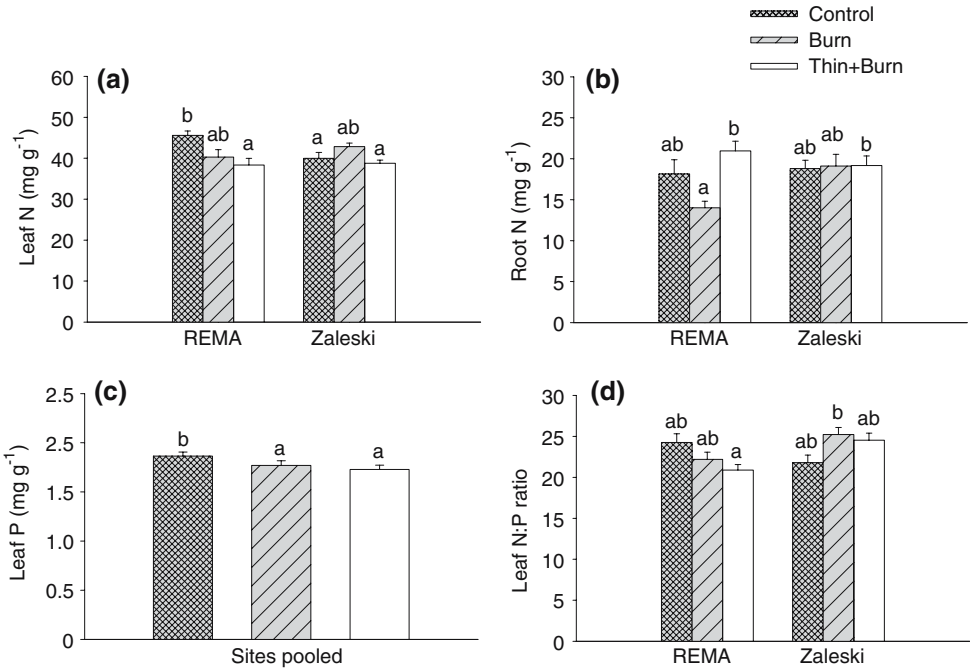

Fig. 1 Effects of silvicultural treatments in 2004 on leaf N (**a**), root N (**b**), leaf P (**c**), and leaf N:P (**d**) in two southern Ohio (USA) forests. Means and SE are given. *Bars with different letters* are significant different at Tukey-adjusted $P < 0.05$. When treatment–site effects were not significant, data from the two sites were pooled

Table 2 Responses of soil nutrient availability to different silvicultural treatments[a]

Treatment	Fourth growing season after fire		First growing season after second fire		
	Total inorganic N (mg/kg)	Soil P (μg/kg)	Total inorganic N (mg/kg)		Soil P (μg/kg)
			REMA	Zalaski	
C	9.75(1.12) b	100.70(19.60) b	22.49(3.44) b	22.74(4.61) ab	609.8(74.9) b
B	5.52(0.68) a	45.19(6.25) a	11.91(2.19) ab	14.91(1.62) ab	339.8(21.8) a
T + B	6.39(0.91) a	65.19(7.71) ab	20.67(3.39) ab	8.58(0.96) a	361.9(43.5) a

[a] Data are given as the mean and standard error (in parenthesis). When treatment–site interactions were not significant, the two different sites were pooled. Since total inorganic N (TIN) in 2005 was significantly affected by the treatment–site interactions, means with SE for each site are presented. Different letters in each column indicate significant differences ($P < 0.05$)

Treatment effects during the first growing season after repeated burning (2005)

C plants had higher leaf [N] and litter [P] than both B and T + B plants (Figs. 2a, 3b). Similarly, stem [N] was greater in C plants than in B plants (Fig. 2b). Litter [N], Leaf [P], stem [P], and soil TIN were all affected significantly by the interactive effect of treatment and site during the first growing season after the second fire (Tables 1, 3). At REMA, litter [N] was higher in C plants than in plants from the other two treatments, and C plants had higher leaf [P] than B plants; however, stem [P] and soil TIN were not affected significantly by the treatments at REMA. At Zaleski, litter [N] and soil TIN were not affected significantly by the second fire. In contrast, T + B plants had lower leaf [P] and stem [P] than C plants (Fig. 2). Across these two study sites, leaf [N], stem [N], litter [P] and available soil [P] were consistently lower in plots from manipulated treatments than in those of the unmanaged control, whereas plots from B to T + B did not exhibit significant fire effects.

