Impacts of fire and fire surrogate treatments on ecosystem nitrogen storage patterns: similarities and differences between forests of eastern and western North America

R.E.J. Boerner, Jianjun Huang, and Stephen C. Hart

Abstract: The Fire and Fire Surrogates (FFS) network is composed of 12 forest sites that span the continental United States, all of which historically had frequent low-severity fire. The goal of the FFS study was to assess the efficacy of three management treatments (prescribed fire, mechanical thinning, and their combination) in reducing wildfire hazard and increasing ecosystem sustainability. This paper describes the impact of the FFS treatments on nitrogen (N) storage and distribution. At the network scale, total ecosystem N averaged 4480 $kg \cdot ha^{-1}$, with ~9% in vegetation, ~9% in forest floor, ~2% in deadwood, and ~80% in soil. The loss of vegetation N to fire averaged (±SE) 25 ± 11 $kg \cdot ha^{-1}$, whereas the mechanical and combined mechanical and fire treatments resulted in N losses of 133 ± 21 and 145 ± 19 $kg \cdot ha^{-1}$, respectively. Western coniferous forests lost more N from each treatment than did eastern forests. None of the manipulative FFS treatments impacted >10%–15% of total N of these ecosystems. Management strategies that maximize ecosystem carbon (C) gain by minimizing loss of N should be a focus in western forests, where C and N cycling are tightly linked, but perhaps not in those eastern forests where atmospheric N deposition has decoupled C and N cycles.

Résumé : Le réseau national sur l'utilisation du feu et d'un substitut du feu comprend 12 stations forestières qui couvrent le continent américain. Toutes ces stations ont subi dans le passé de fréquents incendies de faible intensité. Le but du réseau était d'évaluer l'efficacité de trois traitements d'aménagement (brûlage dirigé, éclaircie mécanique et leur combinaison) pour réduire les risques d'incendie et augmenter la durabilité des écosystèmes. Cet article décrit l'impact des traitements appliqués dans le réseau sur la distribution et le stockage de N. À l'échelle du réseau, N total dans les écosystèmes atteignait en moyenne 4480 $kg \cdot ha^{-1}$, dont ~9 % se retrouvaient dans la végétation, ~9 % dans la couverture morte, ~2 % dans le bois mort et ~80 % dans le sol. La perte de N dans la végétation causée par le feu atteignait en moyenne 25 ± 11 $kg \cdot ha^{-1}$ tandis que l'éclaircie mécanique seule et l'éclaircie mécanique accompagnée du brûlage dirigé causaient des pertes respectives de 133 ± 21 et 145 ± 19 $kg \cdot ha^{-1}$. Les forêts de conifères de l'ouest ont perdu plus de N que les forêts de l'est à la suite de chaque traitement. Aucun des traitements n'a eu d'impact sur plus de 10–15 % de la quantité totale de N dans ces écosystèmes. Les stratégies d'aménagement devraient avoir comme objectif de maximiser le gain en C des écosystèmes en minimisant la perte de N dans les forêts de l'ouest où le recyclage de C et le recyclage de N sont étroitement reliés mais peut-être pas dans les forêts de l'est où les dépôts atmosphériques de N ont découplé les cycles de C et N.

[Traduit par la Rédaction]

Introduction

The forests of North America have been actively managed by humans for several millennia (Mann 2005). The selective removal of trees and other plants of various species and sizes for specific economic uses and the use of dormant-season fire to control forest stand structure both clearly predate European colonization of North America. Since the early twentieth century wildfire has been actively suppressed, even in forests with a long history of frequent low-severity fire. This practice has resulted in changes in community structures, fuel complexes, and rates of element cycling, even as these ecosystems have been exposed to additional anthropogenic stresses, such as atmospheric nitrogen (N) and sulfur (S) deposition, and incipient climate change. Ensuring sustainability of these ecosystems for the

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economic and ecosystem services they supply has become increasingly challenging, as the unintended effects of continued fire suppression interact with these other stressors.

In the last decade, the potential use of forest ecosystems as sinks for anthropogenic CO_2 has added yet another impetus for ensuring the health and sustainability of the North American forests. The decoupling of carbon (C) and N cycles of many forested ecosystems in eastern North America because of human-caused increases in exogenous N inputs (Asner et al. 1997) makes an explicit understanding of the impacts of management on the N cycle particularly important in planning the future C economy.

