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FIRE EFFECTS ON NITROGEN POOLS AND DYNAMICS IN TERRESTRIAL ECOSYSTEMS: A META-ANALYSIS

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Abstract. A comprehensive and quantitative evaluation of the effects of fire on ecosystem nitrogen (N) is urgently needed for directing future fire research and management. This study used a meta-analysis method to synthesize up to 185 data sets from 87 studies published from 1955 to 1999. Six N response variables related to fire were examined: fuel N amount (FNA) and concentration (FNC), soil N amount (SNA) and concentration (SNC), and soil ammonium (NH_4^+) and nitrate (NO_3^-) pools. When all comparisons (fire treatment vs. control) were considered together, fire significantly reduced FNA (58%), increased soil NH_4^+ (94%) and NO_3^- (152%), and had no significant influences on FNC, SNA, and SNC. The responses of N to fire varied with different independent variables, which were vegetation type, fire type, fuel type, fuel consumption amount, fuel consumption percentage, time after fire, and soil sampling depth. The response of FNA to fire was significantly influenced by vegetation type, fuel type, and fuel consumption amount and percentage. The reduction in FNA was linearly correlated with fuel consumption percentage ($r^2 = 0.978$). The response of FNC to fire was only affected by fuel type. None of the seven independent variables had any effect on SNA. The responses of SNC, NH_4^+, and NO_3^- depend on soil sampling depth. The responses of both NH_4^+ and NO_3^- to fire were significantly affected by fire type and time after fire but had different temporal patterns. The soil NH_4^+ pool increased approximately twofold immediately after fire, then gradually declined to the prefire level after one year. The fire-induced increase in the soil NO_3^- pool was small (24%) immediately after fire, reached a maximum of approximately threefold of the prefire level within 0.5–1 year after fire, and then declined. This study has identified the general patterns of the responses of ecosystem N that occur for several years after fire. A key research need relevant to fire management is to understand how the short-term responses of N to fire influence the function and structure of terrestrial ecosystems in the long term.

Key words: biomass; fire; forests; fuel; grasslands; meta-analysis; nitrogen; prescribed burning; response ratio; shrublands; slash burning; wildfire.

Introduction

Prior to the 1930s, fire was generally considered a destructive and undesirable force that occurred with varying frequency in terrestrial ecosystems (Clements 1916, Fowells and Stephenson 1933). This point of view resulted in the suppression of natural fire for almost half a century (Kozlowski and Ahlgren 1974). However, since the 1970s, critical scientific evaluations have indicated a potential usefulness of fire in ecosystem management (Kozlowski and Ahlgren 1974, Raison 1979), e.g., controlling fuel (combustible material) levels and thereby avoiding catastrophic wildfire (Wagle and Eakle 1979), restoring forest ecosystems (Kaye et al. 1999, Vose et al. 1999), maintaining species composition and richness in grasslands (Collins and Wallace 1990, Collins et al. 1995, Pendergrass et al. 1999), and improving water yields in catchment areas (Schindler et al. 1980, Bosch et al. 1984).

As a powerful and instantaneous modifier of the environment, fire potentially has a profound, long-term influence on nutrient cycles in ecosystems by changing the form, distribution, and amount of nutrient as well as by changing species composition, plant growth, soil biota, leaching, and erosion (McNabb and Cromark 1990, Grogan et al. 2000). Much attention has been paid to nitrogen (N) pools and dynamics associated with fire because N often limits primary productivity in natural ecosystems (Christensen 1977, Woodmansee and Wallach 1981, Maars et al. 1983, Fenn et al. 1998). In addition, N is easily lost during fuel combustion (Grier 1975, DeBano et al. 1979, Raison et al. 1985*a*, Gillon and Rapp 1989) because N volatilizes at a relatively low temperature (200°C; Knight 1966, White et al. 1973). The volatilization temperature of N can easily be reached in fire if fine fuel exceeds 3370 kg/ha (Stinson and Wright 1969).

Direct N losses during fuel combustion are usually in the forms of gasification, volatilization, and ash convection (Christensen 1994). It is commonly accepted that N loss through combustion is significantly correlated with fuel consumption and/or fire intensity (DeBano and Conrad 1978, Raison et al. 1985*a*, Schoch and Binkley 1986, Feller 1988, O'Connell and McCaw 1997, Belillas and Feller 1998). Depending on types

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of vegetation, fire, and fuel (Binkley et al. 1992*a*), the amounts of N losses during burning can vary from 8.5 kg/ha in a grassland (Medina 1982) to 907 kg/ha in a coniferous forest (Grier 1975) to 1604 kg/ha in a Brazilian tropical forest (Kauffman et al. 1995).

Reports about the impacts of fire on total soil N are highly variable because of differences in vegetation (Dyrness et al. 1989), topography (Turner et al. 1997, Vose et al. 1999), fire regimes (e.g., frequency, intensity, and season; Covington and Sackett 1984, Blair 1997), and sampling methods (Monleon et al. 1997). However, most studies suggest a consistent pattern that fire can increase the availability of soil ammonium (NH_4^+) and nitrate (NO_3^-; Christensen 1973, Kovacic et al. 1986, Rapp 1990, Covington et al. 1991, Baldwin and Morse 1994, Kaye and Hart 1998). The increases in soil NH_4^+ and NO_3^- have been attributed to the pyrolysis of organic material, increased N mineralization, and the leaching of N from the forest floor into the soil after fire (Covington and Sackett 1984, Grove et al. 1986, Knoepp and Swank 1993, Baldwin and Morse 1994, Kaye and Hart 1998, Lynds and Baldwin 1998).

As one of the most limiting nutrients, N plays an important role in postfire recovery of ecosystem productivity. In order to better understand how N responses may influence postfire ecosystem dynamics, it is imperative to synthesize the highly variable results from individual studies across various ecosystems. Such syntheses, which are also essential to policy making in fire management, have been conducted primarily by narrative literature reviews in the past (Ahlgren and Ahlgren 1960, Kozlowski and Ahlgren 1974, Raison 1979, Wells et al. 1979, Woodmansee and Wallach 1981, Johnson et al. 1998). However, conclusions regarding the effects of fire on ecosystem N, particularly on soil N, remain controversial. One reason for the controversy is that narrative reviews are largely qualitative and subjective (Osenberg et al. 1999). Other possible reasons include the inconsistency in the units of expressing N and in soil sampling depths (DeBano et al. 1998). To help resolve the controversy, a comprehensive evaluation of the effects of fire on ecosystem N with quantitative methods is necessary.

In this study, we synthesized experimental results about the effects of fire on N pools and dynamics in terrestrial ecosystems. These results were drawn from studies concerning different vegetation types, fire types, fuel types, fuel consumption amounts and percentages, time after fire, and soil sampling depth. A meta-analysis approach, which provides statistically unbiased estimates of treatment effects across multiple studies, was used to address the following questions. First, to what extent will various ecosystem N pools be affected by fire? Second, how will vegetation, fire, and fuel as well as soil sampling depth affect N responses to fire? Finally, what are the temporal patterns of N responses after fire?

Materials and Methods

Approach

Meta-analysis is a quantitative method used to compare and synthesize results of multiple independent studies with an attempt to address a common question or to test a common hypothesis. Results from similar studies (e.g., studies of the effects of fire on ecosystem N in this paper) are first gathered and compiled into a common database. These results are then combined to estimate the magnitude of a treatment effect. In this study, a response ratio (RR, the ratio of means for a measured variable between the fire treatment group and the control group) was used as an index of the estimated magnitude of the fire effect. In essence, RR quantifies the proportional change that results from an experimental manipulation or treatment (Curtis and Wang 1998, Hedges et al. 1999). The significance of RR is statistically tested to determine whether a response variable of the treatment group is different from that of the control group. The heterogeneity of RR is calculated to examine whether all studies share a common magnitude of the treatment effect. Finally, the RR is grouped according to independent variables (e.g., vegetation type and time after fire in this study) for the purpose of detecting the differences in RRs among groups. Compared to the traditional qualitative and narrative reviews, meta-analysis has the advantages of objectivity and better control of Type II errors; i.e., failure to reject null hypotheses that are false (Arnqvist and Wooster 1995) and thus has the potential to resolve longstanding scientific debates (Gurevitch et al. 1992).

Extracting data from published results

Our literature survey was intended to be as inclusive as possible. We extracted data from publications in the literature for six N response variables: fuel N amount (FNA), fuel N concentration (FNC), soil N amount (SNA), soil N concentration (SNC), soil ammonium (NH_4^+) pool, and soil nitrate (NO_3^-) pool. We also selected seven independent variables which are relevant to the six response variables. The seven independent variables were vegetation type, fire type, fuel type, fuel consumption amount (FCA), fuel consumption percentage (FCP), time after fire (TAF), and soil sampling depth (Tables 1 and 2). Vegetation type had four groups, which were broad-leaved forests (BF), coniferous forests (CF), grasslands (GL), and shrublands (SB). Fire type had three groups, which were prescribed burning (Pres-B), slash burning (SL-B), and wildfire (WF). Fuel type had four groups, which were aboveground biomass (AGB), forest floor (FF), forest floor plus understory (FF+US), and slash plus forest floor (SL+FF). From 87 studies published between 1955 and 1999 (Table 1), we examined 57, 48, 40, 62, 184, and 185 comparisons (fire treatment vs. control) for the analyses of FNA, FNC, SNA, SNC, NH_4^+, and NO_3^-, respectively (Tables 2 and 3).

TABLE 1. Summary of vegetation type (VT), fire type, fuel type, response variables, and references for studies included in the meta-analysis.