N resorption, P resorption, root [N], root [P], and the leaf N:P and soil N:P ratio were not affected significantly by treatment, site, and/or IMI (Tables 1, 3). However, we found that the manipulative treatments changed the relationship between N resorption rate and initial leaf [N]. In the unmanaged control plots, there was no significant relationship between N resorption rate and initial leaf [N]. In contrast, N resorption efficiency was positively correlated with the initial foliar [N] in the manipulated (B and T + B) sites [N resorption (%) = –17.6 + 1.88 N (mg/g), $r^2 = 0.322$, $P = 0.004$]. When all plots were pooled, there was a significant quadratic trend ($P = 0.014$, Fig. 4a).

When B and T + B plots were pooled, P resorption efficiency was positively correlated with the initial leaf [P] in the manipulated plots. In C sites (when one plot near

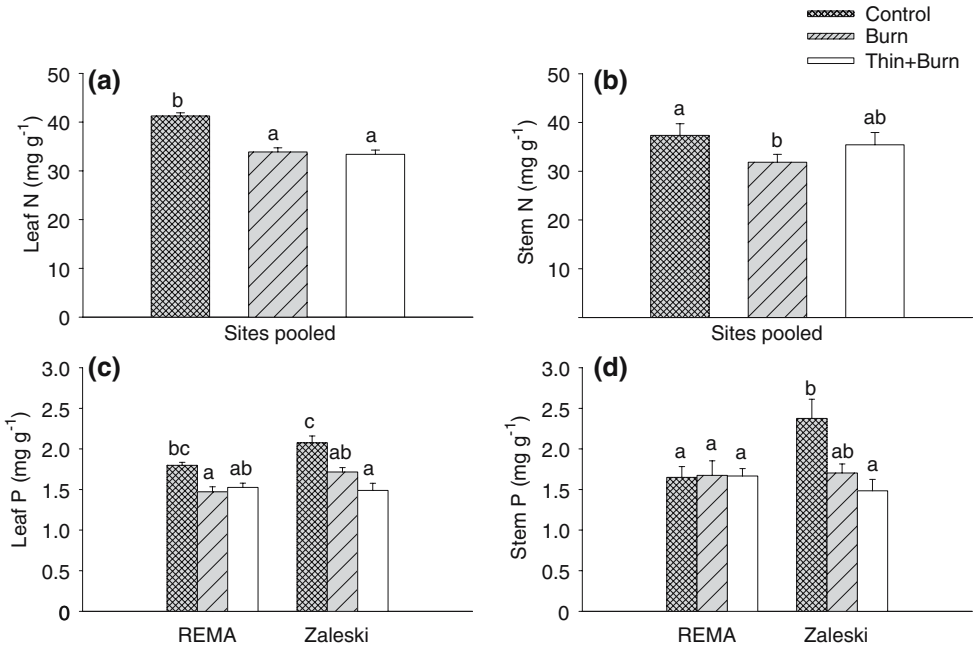

Fig. 2 Effects of silvicultural treatments in 2005 on leaf N (**a**), stem N (**b**), leaf P (**c**), and stem P (**d**). See Fig. 1 for details

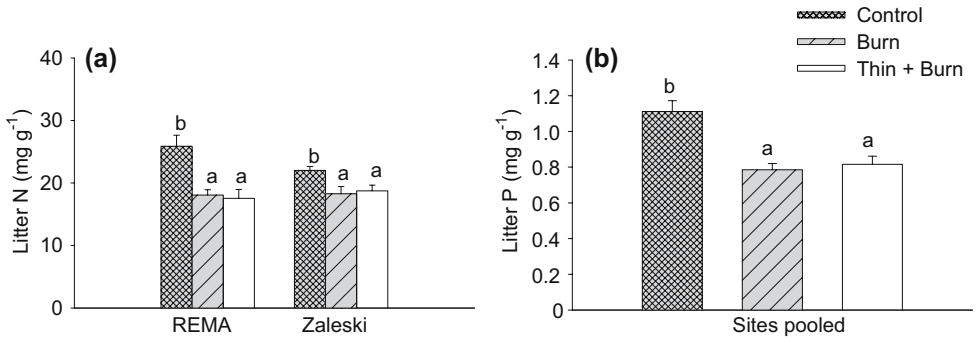

Fig. 3 Effects of silvicultural treatments in 2005 on litter N (**a**), litter P (**b**). See Fig. 1 for details

ridge that appeared to be an outlier was removed) we also observed similar positive correlation. However, at any given leaf [P], P resorption efficiency was lower in C plots where light was more limited, and the manipulated plots were visually separated from the C plots on the efficiency/availability graph (Fig. 4b). Moreover, N resorption efficiency and P resorption efficiency were positively correlated ($P < 0.001$, Fig. 4c).