The Fire and Fire Surrogates (FFS) network is composed of forested ecosystems arrayed across the conterminous United States from Washington and California in the west to Alabama, Ohio, and Florida in the east. All of the forest ecosystems represented in the FFS network share the attribute of having been converted by fire suppression and other management practices from forests that were subject to frequent low-severity fires during pre-Euro-American settlement to forests that are currently subject to infrequent but catastrophic fires. The primary goal of the FFS study was to assess the effectiveness and ecological consequences of alternative management strategies designed to simultaneously reduce wildfire hazard and restore ecosystem structure and function to a more sustainable condition. As such, the FFS study presents a unique opportunity to assess the storage and distribution of N of North American forest ecosystems in relation to geography, fire suppression, and forest management strategies. The specific objectives of this portion of the broader FFS study were to

- characterize the variation in total N ecosystem storage among North American forests in which fire suppression has affected ecosystem structure;
- characterize the distribution of stored N among ecosystem components in such forests;
- determine the proximate effects on N storage and distribution of three management modes intended to reduce wildfire hazard and restore presuppression forest structure: prescribed fire, mechanical thinning, and the combination of the two;
- quantify the geographic similarities and differences among forested ecosystems and in their responses to the FFS treatment alternatives.

Materials and methods

Study sites

The 12 FFS study sites ranged from Washington and California, in the west, to Florida and Ohio, in the east (Table 1). The designated FFS experimental design was a randomized complete block, with three blocks and four treatments (control, prescribed fire, mechanical thinning, and the combination of mechanical thinning and prescribed fire) allocated at random to those three blocks. Because of site-specific constraints, three of the 12 FFS sites were established as completely randomized designs (CA-N, CA-S, WA), with the four treatments allocated at random among the 12 treatment units, and at one site, the Blue Mountains site (OR), four replicates of each treatment were established in a completely randomized design. In addition, the Southern

Table 1. Geographic information for the 12 Fire and Fire Surrogates network sites.

Site	Geographic location	Facility	Forest type	Latitude (N)	Longitude (W)	Elevation (m)	Soil orders
CA-N	Southern Cascade Range, Calif	Klamath National Forest	Western mixed conifer	41°57′	121°86′	1630	Alfisols, Entisols
CA-C	Central Sierra Nevada, Calif.	Blodgett Experimental Forest	Western mixed conifer	38°90′	120°65′	1255	Alfisols
WA	Northeastern Cascade Range, Wash.	Wenatchee National Forest	Ponderosa pine – Douglas-fir	47°26′	120°32′	950	Alfisols, Mollisols
CA-S	Southern Sierra Nevada, Calif.	Sequoia-Kings Canyon National Park	Western mixed conifer	36°59′	118°76′	2025	Inceptisols
OR	Blue Mountains, Ore.	Wallowa-Whitman National Forest	Ponderosa pine – Douglas-fir	45°65′	117°23′	1255	Mollisols, Inceptisols
MT	Northern Rocky Mts., Mont.	Lubrecht Experimental Forest	Ponderosa pine – Douglas-fir	46°90′	113°43′	1150	Alfisols, Inceptisols
AZ	Southwestern Plateau, Ariz.	Coconino and Kaibab National Forests	Ponderosa pine	35°21′	111°85′	220	Alfisols, Mollisols
AL	Gulf Coastal Plain, Ala.	Solon-Dixon Forestry and Education Center	Longleaf pine – slash pine	31°16′	86°68′	50	Ultisols, Entisols
OH	Central Appalachian Plateau, Ohio	Vinton Furnace Experimental Forest, Tar Hollow and Zaleski State Forests	Appalachian oak	39°30′	84°54′	250	Alfisols, Inceptisols
NC	Southern Appalachian Mts., N.C.	Green River Game Lands	Appalachian oak	34°67′	82°84′	600	Ultisols, Inceptisols
SC	Southeastern Piedmont, S.C.	Clemson University Forest	Loblolly pine – oak	35°21′	82°37′	250	Alfisols, Inceptisols
FL	Florida Coastal Plain, Fla.	Myakka River State Park	Florida slash pine	27°26′	82°28′	25	Spodosols

Note: Sites are ordered by longitude from west to east.

Table 2. Mean net change in aboveground biomass carbon (C) and ground-fuel C (forest floor plus downed woody debris) as the result of treatment with prescribed fire, mechanical thinning, or their combination in 12 Fire and Fire Surrogates network sites.