VT	Fire	Fuel	FNA	FNC	SNA	SNC	NH_4^+	NO_3^-	References
BF	Pres-B	AGB		×	×	×			Kauffman et al. (1994)
BF	Pres-B	FF		×					Raison et al. (1985*a*)
BF	Pres-B	FF	×						Raison et al. (1985*b*)
BF	Pres-B	FF					×		Vance and Henderson (1984)
BF	Pres-B	FF+US				×	×	×	Grove et al. (1986)
BF	Pres-B	FF+US		×					O'Connell et al. (1979)
BF	Pres-B	FF+US				×			Raison (1983)
BF	Pres-B	FF+US	×	×					Raison et al. (1985*b*)
BF	Pres-B	SL+FF	×						O'Connell and McCaw (1997)
BF	SL-B	AGB	×						Clinton et al. (1996)
BF	SL-B	AGB	×		×				Kauffman et al. (1993)
BF	SL-B	AGB				×			Uhl and Jordan (1984)
BF	SL-B	SL+FF			×	×	×	×	Ellis and Graley (1983)
BF	SL-B	SL+FF			×	×	×	×	Ellis et al. (1982)
BF	SL-B	SL+FF	×	×	×	×			Ewel et al. (1981)
BF	SL-B	SL+FF				×	×		Humphreys and Lambert (1965)
BF	SL-B	SL+FF				×			Kauffman et al. (1993)
BF	SL-B	SL+FF	×	×	×	×			Kauffman et al. (1995)
BF	SL-B	SL+FF					×		Ludwig et al. (1998)
BF	SL-B	SL+FF				×			Nye and Greenland (1964)
BF	WF	AGB					×	×	Adams and Attiwill (1986)
BF	WF	AGB					×	×	Blank and Zamudio (1998)
BF	WF	AGB					×	×	Busch and Smith (1993)
BF	WF	AGB				×			Kirkpatrick and Dickinson (1984)
BF	WF	AGB				×			Rashid (1987)
BF	WF	AGB					×	×	Weston and Attiwill (1990)
BF	WF	FF		×		×			Beaton (1959)
BF	WF	FF	×		×				Dyrness et al. (1989)
BF	WF	FF+US					×	×	Adams and Attiwill (1986)
BF	WF	FF+US					×	×	Weston and Attiwill (1990)
BF	WF	SL+FF				×			Adams and Boyle (1980)
BF	WF	SL+FF					×	×	Weston and Attiwill (1990)
CF	Pres-B	AGB				×			Anderson and Menges (1997)
CF	Pres-B	FF		×					Alban (1977)
CF	Pres-B	FF	×		×		×	×	Bell and Binkley (1989)
CF	Pres-B	FF	×	×	×	×			Binkley et al. (1992*b*)
CF	Pres-B	FF					×	×	Covington and Sackett (1986)
CF	Pres-B	FF					×	×	Covington and Sackett (1992)
CF	Pres-B	FF		×					De Ronde (1990)
CF	Pres-B	FF		×					Gillon et al. (1995)
CF	Pres-B	FF	×		×				Grier (1975)
CF	Pres-B	FF				×			St. John and Rundel (1976)
CF	Pres-B	FF	×		×				Kaye and Hart (1998)
CF	Pres-B	FF					×	×	Kovacic et al. (1986)
CF	Pres-B	FF			×				Lynham et al. (1998)
CF	Pres-B	FF	×						Maggs (1988)
CF	Pres-B	FF				×		×	Monleon et al. (1997)
CF	Pres-B	FF	×						Richter et al. (1982)
CF	Pres-B	FF	×						Schoch and Binkley (1986)
CF	Pres-B	FF	×	×	×				Vose et al. (1999)
CF	Pres-B	FF+US						×	Boerner et al. (1988)
CF	Pres-B	FF+US	×	×					Christensen (1977)
CF	Pres-B	FF+US		×					Gillon and Rapp (1989)
CF	Pres-B	FF+US	×	×					Nissley et al. (1980)
CF	Pres-B	FF+US					×	×	Rapp (1990)
CF	Pres-B	SL+FF				×			Blackwell et al. (1995)
CF	Pres-B	SL+FF	×						Covington and Sackett (1984)
CF	Pres-B	SL+FF				×			Covington and Sackett (1986)
CF	Pres-B	SL+FF		×		×			Fuller (1955)
CF	Pres-B	SL+FF					×	×	Kaye and Hart (1998)
CF	Pres-B	SL+FF	×						Little and Klock (1985)
CF	Pres-B	SL+FF	×	×					Little and Ohmann (1988)
CF	SL-B	SL+FF					×	×	Covington et al. (1991)
CF	SL-B	SL+FF	×	×					Belillas and Feller (1998)
CF	SL-B	SL+FF		×					Clinton et al. (1996)
CF	SL-B	SL+FF		×					Feller (1988)
CF	SL-B	SL+FF			×				Knoepp and Swank (1993)
CF	SL-B	SL+FF	×	×	×	×			Macadam (1987)
CF	SL-B	SL+FF				×	×	×	Pietikäinen and Fritze (1995)
CF	SL-B	SL+FF		×					Stednick et al. (1982)

TABLE 1. Continued.

VT	Fire	Fuel	FNA	FNC	SNA	SNC	NH_4^+	NO_3^-	References
CF	SL-B	SL+FF					×	×	Vitousek and Matson (1985)
CF	SL-B	SL+FF	×	×					Vose and Swank (1993)
CF	WF	AGB				×			Andreu et al. (1996)
CF	WF	FF	×		×				Dyrness et al. (1989)
CF	WF	FF+US				×			Dumontet et al. (1996)
GL	Pres-B	AGB					×	×	Dudley and Lajtha (1993)
GL	Pres-B	AGB		×	×	×			Kauffman et al. (1994)
GL	Pres-B	AGB	×	×	×	×			Kauffman et al. (1998)
GL	Pres-B	AGB			×				Ram and Ramakrishnan (1992)
GL	Pres-B	AGB	×	×					Redmann (1991)
GL	Pres-B	AGB	×	×					Seastedt (1988)
GL	Pres-B	AGB				×			Seastedt and Ramundo (1990)
GL	Pres-B	AGB					×	×	Turner et al. (1997)
GL	WF	AGB					×		Blank and Zamudio (1998)
SB	Pres-B	AGB					×	×	Christensen (1987)
SB	Pres-B	AGB	×		×				DeBano et al. (1979)
SB	Pres-B	AGB						×	Herman and Rundel (1989)
SB	Pres-B	AGB		×	×	×			Kauffman et al. (1994)
SB	Pres-B	AGB					×	×	Marion et al. (1991)
SB	Pres-B	AGB			×	×	×	×	Singh (1994)
SB	Pres-B	AGB					×	×	Singh et al. (1991)
SB	Pres-B	AGB	×	×					Trabaud (1994)
SB	Pres-B	AGB					×	×	Wilbur and Christensen (1983)
SB	Pres-B	FF					×	×	DeBano et al. (1979)
SB	WF	AGB						×	Arianoutou-Faraggitaki and Margaris (1982)
SB	WF	AGB						×	Baldwin and Morse (1994)
SB	WF	AGB				×	×	×	Christensen and Muller (1975)
SB	WF	AGB				×			Halvorson et al. (1997)
SB	WF	AGB					×	×	Lynds and Baldwin (1998)
SB	WF	AGB			×	×			Marion and Black (1988)

Notes: Vegetation types include broad-leaved forests (BF), coniferous forests (CF), grasslands (GL), and shrublands (SB). Fire types include prescribed burning (Pres-B), slash burning (SL-B), and wildfire (WF). Fuel types include aboveground biomass (AGB), forest floor (FF), forest floor plus understory (FF+US), and slash plus forest floor (SL+FF). Response variables include fuel N amount (FNA), fuel N concentration (FNC), soil N amount (SNA), soil N concentration (SNC), soil ammonium pool (NH_4^+), and soil nitrate pool (NO_3^-).

Meta-analysis assumes the independence of data being synthesized. Violation of this assumption (e.g., including multiple results from a single study) may alter the structure of the data, inflate samples and significance levels for statistical tests, and increase the probability of Type I errors, i.e., rejecting the null hypothesis when it is true (Wolf 1986, Vander Werf 1992). Some researchers consider lack of independence to be a serious problem for meta-analysis, and thus they advocate for the inclusion of only one result from each study (Vander Werf 1992, Tonhasca and Byrne 1994, Koricheva et al. 1998). However, the loss of information caused by the omission of multiple results in each study may become a more serious problem than that caused by violating the assumption of independence (Hedges and Olkin 1985, Gurevitch et al. 1992).

TABLE 2. Independent variables and the groups used in the meta-analysis.

Independent variable	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7	Group 8	Group 9
VT			GL	SB					
Fire	BF	CF	WF						
Fuel	Pres-B	SL-B	FF+US	SL+FF					
TAF1	AGB	FF1–6	7–12	13–36	37–60	>60			
TAF2	0	1–3	4–6	7–12	13–18	19–24	25–36	37–48	49–60
FCA	0	10–20	20–30	30–40	40–60	60–80	80–100	100–150	>150
FCP	≤10≤20	20–30	30–40	40–50	50–60	60–70	70–80	80–90	90–100
Depth	≤2.5	2.6–5.0	5.1–10	10.1–20	20.1–30	>30			

Notes: We used two different time scales because the time resolutions for NH_4^+ and NO_3^- reported in the literature are finer than those for other response variables: TAF1 = time after fire (mo) used for FNA, FNC, SNA, and SNC; TAF2 = time after fire (mo) used for NH_4^+ and NO_3^-. Soil sampling depth (depth, cm) is grouped according to a certain quantitative level; 5.1–10 means soil sampling depth varying from 0–5.1 to 0–10.0 cm. FCA = fuel consumption amount (Mg/ha); FCP = fuel consumption percentage (%). For other abbreviations, see Table 1.

TABLE 3. Statistical tests of the effects of independent variables on the response variables, using between-group heterogeneity (Q_b) of N response to fire.

Variable	k	VT	Fire	Fuel	TAF	FCA	FCP	Depth
FNA	57	12.76**	4.76	9.14*	0.03	49.70***	115.42***	
FNC	48	4.12	0.31	11.96**	7.00	3.41	5.41	
SNA	40	0.75	0.78	1.08	1.01	7.00	6.28	2.64
SNC	62	0.47	2.04	2.72	5.97	1.61	3.47	13.64*
NH_4^+	184	6.90_{29}	25.09_{29}***	1.47_{29}	136.88***	0.17_9	0.77_7	13.97_{28}***
NO_3^-	185	7.57_{36}	9.91_{36}**	2.14_{35}	49.69***	0.92_9	2.66_7	9.11_{36}*

Notes: Each response variable was represented by k comparisons. The subscript numbers are the numbers of comparisons for the peak responses for NH_4^+ and NO_3^- grouped by different independent variables (see *Material and Methods*). See Table 1 and Table 2 for abbreviations.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Many researchers therefore have included more than one result from each study in their meta-analysis (Gurevitch et al. 1992, Poulin 1994, Wooster 1994, Arnqvist and Wooster 1995, Curtis 1996, Curtis and Wang 1998).

In the analyses of FNA, FNC, SNA, and SNC, when more than one vegetation type or stand was burned in one fire or in several fires, the results were considered to be independent and were included. When there were data with different sampling dates from one stand or vegetation type, we only included the result from the earliest sampling date with an attempt to avoid replications of vegetation type, fire type, fuel type, and/or soil sampling depth. When there were several SNA and SNC data from different soil layers in each study, only the value for the surface soil layer was used in our analysis because the surface layer is most sensitive to fire (DeBano and Conrad 1978, Kutiel and Naveh 1987).

Because the level of available soil N (NH_4^+ and NO_3^-) varies seasonally and the response of the available N pools after fire is generally more dynamic than that of total soil N (Covington et al. 1991, Singh et al. 1991, Singh 1994), two steps were used in the analyses of soil NH_4^+ and NO_3^-. First, all the results from different sampling dates in each study (the number of comparisons, k, = 184 and 185 for NH_4^+ and NO_3^-, respectively) were compiled together to examine the temporal dynamics of NH_4^+ and NO_3^- after fire. In this step, the effects of vegetation, fire, fuel, and soil sampling depth on the responses of soil NH_4^+ and NO_3^- were not considered because inclusion of multiple results with different sampling dates in each study caused large replications of these independent variables. Second, subdatasets from the response peaks of soil NH_4^+ (TAF = 0 mo, e.g., immediately after fire, $k = 29$) and NO_3^- (TAF = 7–12 mo, $k = 36$) to fire were selected and analyzed to examine the effects of these independent variables on the responses of soil NH_4^+ and NO_3^- to fire. In the second step, only one comparison was included from each study unless the results came from different vegetation types or stands.

Means, standard deviations, and sample sizes for the treatment and control groups are needed in order to conduct meta-analysis. We only included studies in which means, standard deviations, and sample sizes for the treatment and control groups could be derived or inferred from the information provided. When means and standard deviations for both groups were reported, these data were used directly. When data (means and some measures of variance) were presented in the form of graphs, the figures were enlarged and manually digitized. If raw data of the treatment and control groups were given, means and standard deviations were calculated. When mean and standard error (SE) of each treatment were reported, as in most studies, the standard deviation (SD) was calculated as

$$\mathrm{SD} = \mathrm{SE}\sqrt{n} \tag{1}$$

where n was the sample size. If data were given with a mean and a confidence interval (CI), the standard deviation was calculated as

$$\mathrm{SD} = (\mathrm{CI_u} - \mathrm{CI_l})\sqrt{n}/2u_\mathrm{p} \tag{2}$$

where $\mathrm{CI_u}$ and $\mathrm{CI_l}$ were the upper and lower limits of CI, and u_p was the significant level and equaled 1.96 when $\alpha = 0.05$ and 1.645 when $\alpha = 0.10$. When preburn and postburn fuel N concentrations in different fuel compartments (such as forest floor, understory, and slash with different diameters) were provided, means and standard deviations representing the whole-system FNC were calculated. The units with which measurements have been reported are not important since the calculated response ratios are dimensionless (Curtis 1996).