Linkage between soil conditions and plant leaf nutrient concentration

Plant nutrient concentration, especially leaf nutrient concentrations, were strongly and significantly correlated with soil TIN and available P (Table 4). During the fourth growing season following the first fire, leaf [N], and [P] were strongly correlated with IMI, and leaf [N], leaf [P], and root [P] were strongly correlated with soil TIN. In contrast, during the first growing season after the second fire, IMI was not significantly correlated with any leaf nutrient parameters, whereas soil TIN and available P were still highly correlated with leaf [N] and [P].

N and P resorption efficiencies were not significantly correlated with soil nutrient availability, either when all sites were pooled or when each treatment was considered individually (Table 4; Fig. 4d, e). In addition, leaf [N] and [P] resorption were not significantly correlated with IMI (Tables 3, 4).

We utilized structural equation modeling to further clarify the effects of fire, site, and pre-treatment landscape position effects on post-treatment soil nutrient availability, leaf nutrient concentrations, and the links among them. In this model, we assumed that variations in soil nutrient availability were causally linked to variations in plant tissue nutrient concentrations. The hypothesized model provided a good fit to both long-term and short-term data (Fig. 5). In 2004, the fourth growing season after burning, plant tissue nutrient concentrations were strongly affected

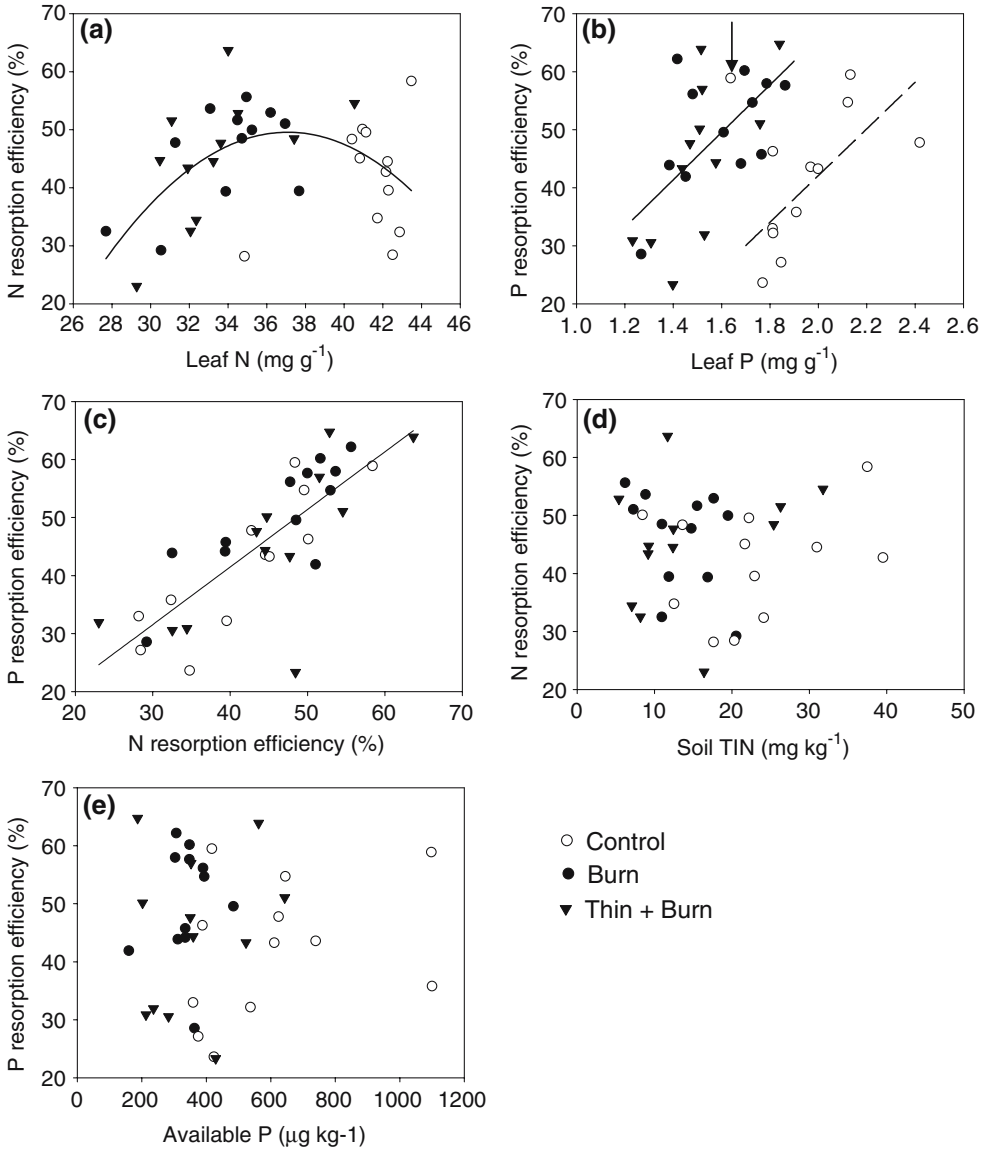

Fig. 4 Relationship between N resorption efficiency and leaf N (**a**), P resorption efficiency and leaf P concentrations (**b**), N resorption efficiency and soil TIN (**c**), P resorption efficiency and soil available P (**d**), and N resorption efficiency and P resorption efficiency (**e**). In **b**, for pooled B and T + B plots, P resorption (%) = –15.9 + 40.9 P (mg/g), r^2 = 0.387, P = 0.001. For the control plot only, when one outlier, as indicated by *arrow*, was removed, P resorption (%) = –38.3 + 40.2 P (mg/g), r^2 = 0.387, P = 0.017

by IMI, treatment, and site, but not by soil nutrient availability. The submodel for plant tissue nutrient concentrations was strong (r^2 = 0.93), and of those independent variables that were linked significantly with plant tissue nutrient concentrations, IMI had the greatest standardized regression weight (b = 0.81). The submodel for soil nutrient availability in 2004 was not as strong as the plant tissue submodel (r^2 = 0.43), and variations in soil nutrient availability were linked significantly to treatment and IMI but not site.