		Aboveground biomass C (%)			Ground-fuel C		
Site	Site code	Fire	Mechanical	Mechanical + fire	Fire	Mechanical	Mechanical + fire
Southern Cascade Range	CA-N	–13.5	–29.4	–22.9	–74.4	na	na
Central Sierra Nevada	CA-C	–15.5	–13.7	–29.9	–66.9	–22.5	–72.6
Northeastern Cascade Range	WA	7.8	–33.8	–35.4	14.0	51.2	14.6
Southern Sierra Nevada	CA-S	–4.4	na	na	–73.7	na	na
Blue Mountains	OR	2.5	–28.3	–58.4	–73.5	–36.2	–62.9
Northern Rocky Mountains	MT	–6.5	–44.6	–57.0	–42.0	28.2	–24.9
Southwestern Plateau	AZ	0.3	–46.4	–45.7	–10.2	108.9	–24.5
Gulf Coastal Plain	AL	–2.5	–24.3	–23.7	–17.3	–6.3	–34.7
Central Appalachian Plateau	OH	–0.7	–27.6	–22.5	–2.2	60.6	29.5
Southeastern Piedmont	SC	–9.9	–26.8	–42.0	–44.6	21.3	–16.0
Southern Appalachians	NC	–9.0	–4.4	–15.3	–35.4	15.4	–30.5
Florida Coastal Plain	FL	–17.1	–21.9	–5.3	–33.8	–22.2	293.8
FFS network mean	FFS	–5.7	–27.4	–32.6	–38.3	19.8	7.2

Note: Data are from Boerner et al. (2008). na denotes data not available.

Sierra Nevada site (CA-S) was located in a National Park, and because of established National Park policy, mechanical treatments could not be implemented. The geography, geology, vegetation, soils, and prior management of each site are described in detail by McIver et al. (2008).

Each treatment unit was a minimum of 10 ha with a surrounding buffer zone of at least 4 ha. Both the treatment unit and the buffer received the experimental treatment. Among the 12 FFS sites, the treatment units (including the buffer) ranged in size from the minimum 14 ha to as large as 80 ha. The 12–16 treatment units within a site were as uniform as possible in landform characteristics, soil, vegetation, and land-use history.

Across the network, the prescribed fire treatment resulted in the removal of an average of 5.7% of the aboveground biomass and 38.3% of the ground-fuel mass (forest floor plus downed woody debris) (Table 2). In contrast, the mechanical treatment resulted in an average removal of 27.4% of aboveground biomass and a net addition of 19.8% to ground fuels. The combined mechanical and fire treatment resulted in the loss of 32.6% of aboveground biomass and a net addition of 7.2% to the ground-fuel mass (Table 2). Details of fire prescriptions, mechanical thinning protocols, and desired future condition profiles for each study site are described by McIver (2001).

In the designated FFS design, each treatment unit was overlain with a 50 m grid, with a minimum of 36 grid points geolocated within each treatment unit. Ten 0.1 ha rectangular permanent sampling plots were located at random within each treatment unit, with one corner anchored at a grid point. Two of the 12 FFS sites (CA-C, OR) deviated from this base design, as they instead had a larger number of 200–405 m^2 circular vegetation plots.

Vegetation components, soil, and fuels were sampled during the pretreatment growing season, the growing season immediately following the completion of the treatment implementation, and, where logistically possible, an additional posttreatment year as late in the funding period as possible (usually the second year after treatment, but the third or fourth year in one to two sites each). In an attempt to compensate for the these variations in the timing of the last sampling, we calculated the rates of change in the N pools on an annual basis; however, even with this adjustment, the lack of a second posttreatment sampling at some sites and the variations in the timing of the last sampling among those that did have one combine to reduce our confidence in our estimates of the network-wide effects of the treatments during the latter sampling period. Two sites (CA-N, OR) had incomplete pretreatment sampling because their treatments had been installed before the designated FFS design was established, and logistic constraints resulted in incomplete pretreatment sampling in one additional site (CA-S).

Field methods

Each live and dead tree ≥10 cm diameter at breast height (1.37 m, DBH) in each permanently marked vegetation plot was labeled, identified, and measured during the pretreatment sampling year and remeasured during each subsequent sampling. Stems that grew to the tree size class were marked, identified, and measured the year they were ≥10 cm DBH and were followed thereafter. Saplings (stems >1.37 m height but <10 cm DBH), seedlings (≤1.37 m height), and the cover of shrubs, forbs, and graminoids were measured in subplots nested within the larger vegetation plots in all sites. Shrub, forb, and graminoid biomasses were only measured directly in sites where these components were judged to be significant fuel sources. The number and size of the subplots varied among FFS sites in relation to stem density and plant diversity (details for each site are given by McIver 2001).