Response ratio

The response ratio, $\mathrm{RR} = \bar{X}_t/\bar{X}_c$, is the ratio of mean in the treatment group ($\bar{X}_t$) to that of the control group ($\bar{X}_c$). For the purpose of statistical tests, RR is converted to the metric of the natural log as

$$\ln \mathrm{RR} = \ln(\bar{X}_t/\bar{X}_c) = \ln(\bar{X}_t) - \ln(\bar{X}_c). \tag{3}$$

If $\bar{X}_t$ and $\bar{X}_c$ are normally distributed and both are >0, ln(RR) is approximately normally distributed (Curtis and Wang 1998) with a mean equal to the true log response ratio and a variance (v) approximately equal to the following:

$$v = \frac{s_t^2}{n_t \bar{X}_t^2} + \frac{s_c^2}{n_c \bar{X}_c^2} \qquad (4)$$

where n_t and n_c are the sample sizes for the treatment and control groups, respectively; s_t and s_c are the standard deviations for all comparisons in the treatment and control groups, respectively.

The meta-analysis calculates a weighted log response ratio ($\ln(RR_{++})$) from individual $\ln(RR_{ij})$ ($i = 1, 2, \ldots, m$; $j = 1, 2, \ldots, k_i$) by giving greater weight to studies whose estimates have greater precision (lower v) so that the precision of the combined estimate and the power of the tests will increase (Hedges and Olkin 1985, Gurevitch and Hedges 1999). Here m is the number of groups, k_i is the number of comparisons in the ith group. The weighted mean log response ratio ($\ln(RR_{++})$) is calculated by

$$\ln RR_{++} = \sum_{i=1}^{m}\sum_{j=1}^{k_i} w_{ij} \ln RR_{ij} \Big/ \sum_{i=1}^{m}\sum_{j=1}^{k_i} w_{ij} \qquad (5)$$

with the standard error as

$$s(\ln RR_{++}) = \sqrt{1 \Big/ \sum_{i=1}^{m}\sum_{j=1}^{k_i} w_{ij}} \qquad (6)$$

where w_{ij} is the weighting factor and is estimated by

$$w_{ij} = 1/v. \qquad (7)$$

The 95% confidence interval for the log response ratio is

$$95\%\text{CI} = \ln RR_{++} \pm 1.96 s(\ln RR_{++}). \qquad (8)$$

The corresponding confidence limits for the response ratio can be obtained by computing their respective antilogs. If the 95% CI of a response variable overlaps with zero, the response ratio is not significantly changed. If the 95% CIs of two groups overlap, the response ratios of the two groups are not significantly different from each other. Otherwise, they are statistically different.

Homogeneity test

The homogeneity test is used to determine whether at least one of the response ratios in a series of comparisons differs from the rest (Gurevitch and Hedges 1993). In this study, we used the homogeneity test to examine the source of variations in response ratios among comparisons and to determine whether different groups of independent variables result in quantitatively different responses. The total heterogeneity (Q_T) is partitioned into within-group heterogeneity (the variation among comparisons within groups, Q_W) and between-group heterogeneity (the variation in weighted response ratio between groups, Q_B) as

$$Q_T = Q_W + Q_B \qquad (9)$$

which is analogous to the practice of partitioning variation in an ANOVA. The total heterogeneity (Q_T) is calculated as

$$Q_T = \sum_{i=1}^{m}\sum_{j=1}^{k_i} w_{ij}[\ln RR_{ij} - \ln RR_{++}]^2 \qquad (10)$$

with ($\Sigma_{i=1}^{m} k_i - 1$) degrees of freedom (df). The between-group heterogeneity (Q_B) is calculated as

$$Q_B = \sum_{i=1}^{m}\sum_{j=1}^{k_i} w_{ij}[\ln RR_{i+} - \ln RR_{++}]^2 \qquad (11)$$

with df $= m - 1$. The within-group heterogeneity is calculated as

$$Q_W = \sum_{i=1}^{m}\sum_{j=1}^{k_i} w_{ij}[\ln RR_{ij} - \ln RR_{i+}]^2 \qquad (12)$$

with df $= (\Sigma_{i=1}^{m} k_i - m)$.

The Q statistic approximately follows a χ^2 distribution, which allows a significance test of the null hypothesis that all response ratios are equal. The greater the value of Q, the greater the heterogeneity in response ratios among comparisons. If Q_B is larger than a critical value, an independent variable has a significant influence on the response ratio (Gurevitch et al. 1992).

In our meta-analysis, the whole datasets in each of the six response variables were divided according to the six (fuel N) or seven (soil N) independent variables in order to explore the ecological causes of fire effects. Those interactions that were not statistically significant between the response variables and independent variables were not examined further in this study except for the interactions of SNA and SNC with TAF. The latter interactions were examined to evaluate the temporal responses of SNA and SNC to fire. In this study, the meta-analysis was conducted using the statistical software MetaWin 1.0 (Rosenberg et al. 1997).

Results

Fire significantly reduced fuel N amount (FNA) by 58% (Fig. 1). The FNA response to fire was strongly influenced by vegetation type ($P < 0.01$; Table 3). The reduction in FNA in response to fire was 71% for broad-leaved forests, 48% for coniferous forests, 60% for grasslands, and 71% for shrublands (Fig. 2a). A paired comparison indicated no overlap of 95% confidence intervals between broad-leaved and coniferous forests, which suggests that the responses of FNA to fire for the two terrestrial ecosystems were significantly different. No significant difference was found among other vegetation types.

Fire-induced responses in FNA also varied with fuel types (Table 3), with reductions of 73% for aboveground biomass (AGB), 54% for forest floor (FF), 64% for FF plus understory (US), and 49% for slash fuel (SL) plus FF (Fig. 2b). The paired comparison indicated that the effects of fire on FNA were significantly different only between AGB and SL+FF.

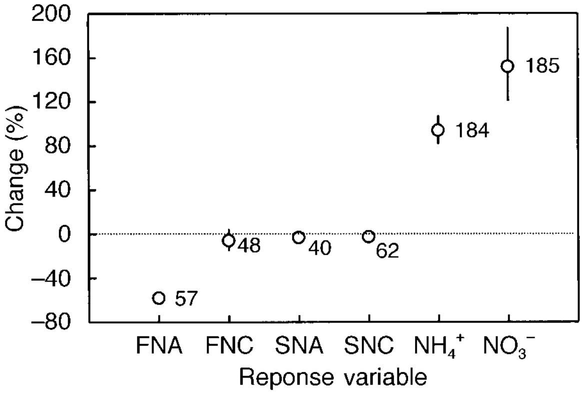

FIG. 1. Percentage of changes in six N response variables after fire. Open circles and vertical lines are means ±95% confidence intervals; numbers are the number of comparisons (k). FNA = fuel N amount, FNC = fuel N concentration, SNA = soil N amount, SNC = soil N concentration, NH_4^+ = soil ammonium pool, and NO_3^- = soil nitrate pool.

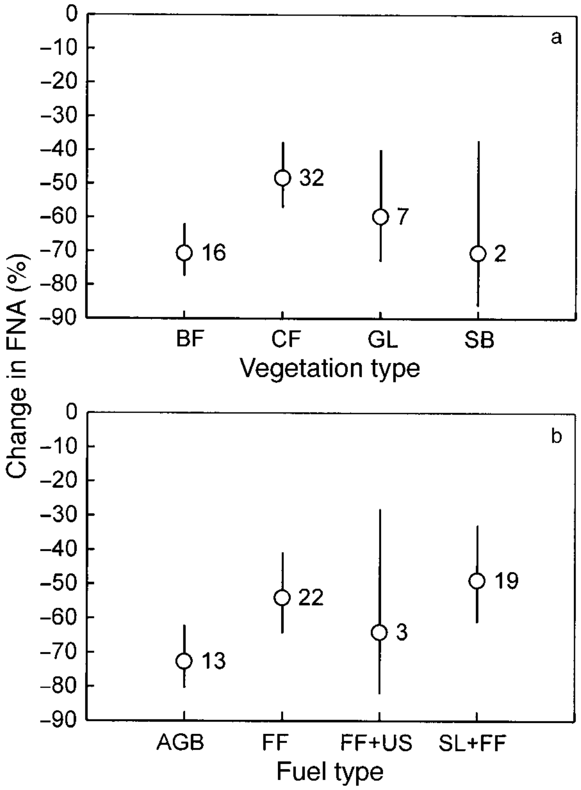

FIG. 2. The effects of (a) vegetation type and (b) fuel type on the response of FNA to fire. Open circles and vertical lines are means ±95% confidence intervals; numbers are the number of comparisons (k). BF = broad-leaved forests, CF = coniferous forests, GL = grasslands, SB = shrublands, AGB = aboveground biomass, FF = forest floor, FF + US = forest floor plus understory, and SL+FF = slash plus forest floor.

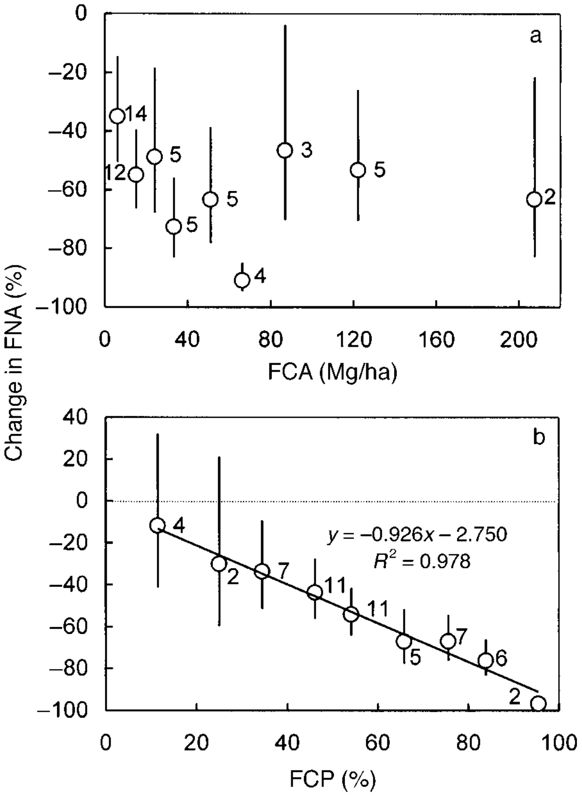

FIG. 3. The effects of (a) FCA and (b) FCP on the response of FNA to fire. Open circles and vertical lines are means ±95% confidence intervals; numbers are the number of comparisons (k). FCA = fuel consumption amount; FCP = fuel consumption percentage. See Fig. 1 for other abbreviations.

Both fuel consumption amount (FCA) and percentage (FCP) had significant influences on the response of FNA to fire (Table 3). When FCA increased from 10 to 80 Mg/ha, the reduction in FNA increased (Fig. 3a). When FCA was >80 Mg/ha, the lack of correlation between FNA and FCA (Fig. 3a) possibly resulted from incomplete burning of coarse fuel and piled slash. When all studies were considered together, no apparent linear relationship emerged between FCA and the fire-induced reduction in FNA. Further partitioning of this dataset according to vegetation type showed a similar variability (Fig. 4a–c). In contrast to the relationship between FNA and FCA, FNA (y) decreased linearly with FCP (x; Fig. 3b) as $y = -0.926x - 2.750$ with a determinant coefficient $r^2 = 0.978$. As FCP increased from 12% to 96%, FNA was reduced by 12% to 97%. When the reduction in FNA was partitioned into different vegetation types, the relationships were still significant for broad-leaved forests (Fig. 4d; $y = -1.114x + 9.517$, $r^2 = 0.965$) and coniferous forests (Fig. 4e; $y = -1.044x + 4.219$, $r^2 = 0.970$). The relationship for grasslands was difficult to interpret because the number of comparisons was small (Fig. 4f).