In 2005, the first growing season after the second fire, plant tissue nutrient concentrations were strongly affected by treatment and soil nutrient availability, but independent of both IMI and study site (model r^2 = 0.96). Thus, the strong linkage among landscape position (IMI), soil nutrient availability, and plant tissue nutrient concentrations we observed during the fourth year after the initial treatment was not present the first year after a second burning treatment.

Discussion

Soil nutrient availability

In our study, fire alone or combined with thinning reduced soil N and P availability, both in the short term (2 months after repeated fire) or over the long term (>3 year following a single fire). Previous studies have shown that fire often reduces long-term soil nutrient pools (Vance and Henderson 1984; Monleon et al. 1997). This reduction can be the result of direct volatilization, post-fire leaching of ash,

Table 3 Results of ANCOVAs[a] comparing effects of different silvicultural treatments on litter nutrient concentration and nutrient resorption efficiency

Parameter	First growing season after second fire		
	Treatment	Treatment–site interaction	IMI covariate
Litter N	15.00***	4.09*	4.73*
N resorption	0.50	2.54	1.53
Litter P	13.33***	1.71	4.31*
P resorption	1.63	1.69	1.88

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

[a] The F values are presented for effects of treatment, treatment–site interaction and IMI covariate

altered soil surface microclimate, and changes in soil microbial activity. In contrast, low-intensity ground fire may have a positive effect on short-term nutrient availability or, in some cases, no detectable effect at all (Boerner 1982, 2006). Fire increases soil temperature through its effect on surface conditions, and it stimulates post-fire microbial N fixation and mineralization, all of which may increase soil N availability (Raison 1979; Boerner 1982; Wan et al. 2001). In addition, inorganic N can also be released directly to soil when the fire temperature is not high enough to result in direct volatilization. Thus, if nutrient availability did increase following either of the fires in our study sites, any increases that did occur must have disappeared within 2 months.

In southern Appalachian oak-hickory forests, the consequences of burning on TIN are determined by the site-specific circumstances under which burning occurred. Boerner et al. (2000) found that both fire behavior and landscape position had major impacts on post-fire soil N. At a site which burned at relatively greater intensity, soil N mineralization and TIN both decreased after fire, whereas at a less intensely burned site, fire resulted in increased TIN in the soils in some landscape positions. These authors concluded that the pattern and magnitude of change in soil inorganic N may be determined by complex interactions among site (landscape) factors and fire behavior, and may not, therefore, be predictable on an a priori basis in all cases.