Standing deadwood was sampled using the same methods as those used for live vegetation. The mass of downed deadwood <150 mm in diameter was estimated using the planar intercept method of Brown (1974) supplemented with strip plots. Two 20 m transects were run from each of the 36 grid points in each treatment unit, and the number of intercepts of woody materials in four size classes (0–6, 6–25, 25–75, and 75–150 mm) was tallied. To assess the mass and spatial distribution of larger woody debris, strip plots (4 m × 20 m) were established at a minimum of 50% of

Fig. 1. Mean (plus one standard error) nitrogen storage (kilograms per hectare) in four ecosystem pools in the 12 Fire and Fire Surrogates network sites. The bar at the extreme right represents the network mean without the FL and CA-S sites. Site codes follow Table 1.

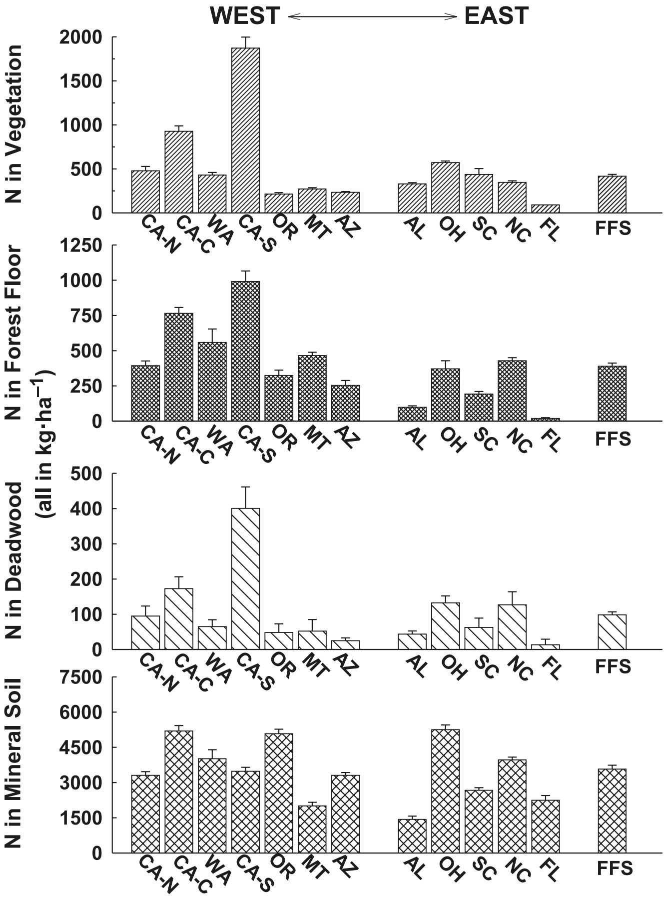
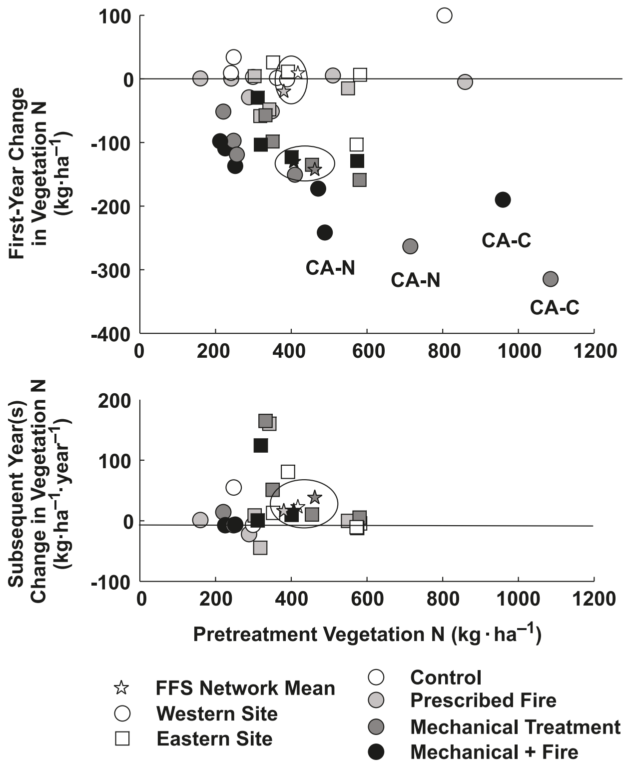