Overall, fire had little influence on fuel N concen-

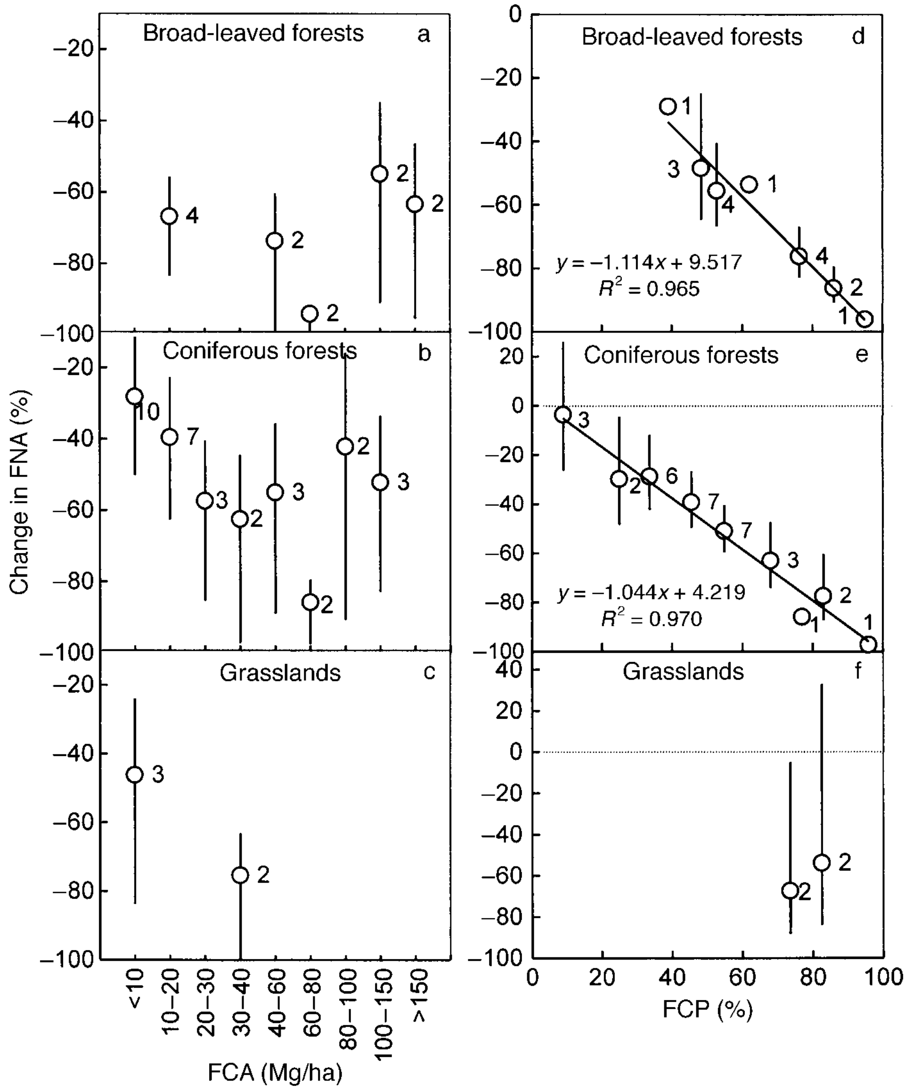

FIG. 4. The effects of FCA (a–c) and FCP (d–f) on the responses of FNA to fire in broad-leaved forests (a, d), coniferous forests (b, e), and grasslands (c, f). Open circles and vertical lines represent means ± 95% confidence intervals; numbers are the number of comparisons (*k*). See Figs. 1 and 3 for abbreviations.

tration (FNC). The effect of fire on FNC varied only with fuel types ($P < 0.01$; Table 3 and Fig. 5). Fire significantly reduced FNC for AGB (21%) and increased FNC for FF+US (38%), but had no significant effect on FNC for FF (−14%) and SL+FF (+0.02%).

The responses of SNA and SNC were not significantly affected by fire (Fig. 1). Of the seven independent variables examined in relation to the effects of fire on SNA and SNC, only soil sampling depth influenced the response of SNC (Table 3). When soil sampling depth was between 0–2.6 cm and 0–5.0 cm, SNC showed a significant reduction after fire (11%, Fig. 6). Responses of SNA and SNC showed little temporal variability after fire (Fig. 7).

Fire caused significant increases in soil NH_4^+ and NO_3^- (94% and 152%, respectively, Fig. 1). There was a substantial temporal variability in soil NH_4^+ and NO_3^- after fire (TAF, $P < 0.001$; Table 3). The increase of soil NH_4^+ was highest immediately after fire (0 month, 199%) and asymptotically decreased to the prefire level with time (Fig. 8a). Soil NO_3^- response to fire lagged behind that of NH_4^+. The fire-induced increase in soil NO_3^- was small immediately after fire (24%), reached a peak (322%) 7–12 mo after fire, and then gradually returned to the prefire level within 5 yr (Fig. 8b). Note that the estimated increase in soil NO_3^- in the period of 25–36 mo after fire was very high, which was determined from only three samples and might be biased.

Subdatasets from the peak responses of soil NH_4^+ (TAF = 0 mo, k = 29) and NO_3^- (TAF = 7–12 mo, k = 36) were drawn to analyze the influences of different independent variables on the responses of soil NH_4^+

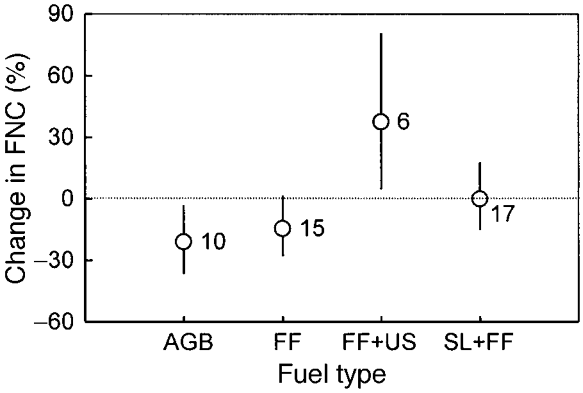

FIG. 5. The effect of fuel type on the response of FNC to fire. Open circles and vertical lines are means ±95% confidence intervals; numbers are the number of comparisons (k). See Figs. 1 and 2 for abbreviations.

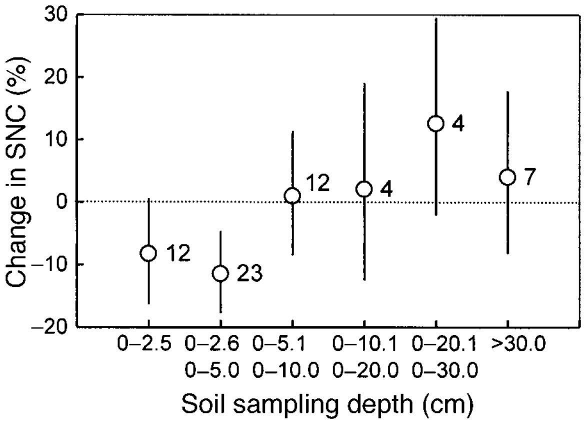

FIG. 6. The effect of soil sampling depth on the response of SNC to fire. Open circles and vertical lines are means ±95% confidence intervals; numbers are the number of comparisons (k). See Fig. 1 for abbreviations.

and NO_3^- to fire. Fire type had significant influences on the peak responses of soil NH_4^+ ($P < 0.001$) and NO_3^- ($P < 0.01$) to fire (Table 3). Soil NH_4^+ increased by 125% for prescribed burning, 358% for slash burning, and 1071% for wildfire (Fig. 9a). The fire-induced peak increase in soil NO_3^- was 129% for prescribed burning, 3750% for slash burning, and 929% for wildfire (Fig. 9b). Similar to SNC, the fire-induced peak responses of soil NH_4^+ ($P < 0.001$, $k = 28$) and NO_3^- ($P < 0.05$, $k = 36$) were significantly affected by soil sampling depth, with the smallest depth having the greatest peak response (Fig. 10). When soil sampling depth was within 2.5 cm, the peak increases in both soil NH_4^+ (614%) and NO_3^- (3277%) were significantly larger than those with the sampling depth from 0–5.0 cm to 0–10.0 cm (64% and 283% for NH_4^+ and NO_3^-, respectively, Fig. 10).

DISCUSSION

In this study, we used a meta-analysis method to search for the general patterns in the effects of fire on ecosystem N pools and dynamics from highly variable results of individual fire research projects reported in the literature. The results of our meta-analysis indicate that fire significantly reduces fuel N amount, increases soil NH_4^+ and NO_3^-, and has no significant effect on fuel N concentration, soil N amount, and soil N concentration. The fire-induced reduction in fuel N amount varies with vegetation type, fuel type, fuel consumption amount, and fuel consumption percentage. Fire-induced increases in soil NH_4^+ and NO_3^- are influenced by fire type, time after fire, and soil sampling depth (Table 3). It appears that our meta-analysis successfully integrates the scientific literature to identify the general patterns of the short-term effects of fire on N pools and dynamics in terrestrial ecosystems. In the following sections, we will discuss these effects in more detail as well as the implications of our results for fire research and management.

Fire and fuel N pools

It is commonly accepted in the literature that fuel N loss is related to fire intensity (Knight 1966, DeBano et al. 1979, Marion et al. 1991, Gillon et al. 1995). The fire intensity was quantitatively represented in this study by two variables: fuel consumption amount and fuel consumption percentage because fuel load was a

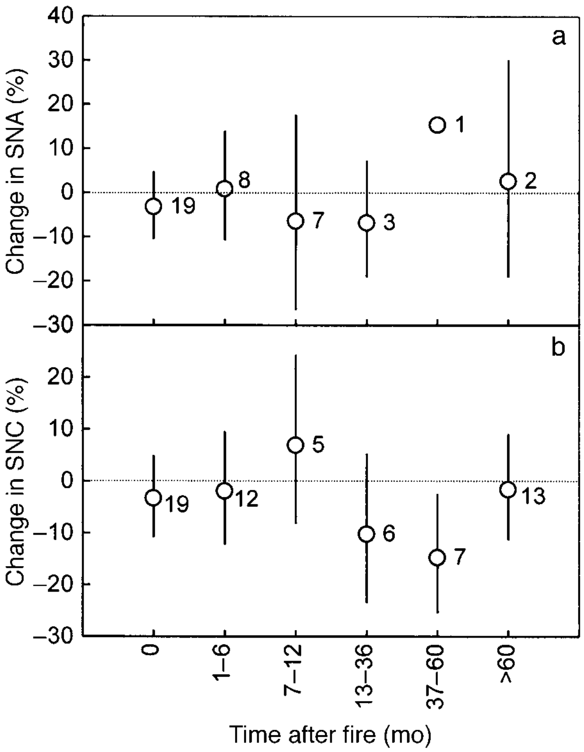

FIG. 7. Temporal dynamics of the responses of (a) SNA and (b) SNC to fire after burning. Open circles and vertical lines are means ±95% confidence intervals; numbers are the number of comparisons (k). See Fig. 1 for abbreviations.

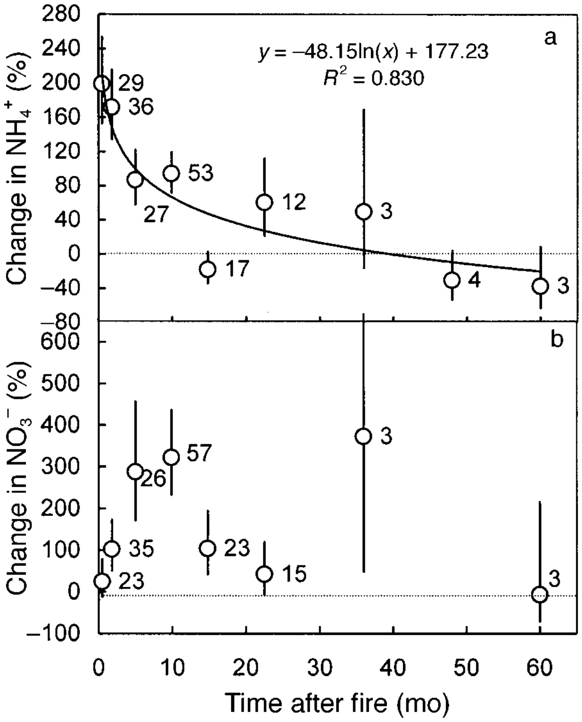

FIG. 8. Temporal dynamics of the responses of soil (a) NH_4^+ and (b) NO_3^- after fire. Open circles and vertical lines are means ±95% confidence intervals; numbers are the number of comparisons (k).