Plant nutrient concentration

Fire can affect plant nutrient status through changes in soil nutrient availability, canopy light penetration and direct damage to the root system. Many previous studies have shown that fire either increased or had no effects on foliar nutrient concentrations (Christensen 1977; Gilliam 1988; Reich et al. 1990; Kruger and Reich 1997; Adams and Rieske 2003). In contrast, our results showed that fire alone or combined with thinning decreased the foliar nutrient concentration both 2 months and 4 years after fire. We attributed these results to two factors. First, unlike many prior studies, in this site both fire alone and the combination of thinning and fire resulted in decreased short-term and long-term soil nutrient availability. Second, this herb exhibits enhanced photosynthetic rate per unit leaf area and greater leaf and total biomass in B and T + B plots relative to the C plots (Huang et al. 2007b); therefore, the greater leaf biomass production in burned areas may have resulted in reduced nutrient concentrations even if absolute uptake had increased.

Structural equation modeling (SEM) has been recognized as a powerful tool to explore causational mechanisms

Table 4 Pearson correlation coefficients for the relation between plant nutrient concentration and soil nutrient availability

Parameter	Fourth growing season after fire				First growing season after second fire			
	IMI	Total inorganic N (TIN)	Soil P	Soil N:P ratio	IMI	TIN	Soil P	Soil N:P ratio
Leaf N	0.48***	0.37**	0.12	0.24	0.23	0.55***	0.66***	–0.11
Stem N	0.29*	0.26	–0.09	0.29*	–0.23	0.28	0.34*	0.05
Root N	0.21	0.40**	0.10	0.11	–0.10	0.02	0.14	–0.11
Leaf P	0.46***	0.20	0.23	–0.06	0.27	0.47**	0.41*	0.07
Stem P	0.20	0.27	0.03	0.04	0.16	0.34*	0.17	0.13
Root P	0.20	0.28*	0.11	–0.01	–0.30	0.15	0.25	–0.10
Leaf N:P ratio	0.06	0.19	–0.09	0.28	–0.13	–0.02	0.16	–0.20
Litter N					0.28	0.30	0.28	0.14
N resorption					–0.15	0.03	0.16	–0.27
Litter P					0.29	0.37*	0.25	0.24
P resorption					–0.12	–0.07	0.06	–0.23

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

n = 49 plots in 2004 and n = 36 plots in 2005

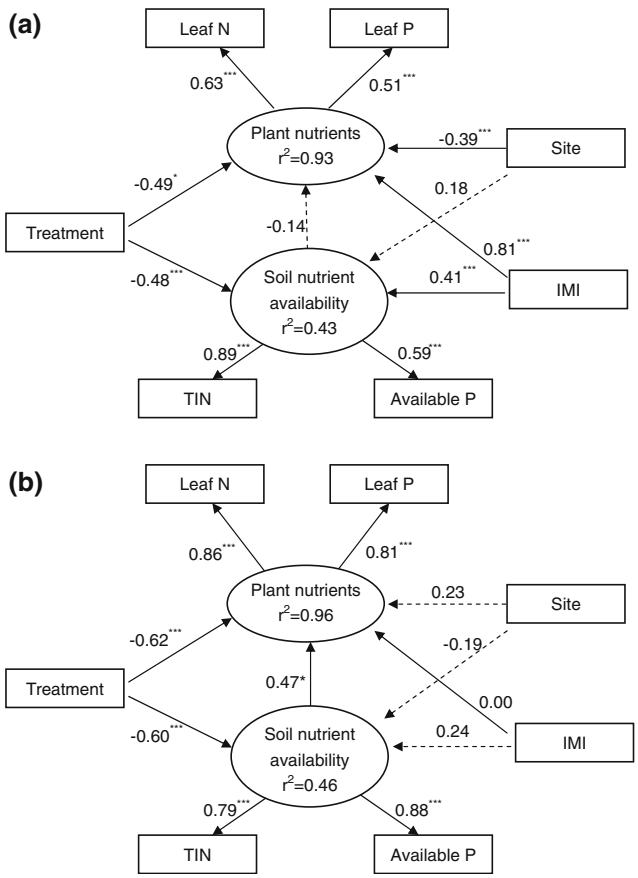

Fig. 5 Structural equation modeling of the relationship between soil chemistry and plant nutrient in combining site, integrated moisture index (IMI), and treatment effects in 2004 (**a**), and 2005 (**b**). *Ovals* are latent variables, *rectangles* are observed variables; standardized regression coefficients for regression linkages and squared multiple correlations for effect variables are indicated. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. The goodness-of-fit for **a** was chi-square = 5.792, $df = 8$, P value = 0.671, GFI = 0.968, RMSE < 0.001; **b** chi-square = 10.599, $df = 8$, P value = 0.250, GFI = 0.927, RMSE = 0.096