Fig. 2. Net changes in nitrogen (N) storage in aboveground vegetation during the first posttreatment year (top) and change from posttreatment year 1 to the next sampling period divided by years elapsed (bottom) resulting from the Fire and Fire Surrogates study treatments. Points specifically mentioned in the text are labeled with their site code. Site codes follow Table 1.



the grid points sampled by the planar intercept method. Within each strip plot, logs or parts of logs ≥1 m in length and >150 mm diameter at the larger end were identified, their length within the strip plots measured, and their diameters measured at their ends or at the points where they intercepted the boundary of the strip plot. Materials in the 75–150 and >150 mm size classes were identified to species where possible, and the decay condition of each piece was noted. Samples from each size subclass in each site were dried and weighed to produce mass estimates. Sampling of woody debris in all size classes was done during the pretreatment year, the initial posttreatment year, and (where possible) a later sampling year.

The mass of the forest floor (organic or O horizon) was considered to be the sum of the Oi, Oe, and Oa (L, F, and H) horizons (where present), exclusive of woody materials as defined above. To estimate forest floor mass, 0.1 m^2 plots were excavated at the end of each of the woody debris transects, the depth of each horizon was measured on all four faces of the excavated plot, and then each forest floor horizon was removed, dried, and weighed separately. This resulted in n = 36–72 for each forest floor horizon in each treatment unit. Regressions of forest floor mass on depth were then constructed for each treatment unit.

In plots that were to be burned (fire only and mechanical plus fire), a series of eight duff pins were installed in each of the 0.1 ha vegetation sampling plots prior to the fire, and the depth of each organic horizon was determined both before and after the fire. The mass–depth regressions generated by destructive sampling were then used to estimate the prefire and postfire organic horizon mass at each of those points.

Mineral soil samples for determination of soil total N concentration were taken from each permanent vegetation plot during midsummer of the pretreatment year, the first posttreatment year, and, for most FFS sites, the second, third, or fourth posttreatment year. Approximately 200 g fresh soil mass was collected 1–2 m from the opposite corners and midpoints of each of the long sides of each 0.10 ha sample plot. The O horizon, if present, was removed prior to sampling the mineral soil. If no distinct boundary occurred between the Oa subordinate O horizon (i.e., humic subhorizon) and the A master horizon, the Oa was included in the sampling of the surface mineral soil. Where a distinct boundary between the A and E horizons occurred, the full depth of the A horizon was sampled. If no E horizon was present, samples of the top 15 cm of the A horizon were taken.

Laboratory methods

We attempted to standardize laboratory methods across the 12 network sites. Bulk density was determined gravi-

Table 3. Nitrogen pools sizes (kilograms per hectare) in deadwood, forest floor, and mineral soil in temperate forest ecosystems.

Source	Ecosystem	Deadwood	Forest floor	Soil	Depth (cm)
Jurgensen et al. 1977	wcf	102 (2–231)	581 (161–1128)	2465 (1152–4030)	30
Debyle 1980	wcf		483 (462–504)	2002	15
Tinker and Knight 2000	wcf	35			
Covington and Sackett 1984	wcf		463		
Grier 1975	wcf		840	1470	36
Frazer et al. 1990	wcf			1715	14
Black and Harden 1995	wcf		790	3050	20
Jurgensen et al. 1977	wcf	35 (2–68)	462 (161–867)	2455 (1152–4030)	30
Monleon et al. 1997	wcf			1107 (1043–1208)	15
Baird et al. 1999	wcf		202 (183–220)	465 (300–630)	60
Johnson et al. 2000	wcf		380 (100–900)	3020 (1200–5100)	A horizon
Johnson and Curtis 2001	wcf	7 (0–14)	232 (202–265)	2529 (1413–3815)	40
Page-Dumroese and Jurgensen 2006	wcf			1294 (709–1975)	30
This study	wcf	75 (48–173)	485 (323–765)	3659 (1103–5643)	30
Wells 1971	scf		359		
McKee 1982	scf		268 (131–408)	694	5
Schoch and Binkley 1986	scf		229		
Groeschl et al. 1990	scf		577	328	10
This study	scf	53 (44–62)	145 (98–191)	1901 (1169–2633)	30
Johnson et al. 1982	edf		150	3863 (3565–3800)	
Vose and Swank 1993	mdc		323 (300–354)		
Knoepp and Swank 1997	mdc			1378 (986–1867)	20
Kaczmarek et al. 1995	edf		357 (254–609)	14 300 (7561–23 286)	30
Vose et al. 1999	mdc	43 (36–50)	329 (233–489)		
Johnson et al. 2000	edf			5867 (3200–9100)	A horizon
Idol et al. 2001	edf	20 (17–23)			
Finér et al. 2003	mdc	68	597	1707	20
Hubbard et al. 2004	edf	36	163		
This study	edf, mdc	130 (127–132)	400 (371–428)	4622 (4300–4944)	30