(data not shown). Although analysis of raw data reached conclusions similar to those by meta-analysis regarding fuel N loss, response ratios used in the meta-analysis facilitated statistical comparisons among different projects with diverse vegetation types and other independent variables.

Vegetation type and fuel type affect the loss of fuel N mainly through the influences of fuel consumption percentage as well as other fuel properties (i.e., amount, flammability, distribution, compaction, size, density, moisture content, and chemical constituents; Binkley et al. 1992*a*, Kauffman et al. 1994). The responses of fuel N amount to fire for broad-leaved forests (−71%), coniferous forests (−48%), and grasslands (−60%) corresponded well with the mean fuel consumption percentage for broad-leaved forests (64%), coniferous forests (48%), and grasslands (62%). Similarly, the magnitude of the N loss during fire for different fuel types (73% for AGB > 54% for FF > 49% for SL+FF) was consistent with that of fuel consumption percentage (68% for AGB > 54% for FF > 48% for SL+FF; note that shrublands and FF+US were not discussed here because of their smaller number of comparisons). Other factors, such as fire regimes (e.g., frequency, intensity, and season), weather conditions (humidity and wind speed), and topography, have also been documented to influence fuel N loss during combustion by affecting major contributor to fire intensity (Whelan 1995). Although fuel N loss during burning significantly varied with both fuel consumption amount and percentage, the response ratio of FNA to fire was more strongly correlated with fuel consumption percentage than amount. The strong correlation resulted largely from the fact that both the response ratio and fuel consumption percentage are relative values. A given absolute quantity of N loss may be converted to different percentages for diverse ecosystems. For example, grasslands have lower aboveground biomass and lower N amount than forests. The mean loss of 120 kg N/ha in grasslands represented 53% of the fuel N amount according to all the datasets in our database whereas the mean loss of 228 kg N/ha accounted for only 43% of the fuel N amount in the coniferous forests. When the amount of N loss (y, kg/ha) was plotted against fuel consumption amount (x, Mg/ha) across all studies, a strong linear regression was found ($y = 6.037x + 41.761$, determinant coefficient $r^2 = 0.802$, $P < 0.001$, $k = 57$). Similar regression relationships between the amount of N loss and FCA have been reported by other researchers (Raison et al. 1985*a*, Little and Ohmann 1988, Hobbs et al. 1991, Marion et al. 1991, Gillon et al. 1995, O'Connell and McCaw 1997). There was no linear correlation between fuel consumption amount and the percentage of fuel N loss or between fuel consumption percentage and the amount of fuel N loss

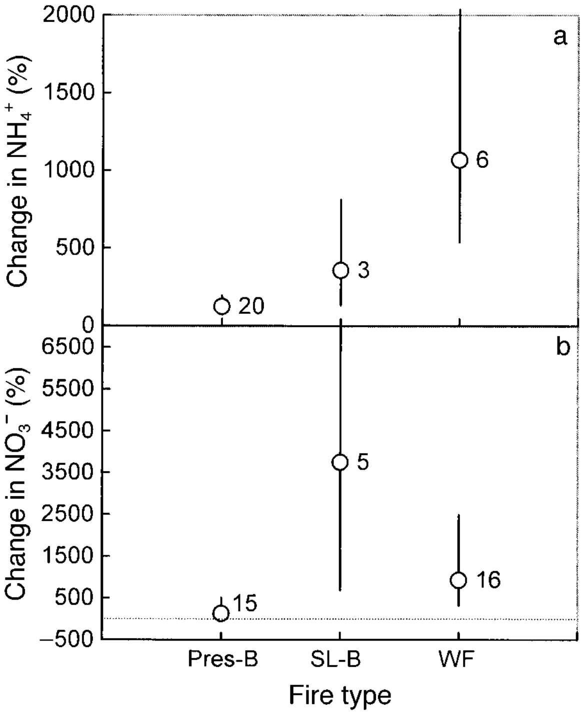

FIG. 9. The effect of fire type on the peak responses of soil (a) NH_4^+ and (b) NO_3^- to fire. Open circles and vertical lines are means ±95% confidence intervals; numbers are the number of comparisons (k). Pres-B = prescribed burning, SL-B = slash burning, and WF = wildfire.

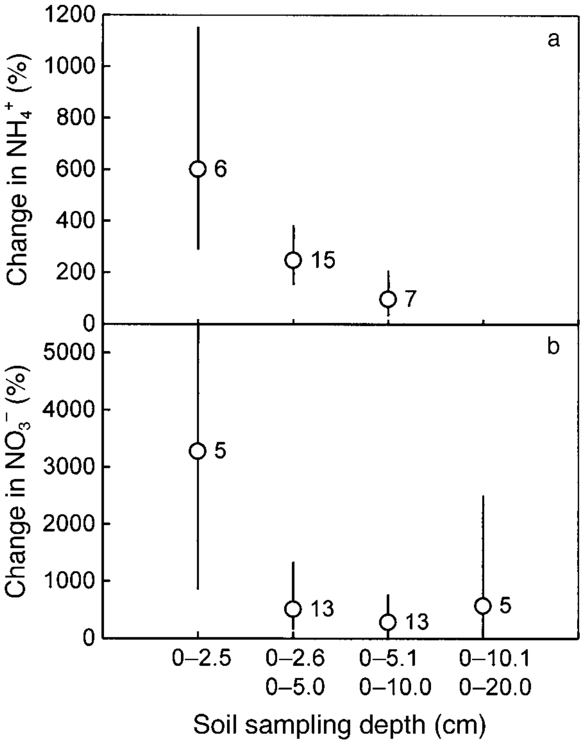

FIG. 10. The effect of soil sampling depth on the peak responses of soil (a) NH_4^+ and (b) NO_3^- to fire. Open circles and vertical lines are means ±95% confidence intervals; numbers are the number of comparisons (*k*).

fire behavior (Trollope 1984, De Ronde 1990, DeBano et al. 1998).

Our results indicate that fire did not significantly affect fuel N concentration (Fig. 1), which suggests that the composition and C/N ratio of fuel do not change substantially. This is consistent with conclusions reached by Schoch and Binkley (1986), Binkley et al. (1992*b*), and O'Lear et al. (1996). The lack of an effect of fire on fuel N concentration was also reflected by the slope of 0.926 between the response of fuel N amount and fuel consumption percentage, which was not significantly different from 1 ($P > 0.05$).

Fire and total soil N pools

It has long been controversial in fire ecology whether or not fire significantly alters total soil N pools. Total soil N has been reported to increase (Klemmedson et al. 1962, Christensen 1973, Covington and Sackett 1986, Kovacic et al. 1986, Schoch and Binkley 1986), decrease (DeBano and Conrad 1978, DeBano et al. 1979, Raison et al. 1985*a, b*, Kutiel and Naveh 1987, Bell and Binkley 1989, Kutiel et al. 1990, Groeschl et al. 1993), or remain unchanged (Alban 1977, Richter et al. 1982, Binkley et al. 1992*a*, Knoepp and Swank 1993) after fire. Our analysis indicates that fire had no significant influence on soil N amount or concentration across all studies.

One of the major reasons why fire does not significantly affect total soil N is that fire-induced change in soil N is relatively small compared with the total amount of soil N within a certain sampling depth (Wright and Bailey 1982, Gillon and Rapp 1989). For example, fire-induced N loss of 65 kg/ha in Arizona chaparral only accounts for 5% of the total of 1300 kg N/ha in the upper soil layer (0–10 cm; DeBano et al. 1998). Across all the studies in our database, the mean change in SNA after fire was 43 kg N/ha, which accounted for only 3% of the preburn SNA (1481 kg N/ha). The relatively small change in total soil N cannot be detected due to the large variations in sampling, measurement, and soil N amount within each study and/or across all studies.

Inconsistency of sampling depth may have also contributed to the lack of statistical significance in the response of soil N to fire. The soil layer that is most influenced by fire is limited to the upper several centimeters. The main reason is that temperatures above 100°C are seldom reached in subsurface soil before the surface soil water evaporates completely (DeBano and Conrad 1978). DeBano and Conrad (1978) and Kutiel and Naveh (1987) suggested that the major changes in soil nutrient pools after fire would take place in the upper 0–2 cm layer of the mineral soil and that the magnitude of the changes would be correlated with the intensity and duration of the fire. If soil samples were stratified into thinner layers, significant responses of N in the topsoil might be detected. For example, in Aleppo pine forest in Israel, Kutiel and Naveh (1987) found a 25% decrease in soil N in the upper 2 cm layer after a wildfire. In our meta-analysis, we found a significant decrease in SNC (11%) with soil sampling depth ranging from 0–2.6 cm to 0–5.0 cm. The diminishing peak responses of soil NH_4^+ and NO_3^- to fire with increasing sampling depth also support this conclusion. Because most studies have not taken this issue into consideration, we recommend using thinner and consistent soil sampling depths to facilitate comparisons across different ecosystem types.

Many factors may influence the postfire pools of total soil N. These factors include soil moisture (Wright and Bailey 1982), N deposition (Christensen and Muller 1975, Grier 1975, Christensen 1994), N transformations (fixation, nitrification, ammonification, denitrification; Kutiel et al. 1990), leaching (DeBano and Conrad 1978), soil erosion (DeBano and Conrad 1978, Diaz-Fierros et al. 1990), plant uptake (Richter et al. 1982, Kaye et al. 1999), microbial immobilization (Adams and Attiwill 1991, Kaye et al. 1999), and spatial heterogeneity (Turner et al. 1997, Grogan et al. 2000). These factors and their variabilities complicate the temporal variation in total soil N after fire and may be responsible for the inconsistency of results reported in the scientific literature. The inconsistent results yield a large standard deviation and reduce the statistical power to detect changes in total soil N pools after fire.

Fire and available soil N

Available soil N (NH_4^+ and NO_3^-) can be readily taken up and assimilated by plants and thus is important for plant growth and recovery of primary productivity after fire (Raison 1979). Although the total soil N pools are not significantly affected by fire, there are significant increases in soil NH_4^+ and NO_3^- after fire. This result is consistent with those of other studies (Klemmedson et al. 1962, Christensen 1973, Dunn and DeBano 1977, Kovacic et al. 1986, Kutiel et al. 1990, Rapp 1990, Singh et al. 1991, Covington and Sackett 1992, Knoepp and Swank 1993, Singh 1994, Kaye and Hart 1998). Knoepp and Swank (1993) suggested that the increase in soil NH_4^+ after fire results from two processes: (1) volatilization of organic N from the soil surface and its condensation after downward movement into cooler soil layer and (2) increases in N mineralization caused by altered micro-climate, soil temperature and pH value, and microbial activities.

The temporal patterns of soil NH_4^+ and NO_3^- responses to fire identified in our meta-analysis are similar to those found by Covington et al. (1991) and DeBano et al. (1998). Elevated soil NH_4^+ generally persists for several months (Wilbur and Christensen 1983, Adams and Attiwill 1986) and then declines to the prefire level one year after fire (Covington et al. 1991, Monleon et al. 1997) because of increased nitrification, leaching (Dudley and Lajtha 1993), microbial immobilization, and plant uptake (Kaye et al. 1999). The increased soil NH_4^+, together with the altered soil pH, temperature, microbial activity, and decreased allelopathy, contributes to the increased soil N nitrification rates after fire (Christensen 1973) and results in the NO_3^- increase (Christensen 1973, Raison 1979, Kovacic et al. 1986, Kutiel and Naveh 1987, Covington et al. 1991, Baldwin and Morse 1994, Kaye and Hart 1998).