in ecological data (Grace and Keeley 2006; Vile et al. 2006). Our SEM indicated that fire alone or combined with thinning had significant impacts on soil nutrient availability and plant nutrient concentrations both in the short term and over the long term; however, the SEM also suggested that the mechanisms underlying the short- and long-term linkage changes may have differed. Two months after fire, SEM indicates that the treatments had indirect effects on plant nutrient mediated through the effects of the treatments on soil nutrient availability. Even though fire influenced long-term soil nutrient availability and leaf nutrient concentrations, the variations in leaf nutrient characteristics could not be directly linked to soil nutrient dynamics. Other factors, such as an altered light regime after fire and/or thinning or interactions between the treatments and landscape position, may have been more important in controlling leaf nutrient concentrations than the proximate changes in soil nutrient availability.

We used the integrated moisture index (IMI) metric of Iverson et al. (1997) to describe landscape-scale, topographically generated variations in long-term soil moisture potential in these dissected study areas. Structural equation modeling demonstrated that neither foliar nutrient concentrations nor soil nutrient availability varied significantly along these gradients 2 months after fire (i.e., IMI was uncorrelated with tissue and soil nutrients in 2005). In contrast, after the initial effects of the fire on forest floor microclimate had dissipated, the importance of gradients of temperature and moisture became more important, and both soil nutrient availability and foliar concentrations came under the control of those gradients once again (i.e., soil nutrient availability and foliar concentrations were correlated with IMI in 2004).

What role temporal variations in the rate of N-fixation by rhizobial symbionts of *D. nudiflorum* might play in this is, at this point, uncertain. During the fourth growing season after the first fire (2004), the root systems of *D. nudiflorum* plants from B to T + B plots had considerably more nodules than those from the C site. In contrast, in 2005, 2 months after the second fire there were no obvious differences in the nodulation of plants from burned to unburned sites, and we could detect no N-fixation activity in 2005 in plants from either burned or unburned plots. As nodule development and support is a facultative process and as nodulation is inhibited when inorganic N availability is high, it seems reasonable to hypothesize that N availability was significantly lower in the B plots during the fourth post-fire growing season than in either the B plots 2 months after the second fire or in the C plots in either year. Measurement of N-fixation activity in *D. nudiflorum* plants in the 2005 B plots during the 2008 and 2009 growing seasons will help test this hypothesis.

Plant nutrient resorption

We originally hypothesized that B and T + B would increase soil nutrient availability and foliar nutrient concentration, and we expected nutrient resorption would therefore be lower in the manipulated sites. We actually found the burning alone or combined with thinning had no effect on nutrient resorption. Over all treatments, average N resorption efficiency is 44.3% and P resorption is 45.8%. This result is contrary to that of a study in northern hardwoods (Latty et al. 2004) but consistent with those of a study in oak-pine forest in the New Jersey Pine Barrens (Boerner et al. 1988).

Linkage between nutrient resorption and site fertility and initial foliar nutrient concentration

Boerner (1984, 1986) related nutrient resorption to soil fertility in eastern deciduous forests of North America; however, this author found that woody plant and herbaceous species displayed different patterns of correlation between nutrient resorption and soil nutrient availability. Proportional resorption of N and P was found to be greater in individuals of three tree species (*Quercus alba*, *Acer rubrum*, and *Fagus grandifolia*) when growing on less fertile sites than on more fertile sites (Boerner 1984). In the same study region, Boerner (1986) reported that nutrient resorption in two understory herbs generally decreased with decreasing nutrient availability. We observed that nutrient resorption by *D. nudiflorum* was unrelated to soil nutrient availability, which is consistent with the conclusions of a review of the literature on N and P resorption in perennial plants that did not reveal any relationship between site/plant nutrition and resorption efficiency (Aerts 1996).