Note: Values are means, and the range is provided for studies that included multiple sites. Ecosystem codes are as follows: wcf, western coniferous forest; scf, southern coniferous forest; mdc, mixed deciduous and coniferous forest; edf, eastern deciduous forest.

metrically on a minimum of 20 intact soil cores per treatment unit or estimated from a minimum of 200 soil strength (penetrometer) measurements per treatment unit using site-specific regressions of bulk density on soil strength. Organic C and total N concentrations in soil and O horizons were determined by microDumas oxidation. Results from the six subsamples taken in or around each sample plot were averaged to give a single datum for each plot.

Estimation of standing N stocks

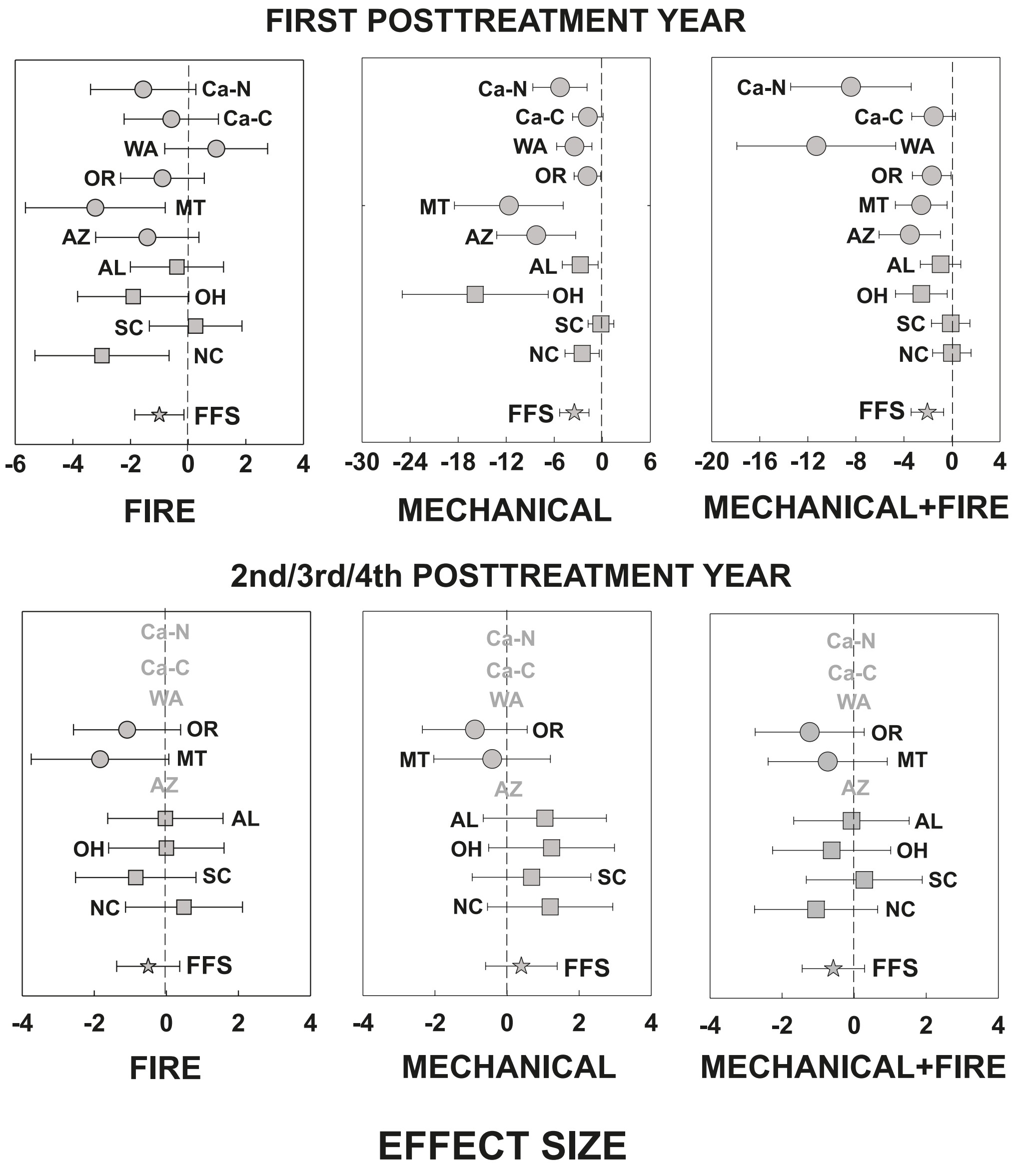
We relied on allometric equations to convert live and dead tree basal area and height measurements to biomass, using equations from the compilation of North American tree species biomass regressions of Jenkins et al. (2004). Although we initially employed species-specific equations for the dominant species where possible, inconsistencies among equations for a given species and among equations for closely related species led us to abandon this approach and favor the 10 species-group equations given by Jenkins et al. (2004), all of which had r^2 >0.938. Total dry biomass estimates from the species-group equations were then allocated into foliage, stem and branch bark, and stem and branch wood using the component ratio equations of Jenkins et al. (2003, cited in Jenkins et al. 2004). Within species groups, stemwood biomass estimates were adjusted using estimates of wood specific gravity derived from Jenkins et al. (2004).