Implications for fire research and management

Our meta-analysis has identified the general patterns of the short-term effects of fire on N pools and dynamics in terrestrial ecosystems. However, the long-term effects of fire on ecosystem N are yet to be evaluated. Nitrogen pools in natural ecosystems have been built up over decades, centuries, even millennia, and much of the N is locked into very slowly cycling pools. Rapid and substantial losses of N through fuel combustion may presumably alter the long-term dynamics of N cycling (Ojima et al. 1990, 1994, Seastedt and Ramundo 1990, Binkley et al. 1992*a*, Blair 1997) and influence primary productivity, species composition, and community succession (McNabb and Cromack 1990, DeBano 1991, Raison et al. 1993, Ojima et al. 1994, Seastedt et al. 1994, Hoffmann 1999). Frequent burning depletes ecosystem N pools because N replenishment is usually less than fire-induced N loss. Models simulating annual burning in tallgrass prairie suggest that soil N pools are stable initially (1–3 yr) and then decrease whereas soil N pools increase continually in the absence of burning (Ojima et al. 1990). However, few studies have been done on how the short-term responses of N to fire influence the function and structure of terrestrial ecosystems in the long term. To improve our understanding on these issues, properly designed and long-term experimental studies are needed. Such studies should use consistent methods to facilitate comparison and integration of results across various terrestrial ecosystems.

The responses of different ecosystems to fire-induced N changes vary with their vegetation type, inherent fertility, and ability to replenish N. Some ecosystems (e.g., tropical forests and savanna) are more sensitive to N loss than other ecosystems because they retain a relatively large proportion of N in the biomass (Menaut et al. 1992). In such N-limited ecosystems, fire-induced N loss can severely impact the long-term primary productivity (DeBano et al. 1998). In contrast, the coniferous forests in western Oregon are reported to maintain productive stands after losing >1.1 Mg/ha of N during stand-replacing fires (McNabb and Cromack 1990). Therefore, frequent burning as a management practice may benefit ponderosa pine forests but may be harmful for tropical forests and savanna.

Different ecosystems have different mechanisms and abilities to replenish N after fire. For example, it requires 10 yr or more for Australian eucalypt forests to naturally replace an ~50% fuel N loss caused by repeated low-intensity burning (Raison et al. 1993). On the other hand, the neotropical dry forests of northeastern Brazil need >100 yr of fallow to replace a loss of more than 500 kg N/ha (equivalent to 95% aboveground biomass N) in a severe fire (Kauffman et al. 1993). Thus, fire regimes (including frequency, interval, and season) should be determined according to the ability of different ecosystems to replenish N.

The high level of available soil N (NH_4^+ and NO_3^-) after fire may compensate for the ecosystem N reduction during burning and enhance postfire plant growth (DeBano et al. 1977, 1998). Therefore, frequent burning can be used to enhance soil N availability in some ecosystems (e.g., southwestern ponderosa pine forests in USA, Covington and Sackett 1986). Elevated soil N availability after fire, however, may not be desirable in other ecosystems. For example, a twofold increase in available soil N in South Africa lowland fynbos after fire can be detrimental to the survival of indigenous species adapted to an N impoverished habitat (Musil and Midgley 1990). Hence, fire-induced increase of soil N availability may be used to promote plant growth and primary productivity in ponderosa pine forests after fire but may adversely change species composition in South Africa lowland fynbos.

Vegetation-specific responses of ecosystems to fire and fire-induced N changes necessitate appropriate fire management programs for different ecosystems. The positive vs. negative, short-term vs. long-term effects of fire on ecosystem N, species composition, and primary productivity should be weighed for implementation of any fire management programs. Mechanisms and practices to restore and replenish N after fire should also be implemented to maintain the long-term balance of N cycling and primary productivity, particularly in N-limited ecosystems.

In conclusion, our meta-analysis indicates that fire significantly reduces fuel N amount, increases soil ammonium and nitrate availability, but does not affect fuel N concentration or total soil N amount or concentration. The reduction of fuel N amount during fire varies with vegetation type, fuel type, and fuel consumption amount and percentage. The fire-induced increases in soil ammonium and nitrate vary with fire type, time after fire, and soil sampling depth. While the general patterns of the short-term effects of fire on N pools and dynamics emerge clearly from our study, the long-term effects of fire on ecosystem N, species composition, and primary productivity are yet to be evaluated. Finally, our study illustrates vegetation-specific responses of N to fire that necessitate appropriate fire management programs for different terrestrial ecosystems.

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Literature Cited

Adams, M. A., and P. M. Attiwill. 1986. Nutrient cycling and N mineralization in Eucalypt forests of southeastern Australia. II. Indices of N mineralization. Plant and Soil **92**:341–362.

Adams, M. A., and P. M. Attiwill. 1991. Nutrient balance in forests of northern Tasmania. 2. Alteration of nutrient availability and soil water chemistry as a result of logging, slash-burning and fertilizer application. Forest Ecology and Management **44**:115–131.

Adams, P. W., and J. R. Boyle. 1980. Effects of fire on soil nutrients in clearcut and wholetree sites in central Michigan. Soil Science Society of America Journal **44**:847–850.

Ahlgren, I. F., and C. E. Ahlgren. 1960. Ecological effects of forest fires. Botanical Review **26**:483–533.

Alban, D. H. 1977. Influence on soil properties of prescribed burning under mature red pine. USDA Forest Service, Research Paper **NC-139**. North Central Forest Experimental Station, St. Paul, Minnesota, USA.

Anderson, R. C., and E. S. Menges. 1997. Effects of fire on sandhill herbs: nutrients, mycorrhizae, and biomass allocation. American Journal of Botany **84**:938–948.

Andreu, V., J. L. Rubio, J. Forteza, and R. Cerni. 1996. Post-fire effects on soil properties and nutrient losses. International Journal of Wildland Fire **6**:53–58.

Arianoutsou-Faraggitaki, M., and N. S. Magaris. 1982. Decomposers and the fire cycle in a phryganic (east Mediterranean) ecosystem. Microbial Ecology **8**:91–98.

Arnqvist, G., and D. Wooster. 1995. Meta-analysis: synthesizing research findings in ecology and evolution. Trends in Ecology and Evolution **10**:236–240.

Baldwin, I. T., and L. Morse. 1994. Up in smoke. II. Germination of *Nicotiana attenuata* in response to smoke-derived cues and nutrients in burned and unburned soils. Journal of Chemical Ecology **20**:2373–2391.

Beaton, J. D. 1959. The influence of burning on soil in the timber range area of Lac Le Jeune, British Columbia. II. Chemical properties. Canadian Journal of Soil Science **39**: 6–11.

Belillas, C. M., and M. C. Feller. 1998. Relationship between fire severity and atmospheric and leaching nutrient losses in British Columbia's Coastal Western Hemlock Zone Forests. International Journal of Wildland Fire **8**:87–101.

Bell, R. L., and D. Binkley. 1989. Soil N mineralization and immobilization in response to periodic prescribed fire in a loblolly pine plantation. Canadian Journal of Forest Research **19**:816–820.

Binkley, D., et al. 1992*a*. Group report: impacts of fires on ecosystems. Pages 359–372 *in* P. J. Crutzen and J. G. Goldammer, editors. Fire in the environment: the ecological, atmospheric, and climatic importance of vegetation fires. John Wiley & Sons, Chichester, UK.

Binkley, D., D. Richter, M. B. David, and B. Caldwell. 1992*b*. Soil chemistry in a loblolly/longleaf pine forest with interval burning. Ecological Applications **2**:157–164.

Blackwell, B., M. C. Feller, and R. Trowbridge. 1995. Conversion of dense lodgepole pine stands in west-central British Columbia into young lodgepole pine plantations using prescribed fire. 2. Effect of burning treatments on tree seedling establishment. Canadian Journal of Forest Research **25**:175–183.

Blair, J. M. 1997. Fire, N availability, and plant response in grasslands: a test of the transient maxima hypothesis. Ecology **78**:2359–2368.

Blank, R. R., and D. C. Zamudio. 1998. The influence of wildfire on aqueous-extractable soil solutes in forested and wet meadow ecosystems along the eastern front of the Sierra-Nevada Range, California. International Journal of Wildland Fire **8**:79–85.

Boerner, R. E. J., T. R. Lord, and J. C. Peterson. 1988. Prescribed burning in the oak–pine forest of the New Jersey Pine Barrens: effects on growth and nutrient dynamics of two *Quercus* species. The American Midland Naturalist **120**:108–119.

Bosch, J. M., R. E. Schulze, and F. J. Kruger. 1984. The effect of fire on water yield. Pages 327–348 *in* P. D. Booysen and N. M. Tainton, editors. Ecological studies 48: ecological effects of fire in South African ecosystems. Springer-Verlag, New York, New York, USA.

Busch, D. E., and S. D. Smith. 1993. Effects of fire on water and salinity relations of riparian woody taxa. Oecologia **94**: 186–194.

Christensen, N. L. 1973. Fire and nutrient cycle in California chaparral. Science **181**:66–68.

Christensen, N. L. 1977. Fire and soil-plant nutrient relations in a pine-wiregrass Savanna on the coastal plain of North Carolina. Oecologia **31**:27–44.

Christensen, N. L. 1987. The biogeochemical consequences of fire and their effects on the vegetation of the coastal plain of southeastern United States. Pages 1–22 *in* L. Trabaud, editor. The role of fire in ecological systems. SPB Academic Publishing, the Hague, the Netherlands.

Christensen, N. L. 1994. The effect of fire on physical and chemical properties of soil in Mediterranean-climate shrublands. Pages 79–95 *in* J. M. Moreno and W. C. Oechel, editors. The role of fire in Mediterranean-type ecosystems. Springer-Verlag, New York, New York, USA.

Christensen, N. L., and C. H. Muller. 1975. Effect of fire on factors controlling plant growth in Adenostoma Chaparral. Ecological Monographs **45**:29–55.

Clements, F. E. 1916. Plant succession—an analysis of the development of vegetation. Carnegie Institute. Washington Publishing, Washington, D.C., USA.

Clinton, B. D., J. M. Vose, and W. T. Swank. 1996. Shifts in aboveground and forest floor carbon and nitrogen pools after felling and burning in the southern Appalachians. Forest Science **42**:431–441.

Collins, S. L., S. M. Glenn, and D. J. Gibson. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. Ecology **76**:486–492.

Collins, S. L., and L. L. Wallace. 1990. Fire in North American tallgrass prairie. University of Oklahoma Press, Norman, Oklahoma, USA.

Covington, W. W., L. F. DeBano, and T. G. Huntsberger. 1991. Soil N changes associated with slash pile burning in pinyon-juniper woodlands. Forest Science **37**:347–355.

Covington, W. W., and S. S. Sackett. 1984. The effect of a prescribed burn in southwestern ponderosa pine on organic matter and nutrients in woody debris and forest floor [*Pinus ponderosa*, nutrient cycling, ecological role of fire]. Forest Science **30**:183–192.

Covington, W. W., and S. S. Sackett. 1986. Effect of periodic burning on soil N concentrations in ponderosa pine. Soil Science Society of America Journal **50**:452–457.

Covington, W. W., and S. S. Sackett. 1992. Soil mineral N changes following prescribed burning in ponderosa pine. Forest Ecology and Management **54**:175–191.

Curtis, P. S. 1996. A meta-analysis of leaf gas exchange and N in trees grown under elevated carbon dioxide. Plant, Cell and Environment **19**:127–137.