Empirical studies have provided conflicting results on the relationship between nutrient resorption efficiency and foliar nutrient concentration in both intraspecific and interspecific comparisons (Chapin and Kedrowski 1983; Shaver and Melillo 1984; Schlesinger et al. 1989; Del Arco et al. 1991; Rejmánková 2005; Huang et al. 2007a). In a recent literature review based on global database, Kobe et al. (2005) found that resorption efficiency generally declined with increasing leaf nutrient status, both within and among species. In our study, plants from the B to T + B treatments exhibited a significant positive relationship between nutrient resorption efficiency and initial foliar nutrient concentration, but this relationship was not present in the plants from the C plot. In the manipulated plots, with decreased soil nutrient availability and increased light availability, plants tended to retranslate more nutrients to support a ''rapid growth strategy'' (Aerts and Chapin 2000). In contrast, in the C plots, soil nutrient availability was higher but photosynthetically active radiation flux was much lower. Plant growth in the C plots is likely limited by light rather than nutrients, and plants do not need to resorb much N or P to meet future demands.

Conclusions

Our results showed that burning (B) alone or combined with thinning (T + B) resulted in both decreased soil nutrient availability and leaf nutrient concentrations. Four years after a single, low-intensity fire, leaf N concentrations in *D. nudiflorum*, a N-fixing herb, were affected primarily by broad landscape-scale gradients of soil moisture and microclimate. In contrast, 2 months after a second fire, leaf nutrient concentrations were strongly dependant on proximate soil nutrient availability, as affected by fire, and not on broad-scale topographic patterns. Variations in leaf nutrient resorption efficiency were independent of soil nutrient availability and could not be explained by initial foliar nutrient concentration alone. Altered soil surface microclimates after different ecological restoration treatments, especially differences in understory light conditions, may also be important in explaining variations in nutrient resorption. These findings enrich our understanding of the effects of different ecosystem restoration treatments on soil nutrient availability, plant tissue nutrient dynamics, and plant–soil interactions at different temporal scales.

Acknowledgments This is publication no. 117 of the Fire and Fire Surrogate Network Project funded by the Joint Fire Sciences Program. We thank Jennifer Brinkman, Aditi Shenoy, Philip Ruse, Carla Giai, Jessica Miesel for field and laboratory assistance. We also gratefully acknowledge Dr. Hormoz BassiriRad and three anonymous reviewers for their comments on the previous version.

References

Adams AS, Rieske LK (2003) Prescribed fire affects white oak seedling phytochemistry: implications for insect herbivory. For Ecol Manage 176:37–47

Aerts R (1990) Nutrient-use efficiency in evergreen and deciduous species from healthlands. Oecologia 84:391–397

Aerts R (1996) Nutrient resorption from senescing leaves of perennials: are there general patterns? J Ecol 84:597–608

Aerts R, de Caluwe H (1994) Nitrogen use efficiency of Carex species in relation to nitrogen supply. Ecology 75:2362–2372

Aerts R, Chapin FS (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Adv Ecol Res 30:1–67

APHA (1976) Standard methods for the examination of water and wastewater, 15th edn. American Public Health Association, Washington, D.C.

Boerner REJ (1982) Fire and nutrient cycling in temperate ecosystems. BioScience 32:187–192

Boerner REJ (1984) Foliar nutrient dynamics and nutrient use efficiency of four deciduous tree species in relation to site fertility. J Appl Ecol 21:1029–1040

Boerner REJ (1986) Seasonal nutrient dynamics, nutrient resorption, and mycorrhizal infection intensity of two perennial forest herbs. Am J Bot 73:1249–1257

Boerner REJ (2006) Unraveling the Gordian knot: interactions among vegetation, soil, and topography in the Central and Southern Appalachians. J Torrey Bot Soc 133:321–361

Boerner REJ, Lord TR, Peterson JC (1988) Effects of prescribed burning on nutrient uptake, use efficiency and growth of two species of oaks in the New Jersey Pine Barrens. Am Midl Nat 120:108–119

Boerner REJ, Morris SJ, Sutherland EK, Hutchinson TF (2000) Spatial variability in soil nitrogen dynamics after prescribed burning in Ohio mixed-oak forests. Landsc Ecol 15:425–439

Boerner REJ, Brinkman JA, Sutherland EK (2004) Effect of fire at two frequencies on forest soils in a nitrogen-enriched landscape. Can J For Res 34:609–618

Boerner REJ, Brinkman JA, Yaussy DA (2006) Ecosystem restoration treatments affect soil physical and chemical properties in Appalachian mixed-oak forests. In: Buckley D (ed) Proc 15th Central Hardwood For Conf. USDA For Serv Gen Tech Rep, SRS-nn, Asheville, pp 131–138