For woody stems <10 cm DBH, we used a single biomass estimate for each species group as the geometric mean of the estimated biomass of 2.5, 5.0, 7.5, and 10.0 cm diameter stems, and we used that single estimate for all saplings of that group in the 2.5–10 cm DBH range. We validated these sapling estimates against output from a set of regressions that was based on stems that spanned those sizes (the *Cornus florida* equations from Boerner and Kost 1986).

As indicated above, C and N concentrations in soil organic matter and forest floor – organic horizon layers were determined empirically in each site. In contrast, analysis of C and N in vegetation and deadwood compartments were available for only a few sites; thus we depended on literature sources for estimates of N concentration in vegetation and deadwood in most sites. From the literature, we obtained estimates of N concentration in wood, branches, bark, and foliage for all of the tree species that accounted for >2% of the biomass in any given site, for coarse woody debris by decay class, and for understory vegetation (full listing of citations for C and N concentrations is given by Boerner et al. 2008).

As the depths of the rooting zone varied from ~30 to >150 cm among FFS sites, we adopted the approach of

Fig. 3. Summary of the meta-analysis of the effects of three Fire and Fire Surrogates (FFS) study treatments on aboveground vegetation nitrogen during the first posttreatment sampling year (top) and from posttreatment year 1 to the next sampling period divided by years elapsed (bottom). Symbols represent mean effect size, with horizontal lines depicting the 95% confidence interval for the mean effect size. Circles denote western sites, squares denote eastern sites, and the FFS network mean is indicated by the star. Sites for which insufficient data were available to test a given treatment–year combination are indicated by the site code in gray along the zero effect line. Site codes follow Table 1.



Johnson and Curtis (2001) for generating a single, depth-weighted estimate of total soil N in the rooting zone for use in further analysis, with the modal depth of the rooting zone among the FFS sites (30 cm) chosen as the arbitrary depth for estimation.

Data analysis

Although analysis of the effects of the FFS treatments on N stocks within a site could be analyzed in a straightforward manner using analysis of variance approaches, we felt this was not the most appropriate manner in which to analyze the results at the network scale. First, the specifics of the experimental design varied in subtle though important ways among the 12 sites. For example, some sites had sufficient pretreatment measurements to use pretreatment conditions as covariates, whereas others did not. Similarly, some sites established their treatment units in a spatial manner that would permit analysis as a complete block design, whereas others did not. In light of such differences, we judged that resorting to a least-common-denominator analysis of variance model would serve little purpose. Second, the variations among network sites in the total N stock and the variability in the distribution of N among vegetation, deadwood, forest floor, and soil were so great and the absolute magnitude of the effects of the FFS treatments were both so modest that any single analysis of variance based approach would be unproductive.

Instead, we first took a meta-analytical approach, as this would allow us to treat each network site as a single experiment with $n = 3$ for each treatment at each site (except OR in which $n = 4$). To adjust for the bias that can be introduced into the calculation of the site-specific effect size by low replication levels, we adjusted the effect size for the sample size using Hedge's d (Rosenberg et al. 2000). To calculate the cumulative effect size at the FFS network scale, we used a random-effects model because we assumed that variability among effect sizes was due to both subject-level "noise" and true unmeasured differences across studies (Raudenbush 1994; Rosenberg et al. 2000). This, in turn, required estimation of both the pooled study variance and the total heterogeneity of a given sample, with the latter being used to test the hypothesis that all effect sizes were equal with the χ^2 distribution with $k - 1$ degrees of freedom (Gurevitch and Hedges 1993).