Curtis, P. S., and X. Z. Wang. 1998. A meta-analysis of elevated CO_2 effects on woody plant mass, form and physiology. Oecologia **113**:299–313.

DeBano, L. F. 1991. The effect of fire on soil properties. Pages 151–156 *in* A. E. Harvey and L. F. Neuenschwander, editors. Proceedings—management and productivity of Western-Montane forest soils. USDA Forest Service, General Technical Report **INT-280**.

DeBano, L. F., and C. E. Conrad. 1978. The effect of fire on nutrients in a chaparral ecosystem. Ecology **59**:489–497.

DeBano, L. F., P. H. Dunn, and C. E. Conrad. 1977. Fire's effect on physical and chemical properties of chaparral soils. Pages 65–74 *in* USDA Forest Service, General Technical Report **WO-3**.

DeBano, L. F., G. E. Eberlein, and P. H. Dunn. 1979. Effects of burning on chaparral soils: I. Soil N. Soil Science Society of America Journal **43**:504–509.

DeBano, L. F., D. Neary, and P. F. Folliott. 1998. Fire's effects on ecosystems. John Wiley & Sons, New York, New York, USA.

De Ronde, C. 1990. Impact of prescribed fire on soil properties—comparison with wildfire effects. Pages 127–126 *in* J. G. Goldammer and M. T. Jenkins, editors. Fire in ecosystem dynamics: Mediterranean and northern perspectives. SPB Academic Publishing, the Hague, the Netherlands.

Diaz-Fierros, F., E. Benito, A. Vega, A. Castelao, B. Soto, R. Perez, and T. Taboada. 1990. Solute loss and soil erosion in burnt areas from Galicia (NW Spain). Pages 103–116 *in* J. G. Goldammer and M. J. Jenkins, editors. Fire in the ecosystem dynamics: Mediterranean and northern perspectives. SPB Academic Publishing, the Hague, the Netherlands.

Dudley, J. L., and K. Lajtha. 1993. The effects of prescribed burning on nutrient availability and primary production in sandplain grasslands. The American Midland Naturalist **130**:286–298.

Dumontet, S., H. Dienel, A. Scopa, A. Mazzatura, and A. Saracino. 1996. Post-fire soil microbial biomass and nutrient content of a pine forest soil from a dunal Mediterranean environment. Soil Biology and Biochemistry **28**: 1467–1475.

Dunn, P. H., and L. F. DeBano. 1977. Fire's effect on biological and chemical properties of chaparral soils. Pages 75–84 *in* USDA Forest Service, General Technical Report **WO-3**.

Dyrness, C. T., K. Van Cleve, and J. D. Levison. 1989. The effect of wildfire on soil chemistry in four forest types in interior Alaska. Canadian Journal of Forest Research **19**: 1389–1396.

Ellis, R. C., and A. M. Graley. 1983. Gains and losses in soil nutrients associated with harvesting and burning eucalypt rainforest. Plant and Soil **74**:437–450.

Ellis, R. C., R. K. Lowry, and S. K. Davis. 1982. The effect of regeneration burning upon the nutrient status of soil in two forest types in southern Tasmania. Plant and Soil **65**: 171–186.

Ewel, J., C. Berish, B. Brown, N. Price, and J. Raich. 1981. Slash and burn impact on a Costa Rican wet forest site. Ecology **62**:816–829.

Feller, M. C. 1988. Relationships between fuel properties and slashburning-induced nutrient losses. Forest Science **34**: 998–1015.

Fenn, M. E., M. A. Poth, J. D. Aber, J. S. Baron, B. T. Bormann, D. W. Johnson, A. D. Lemly, S. G. McNulty, D. F. Ryan, and R. Stottlemyer. 1998. N excess in North American ecosystem: predisposing factors, ecosystem responses, and management strategies. Ecological Applications **8**: 706–733.

Fowells, H. A., and R. E. Stephenson. 1933. Effect of burning on forest soils. Soil Science **38**:175–181.

Fuller, W. H., S. Shannon, and P. S. Burgess. 1955. Effect of burning on certain forest soils of Northern Arizona. Forest Science **1**:44–50.

Gillon, D., V. Gomendy, C. Houssard, J. Maréchal, and J. C. Valette. 1995. Combustion and nutrient losses during laboratory burns. International Journal of Wildland Fire **5**:1–12.

Gillon, D., and M. Rapp. 1989. Nutrient losses during a winter low-intensity prescribed fire in a Mediterranean forest. Plant and Soil **120**:69–77.

Grier, C. C. 1975. Wildfire effects on nutrient distribution and leaching in a coniferous ecosystem. Canadian Journal of Forest Research **5**:599–607.

Groeschl, D. A., J. E. Johnson, and D. W. Smith. 1993. Wildfire effects on forest floor and surface soil in a Table Mountain Pine–pitch pine forest. International Journal of Wildland Fire **3**:149–154.

Grogan, P., T. D. Bruns, and F. S. Chapin III. 2000. Fire effects on ecosystem nitrogen cycling in a California bishop pine forest. Oecologia **122**:537–544.

Grove, T. S., A. M. O'Connell, and G. M. Dimmock. 1986. Nutrient changes in surface soils after intense fire in jarrah (*Eucalyptus marginata* Donn ex Sm.) forest. Australian Journal of Ecology **11**:303–317.

Gurevitch, J., and L. V. Hedges. 1993. Meta-analysis: Combining the results of independent experiments. Pages 378–389 *in* S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York, New York, USA.

Gurevitch, J., and L. V. Hedges. 1999. Statistical issues in ecological meta-analyses. Ecology **80**:1142–1149.

Gurevitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. The American Naturalist **140**:539–572.

Halvorson, J. J., H. Bolton, Jr., and J. L. Smith. 1997. The pattern of soil variables related to *Artemisia tridentata* in a burned shrub-steppe site. Soil Science Society of America Journal **61**:287–294.

Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. Ecology **80**:1150–1156.

Hedges, L., and I. Olkin. 1985. Statistical methods for meta-analysis. Academic Press, Orlando, Florida, USA.
Herman, D. J., and P. W. Rundel. 1989. Nitrogen isotope fractionation in burned and unburned chaparral soils. Soil Science Society of America Journal **53**:1229–1236.
Hobbs, N. T., D. S. Schimel, C. E. Owensby, and D. S. Ojima. 1991. Fire and grazing in the tallgrass prairie: contingent effect on nitrogen budgets. Ecology **72**:1374–1382.
Hoffmann, W. A. 1999. Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. Ecology **80**:1354–1369.
Humphreys, F. R., and M. J. Lambert. 1965. An examination of a forest site which has ash-bed effect. Australian Journal of Soil Research **3**:81–94.
Johnson, D. W., R. B. Susfalk, R. A. Dahlgren, and J. M. Klopatek. 1998. Fire is more important than water for N fluxes in semi-arid forests. Environmental Science and Policy **1**:79–86.
Kauffman, J. B., D. L. Cummings, and D. E. Ward. 1994. Relationships of fire, biomass and nutrient dynamics along a vegetation gradient in the Brazilian cerrado. Journal of Ecology **82**:519–531.
Kauffman, J. B., D. L. Cummings, and D. E. Ward. 1998. Fire in the Brazilian Amazon: 2. Biomass, nutrient pools, and losses in cattle pastures. Oecologia **114**:415–427.
Kauffman, J. B., D. L. Cummings, D. E. Ward, and R. Babbitt. 1995. Fire in the Brazilian Amazon: 1. Biomass, nutrient pools, and losses in slashed primary forests. Oecologia **104**: 397–408.
Kauffman, J. B., R. L. Sanford, Jr., D. L. Cummings, I. H. Salcedo, and E. V. S. Sampaio. 1993. Biomass and nutrient dynamics associated with slash fires in neotropical dry forest. Ecology **74**:140–151.
Kaye, J. P., and S. C. Hart. 1998. Ecological restoration alters N transformations in a ponderosa pine-bunchgrass ecosystem. Ecological Applications **8**:1052–1060.
Kaye, J. P., S. C. Hart, R. C. Cobb, and J. E. Stone. 1999. Water and nutrient outflow following the ecological restoration of a ponderosa pine-bunchgrass ecosystem. Restoration Ecology **7**:252–261.
Kirkpatrick, J. B., and K. J. M. Dickinson. 1984. The impact of fire on Tasmanian alpine vegetation and soils. Australian Journal of Botany **32**:613–629.
Klemmedson, J. O., A. M. Schulitz, H. Jenny, and H. H. Biswell. 1962. Effect of prescribed burning of forest litter on total soil N. Soil Science Society of America Proceedings **26**:200–202.
Knight, H. 1966. Loss of nitrogen from the forest floor by burning. Forestry Chronicle **42**:149–152.
Knoepp, J. D., and W. T. Swank. 1993. Site preparation burning to improve southern Appalachian pine-hardwood stands: N responses in soil, soil water, and streams. Canadian Journal of Forest Research **23**:2263–2270.
Koricheva, J., S. Larsson, E. Haukioja, and M. Keinanen. 1998. Regulation of woody plant secondary metabolism by resource availability: hypothesis testing by means of meta-analysis. Oikos **83**:212–226.
Kovacic, D. A., D. M. Swift, J. E. Ellis, and T. E. Hankonson. 1986. Immediate effects of prescribed burning on mineral soil N in ponderosa pine of New Mexico. Soil Science **141**: 71–76.
Kozlowski, T. T., and C. E. Ahlgren. 1974. Fire and ecosystems. Academic Press, New York, New York, USA.
Kutiel, P., and Z. Naveh. 1987. The effect of fire in a pine forest soil. Plant and Soil **104**:269–274.
Kutiel, P., Z. Naveh, and H. Kutiel. 1990. The effect of a wildfire on soil N and vegetation in an Allepo pine forest on Mount Carmel, Israel. Pages 85–94 *in* J. G. Goldammer and M. J. Jenkins, editors. Fire in ecosystem dynamics: Mediterranean and northern perspectives. SPB Academic Publishing, the Hague, the Netherlands.
Little, S. N., and G. O. Klock. 1985. The influence of residue removal and prescribed fire on distributions of forest nutrients. USDA Forest Service, Research Paper **PNW-338**.
Little, S. N., and J. L. Ohmann. 1988. Estimating N loss from forest floor during prescribed fires in Douglas-Fir/Western Hemlock clearcuts. Forest Science **34**:152–164.
Ludwig, B., P. K. Khanna, R. J. Raison, and K. L. Jacobsen. 1998. Modelling cation composition of soil extracts under ashbeds following an intense slashfire in a eucalypt forest. Forest Ecology and Management **103**:9–20.
Lynds, G. Y., and I. T. Baldwin. 1998. Fire, N, and defensive plasticity in *Nicotiana attenuata.* Oecologia **115**:531–540.
Lynham, T. J., G. M. Wickware, and J. A. Mason. 1998. Soil chemical changes and plant succession following experimental burning in immature jack pine. Canadian Journal of Soil Science **78**:93–104.
Maars, R. H., R. D. Roberts, and R. A. Skeffington. 1983. Nitrogen in the development of ecosystems. Pages 131–137 *in* J. A. Lee, S. McNeill, and I. H. Rorison, editors. Nitrogen as an ecological factor. Blackwell Science Publishing, Oxford, UK.
Macadam, A. M. 1987. Effects of broadcast slash burning on fuels and soil chemical properties in the sub-boreal spruce zone of central British Columbia. Canadian Journal of Forest Research **17**:1577–1584.
Maggs, J. 1988. Organic matter and nutrients in the forest floor of a *Pinus elliottii* plantation and some effects of prescribed burning and superphosphate addition. Forest Ecology and Management **23**:105–119.
Marion, G. M., and C. H. Black. 1988. Potentially available N and phosphorus along a chaparral fire cycle chronosequence. Soil Science Society of America Journal **52**:1155–1162.
Marion, G. M., J. M. Moreno, and W. C. Oechel. 1991. Fire severity, ash deposition, and clipping effects on soil nutrients in chaparral. Soil Science Society of America Journal **55**:235–240.
McNabb, D. H., and K. Cromack, Jr. 1990. Effects of prescribed fire on nutrients and soil productivity. Pages 125–142 *in* J. D. Walstad, S. R. Radosevich, and D. V. Sandberg, editors. Natural and prescribed fire in Pacific Northwest forests. Oregon State University Press, Corvallis, Oregon, USA.
Medina, E. 1982. N balance in the Trachypogon grasslands of Central Venezuela. Plant and Soil **67**:305–314.
Menaut, J.-C., L. Abbadie, and P. M. Vitousek. 1992. Nutrient and organic dynamics in tropical ecosystems. Pages 215–231 *in* P. J. Crutzen and J. G. Goldammer, editors. Fire in the environment: the ecological, atmospheric, and climatic importance of vegetation fires. John Wiley & Sons, Chichester, UK.
Monleon, V. J., K. Cromack, Jr., and J. D. Landsberg. 1997. Short- and long-term effects of prescribed underburning on N availability in ponderosa pine stands in central Oregon. Canadian Journal of Forest Research **27**:369–378.
Musil, C. F., and C. F. Midgley. 1990. The relative impact of invasive Australian acacies, fire and season on the soil chemical status of a sand plain lowland fynbos community. South African Journal of Botany **56**:419–427.
Nissley, S. D., R. J. Zasoski, and R. E. Martin. 1980. Nutrient changes after prescribed surface burning of Oregon ponderosa pine stands. Pages 214–219 *in* R. E. Martin, E. L. Edmonds, D. A. Faulkner, J. B. Harrington, D. M. Fuquay, B. J. Stocks, and S. Barr, edtiors. Proceedings of the sixth conference on fire and forest meteorology (April 22–24, 1980, Seattle, Washington). Society of American Foresters, Washington D.C., USA.