Bowman WD, Theodose TA, Fisk MC (1995) Physiological and production responses of plant growth forms to increases in limiting resources in alpine tundra: implications for differential community response to environmental change. Oecologia 101:217–227

Chapin FS, Kedrowski RA (1983) Seasonal changes in nitrogen and phosphorous fractions and autumn retranslocation in ever2 green and deciduous Taiga tree. Ecology 64:376–391

Chapin FS, Moilanen L (1991) Nutrient controls over nitrogen and phosphorus resorption from Alaskan birch leaves. Ecology 72:709–715

Christensen NL (1977) Fire and soil–plant nutrient relations in a pine-wiregrass savanna on the coastal plain of North Carolina. Oecologia 31:27–44

Del Arco JM, Eacudero A, Garrido MV (1991) Effects of site characteristics on nitrogen retranslocation from senescing leaves. Ecology 72:701–708

Gilliam FS (1988) Interactions of fire with nutrients in the herbaceous layer of a nutrient-poor coastal plain forest. Bull Torrey Bot Club 115:265–271

Grace JB, Keeley JE (2006) A structural equation model analysis of postfire plant diversity in California shrublands. Ecol Appl 16:503–514

Huang J, Wang X, Yan E (2007a) Leaf nutrient concentration, nutrient resorption and litter decomposition in an evergreen broad-leaved forest in eastern China. For Ecol Manage 239:150–158

Huang J, Boerner REJ, Rebbeck J (2007b) Ecophysiological responses of two herbaceous species to prescribed burning, alone or in combination with overstory thinning. Am J Bot (in press)

Hutchinson TF, Boerner REJ, Sutherland S, Sutherland EK, Ortt M, Iverson LR (2005) Prescribed fire effects on the herbaceous layer of mixed-oak forests. Can J For Res 35:877–890

Ice GG, Neary DG, Adams PW (2004) Effects of wildfire on soils and watershed processes. J For 102:16–20

Iverson LR, Dale ME, Scott CT, Prasad A (1997) A GIS-derived integrated moisture index to predict forest composition and productivity of Ohio forests (USA). Landsc Ecol 12:331–348

Kobe RK, Lepczyk CA, Iyer M (2005) Resorption efficiency decreases with increasing green leaf nutrients in a global data set. Ecology 86:2780–2792

Kruger EL, Reich PB (1997) Responses of hardwood regeneration to fire in mesic forest openings II. Leaf gas exchange, nitrogen concentration and water status. Can J For Res 27:1832–1840

Latty FL, Canham CD, Marks PL (2004) The effects of land-use history on soil properties and nutrient dynamics in northern hardwood forests of the Adirondack mountains. Ecosystem 7:193–207

Monleon CJ, Cromack K, Landsberg JD (1997) Short- and long-term effects of prescribed underburning on nitrogen availability in ponderosa pine stands in central Oregon. Can J For Res 27:369–378

Raison RJ (1979) Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: a review. Plant Soil 51:73–108

Rejmánková E (2005) Nutrient resorption in wetland macrophytes: comparison across several regions of different nutrient status. New Phytol 167:471–482

Reich PB, Abrams MD, Ellsworth DS, Kruger EL, Tabone TJ (1990) Fire affects ecophysiology and community dynamics of central Wisconsin oak forest regeneration. Ecology 71:2179–2190

SAS Institute (2001) SAS proprietary software release, version 8.0. SAS Institute, Cary, N.C.

Schlesinger WH, DeLucia EH, Billings WD (1989) Nutrient-use efficiency of woody plants on contrasting soils in the western Great Basin, Nevada. Ecology 70:105–113

Shaver GR, Melillo JM (1984) Nutrient budgets of marsh plants: efficiency concepts and relation to availability. Ecology 65:1491–1510

Sims GK, Ellsworth TR, Mulvaney RL (1995) Microscale determination of inorganic N in water and soil extracts. Comm Soil Sci Plant Anal 26:303–316

Sutherland EK, Hutchinson TF (2003) Characteristics of mixed-oak forest ecosystems in southern Ohio prior to the reintroduction of fire. USDA, For Serv, N E Res Stn, Gen Tech Rep NE-299, Newtown Square

Vance ED, Henderson GS (1984) Soil nitrogen availability following long-term burning in an oak-hickory forest. Soil Sci Soc Am J 48:184–190

Vile D, Shipley B, Garnier E (2006) A structural equation model to integrate changes in functional strategies during old-field succession. Ecology 87:504–517

Wan S, Hui D, Luo Y (2001) Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. Ecol Appl 11:1349–1365