Nye, P. H., and D. J. Greenland. 1964. Changes in the soil after clearing tropical forest. Plant and Soil **11**:101–112.

O'Connell, A. M., T. S. Grove, and G. M. Dimmock. 1979. The effects of a high intensity fire on nutrient cycling in jarrah forest. Australian Journal of Ecology **4**:331–337.

O'Connell, A. M., and W. L. McCaw. 1997. Prescribed burning of thinning slash regrowth stands of karri (*Eucalyptus diversicolor*). 2. N budgets in pre- and post-burn fuel. International Journal of Wildland Fire **7**:41–49.

Ojima, D. S., W. J. Parton, D. S. Schimel, and C. E. Owensby. 1990. Simulated impacts of annual burning on prairie ecosystems. Pages 118–132 *in* S. L. Collins and L. L. Wallace, editors. Fire in North American tallgrass prairie. University of Oklahoma Press, Norman, Oklahoma, USA.

Ojima, D. S., D. S. Schimel, W. J. Parton, and C. E. Owensby. 1994. Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. Biogeochemistry **24**:67–84.

O'Lear, H. A., T. R. Seastedt, J. M. Briggs, J. M. Blair, and R. A. Ramundo. 1996. Fire and topographic effects on decomposition rates and N dynamics of buried wood in tallgrass prairie. Soil Biology and Biochemistry **28**:323–329.

Osenberg, C. W., O. Sarnelle, S. D. Cooper, and R. D. Holt. 1999. Resolving ecological questions through meta-analysis: goals, metrics, and models. Ecology **80**:1105–1117.

Pendergrass, K. L., P. M. Miller, J. B. Kauffman, and T. N. Kaye. 1999. The role of prescribed burning in maintenance of an endangered plant species, *Lomatium bradshawii*. Ecological Applications **9**:1420–1429.

Poulin, R. 1994. Meta-analysis of parasite-induced behavioral changes. Animal Behavior **48**:137–146.

Pietikäinen, J., and H. Fritze. 1995. Clear-cutting and prescribed burning in coniferous forest: comparison of effects on soil fungal and total microbial biomass, respiration activity and nitrification. Soil Biology and Biochemistry **27**: 101–109.

Raison, R. J. 1979. Modification of the soil environment by vegetation fires, with particular reference to N transformations: a review. Plant and Soil **51**:73–108.

Raison, R. J. 1983. Effects of regeneration burning on the properties of forest soils in southern Tasmania: comments on recent study by Ellis *et al.* (1982). Plant and Soil **74**: 453–455.

Raison, R. J., P. K. Khanna, and P. V. Woods. 1985*a.* Mechanisms of element transfer to the atmosphere during vegetation fires. Canadian Journal of Forest Research **15**:132–140.

Raison, R. J., P. K. Khanna, and P. V. Woods. 1985*b.* Transfer of elements to the atmosphere during low-intensity prescribed fires in three Australian subalpine Eucalypt forests. Canadian Journal of Forest Research **15**:657–664.

Raison, R. J., A. M. O'Connell, P. K. Khanna, and H. Keith. 1993. Effects of repeated fire on nitrogen and phosphorus budgets and cycling processes in forest ecosystems. Pages 347–363 *in* L. Tradbuad and P. Prodon, editors. Fire in Mediterranean ecosystems. Commission of the European countries, Ecosystem research report 5, Brussels, Belgium.

Ram, S. C., and P. S. Ramakrishnan. 1992. Fire and nutrient cycling in Seral grassland of Cherrapunji in Northeastern India. International Journal of Wildland Fire **2**:131–138.

Rapp, M. 1990. N status and mineralization in natural and disturbed Mediterranean forests and coppices. Plant and Soil **128**:21–30.

Rashid, G. H. 1987. Effects of fire on soil carbon and N in a Mediterranean oak forest of Algeria. Plant and Soil **103**: 89–93.

Redmann, R. E. 1991. N losses to the atmosphere from grassland fires in Saskatchewan, Canada. International Journal of Wildland Fire **1**:239–244.

Richter, D. D., C. W. Raiston, and W. R. Harms. 1982. Prescribed fire: effects on water quality and forest nutrient cycling. Science **215**:661–663.

Rosenberg, M. S., D. C. Adams, and J. Gurevitch. 1997. MetaWin: statistical software for meta-analysis with resampling tests. Version 1.0. Sinauer, Sunderland, Massachusetts, USA.

Schindler, D. W., R. W. Newbury, K. G. Beaty, J. Prokopowich, T. Kuszczynski, and J. A. Dalton. 1980. Effects of a windstorm and forest fire on chemical losses from forested watersheds and on the quality of receiving streams. Canadian Journal of Fishery and Aquatic Science **37**:328–334.

Schoch, P., and D. Binkley. 1986. Prescribed burning increased N availability in a mature loblolly pine stand. Forest Ecology and Management **14**:13–22.

Seastedt, T. R. 1988. Mass, N, and phosphorus dynamics in foliage and root detritus of tallgrass prairie. Ecology **69**: 59–65.

Seastedt, T. R., C. C. Coxwell, D. S. Ojima, and W. J. Parton. 1994. Controls of plant and soil carbon in a semihumid temperate grassland. Ecological Applications **4**:344–353.

Seastedt, T. R., and R. A. Ramundo. 1990. The influence of fire on belowground processes of tallgrass prairie. Pages 99–117 *in* S. L. Collins and L. L. Wallace, editors. Fire in North American tallgrass prairies. University of Oklahoma Press, Norman, Oklahoma, USA.

Singh, R. S. 1994. Changes in soil nutrients following burning of dry tropical savanna. International Journal of Wildland Fire **4**:187–194.

Singh, R. S., A. S. Raghubanshi, and J. S. Singh. 1991. N-mineralization in dry tropical savanna: effects of burning and grazing. Soil Biology and Biochemistry **23**:269–273.

Stednick, J. D., L. N. Tripp, and R. J. McDonald. 1982. Slash burning effects on soil and water chemistry in southeastern Alaska. Journal of Soil and Water Conservation **37**:126–128.

Stinson, K. J., and H. A. Wright. 1969. Temperatures of headfires in the southern mixed prairie of Texas. Journal of Range Management **22**:169–174.

St. John, T. W., and P. W. Rundel. 1976. The role of fire as a mineralizing agent in a Sierran Coniferous Forest. Oecologia **25**:35–45.

Tonhasca, A., and D. N. Byrne. 1994. The effects of crop diversification on herbivorous insects: a meta-analysis approach. Ecological Entomology **19**:239–244.

Trabaud, L. 1994. The effect of fire on nutrient losses and cycling in a *Quercus coccifera* garrigue (Southern France). Oecologia **99**:379–386.

Trollope, W. S. W. 1984. Fire behavior. Pages 199–217 *in* P. de V. Booysen and N. M. Tainton, editors. Ecological effects of fire in South African ecosystems. Ecological Studies 48. Springer-Verlag, New York, New York, USA.

Turner, C. L., J. M. Blair, R. J. Schartz, and J. C. Neel. 1997. Soil N and plant responses to fire, topography, and supplemental N in tallgrass prairie. Ecology **78**:1832–1843.

Uhl, C., and C. F. Jordan. 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia. Ecology **65**:1476–1490.

Vance, E. D., and G. S. Henderson. 1984. Soil N availability following long-term burning in an oak-hickory forest. Soil Science Society of America Journal **48**:184–190.

Vander Werf, E. 1992. Lack's clutch size hypothesis: an examination of the evidence using meta-analysis. Ecology **73**: 1699–1705.

Vitousek, P. M., and P. A. Matson. 1985. Disturbance, N availability, and N losses in an intensively managed loblolly pine plantation. Ecology **66**:1360–1376.

Vose, J. M., and W. T. Swank. 1993. Site preparation burning to improve southern Appalachian pine-hardwood stands:

aboveground biomass, forest floor mass, and N and carbon pools. Canadian Journal of Forest Research **23**:2255–2262.

Vose, J. M., W. T. Swank, B. D. Clinton, J. D. Knoepp, and L. W. Swift. 1999. Using stand replacement fires to restore southern Appalachian pine–hardwood ecosystems: effects on mass, carbon, and nutrient pools. Forest Ecology and Management **114**:215–226.

Wagle, R. F., and T. W. Eakle. 1979. A controlled burn reduces the impact of a subsequent wild fire in a ponderosa pine vegetation type. Forest Science **25**:123–129.

Wells, C. G., R. E. Campell, L. F. DeBano, C. E. Lewis, R. L. Fredriksen, E. C. Franklin, R. C. Froelich, and P. H. Dunn. 1979. Effects of fire on soil: a state-of-knowledge review. USDA Forest Service, General Technical Report **WO-7**.

Weston, C. J., and P. M. Attiwill. 1990. Effects of fire and harvesting on N transformations and mobility in soils of *Eucalyptus regnans* forests of southeastern Australia. Oecologia **83**:20–26.

Whelan, R. J. 1995. The ecology of fire. Cambridge University Press, Cambridge, UK.

White, E. W., W. W. Thompson, and F. R. Gartner. 1973. Heat effects on nutrient release from soils under ponderosa pine. Journal of Range Management **26**:22–24.

Wilbur, R. B., and N. L. Christensen. 1983. Effects of fire on nutrient availability in a North Carolina Coastal Plain Pocosin. The American Midland Naturalist **110**:54–62.

Wolf, F. M. 1986. Meta-analysis: quantitative methods for research synthesis. SAGE Publications, Beverly Hills, California, USA.

Woodmansee, R. G., and L. S. Wallach. 1981. Effects of fire on biogeochemical cycles. Pages 649–669 *in* F. E. Clark and T. Roswall, editors. Terrestrial N cycles: processes, ecosystem strategies and management impacts. Ecology Bulletin 33. Swedish Natural Science Research Council, Stockholm, Sweden.

Wooster, D. 1994. Predator impacts on stream benthic prey. Oecologia **99**:7–15.

Wright, H. A., and A. W. Bailey. 1982. Fire ecology: United States and Southern Canada. John Wiley & Sons, New York, New York, USA.