Taking this approach required us to delete two of the 12 sites from the analysis: CA-S and FL. The full experimental design could not be implemented at the southern Sierra Nevada site (CA-S), as National Park regulations precluded the mechanical and combined mechanical and fire treatments. Including this site in the analysis would have biased the network-wide effect size estimates for the fire-only treatment, relative to that of the other two treatments. A wildfire during the first posttreatment year compromised two of three control units in the Florida Coastal Plain site (FL). With only a single control unit, we were unable to calculate estimates of dispersion for the control, thus making comparisons with the treated units impossible.

Results and discussion

Pretreatment pool sizes

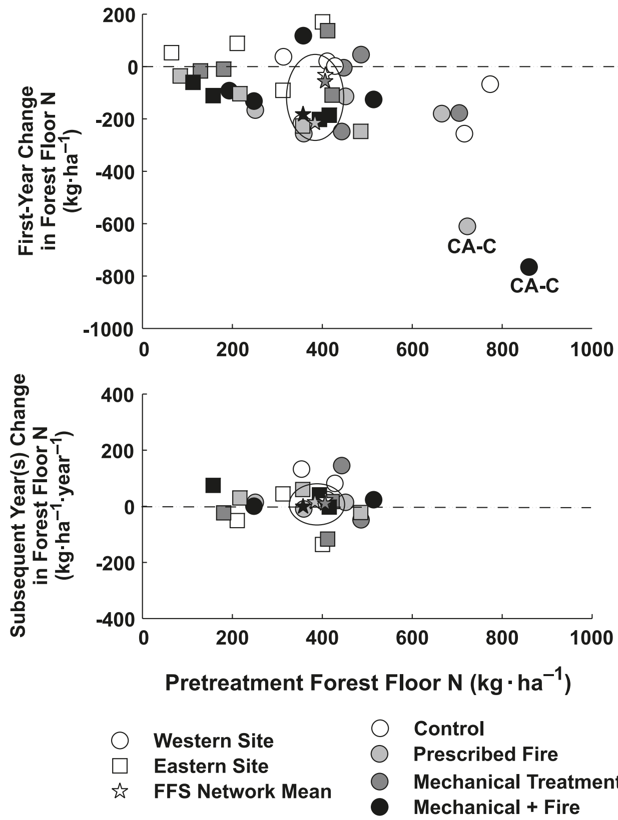
Prior to treatment, total ecosystem N storage across the network averaged (± one standard error) 4480 ± 197 kg·ha^{-1}, with approximately 9.3% ± 4.1% of the N in aboveground vegetation, 8.7% ± 4.4% in the forest floor, 1.8% ± 0.5% in deadwood, and 79.7% ± 3.7% in the mineral soil. The proportional distribution of N among those four components was similar to that reported for other temperate forests (e.g., Finér et al. 2003).

Aboveground vegetation N storage ranged from 200 to 500 kg·ha^{-1} in nine of the 12 sites, with two sites having two- to three-fold more N in vegetation (CA-S and CA-C) and one (FL) having considerably less (Fig. 1). This range compares well with previous estimates of standing stocks of N in aboveground vegetation of 415–450 kg·ha^{-1} (Johnson et al. 1982) and 259–439 kg·ha^{-1} (Clinton et al. 1996) in eastern deciduous forests, 312 kg·ha^{-1} in mixed forests (Finér et al. 2003), and 248 kg·ha^{-1} (Gessel et al. 1973) in coniferous forests.

Nitrogen storage in forest floor and deadwood (standing plus downed) averaged 408 ± 26 and 99 ± 8 kg·ha^{-1}, respectively, and varied among sites in parallel with vegetation N (Fig. 1). Forest floor N storage in the FFS sites was similar to results reported for other North American forests (Table 3). The strong parallels in vegetation and forest floor N pool sizes between the FFS forests and those forests studied previously (Table 3) supports our view that the suite of forested ecosystems selected for the FFS network were relatively representative of their regions.

Although our estimates of standing N stocks in deadwood fall well within the broad range reported for coniferous forests

Fig. 4. Net changes in nitrogen (N) storage in the forest floor during the first posttreatment year (top) and change from posttreatment year 1 to the next sampling period divided by years elapsed (bottom) resulting from the Fire and Fire Surrogates study treatments. Points specifically mentioned in the text are labeled with their site code. Format follows Fig. 3.

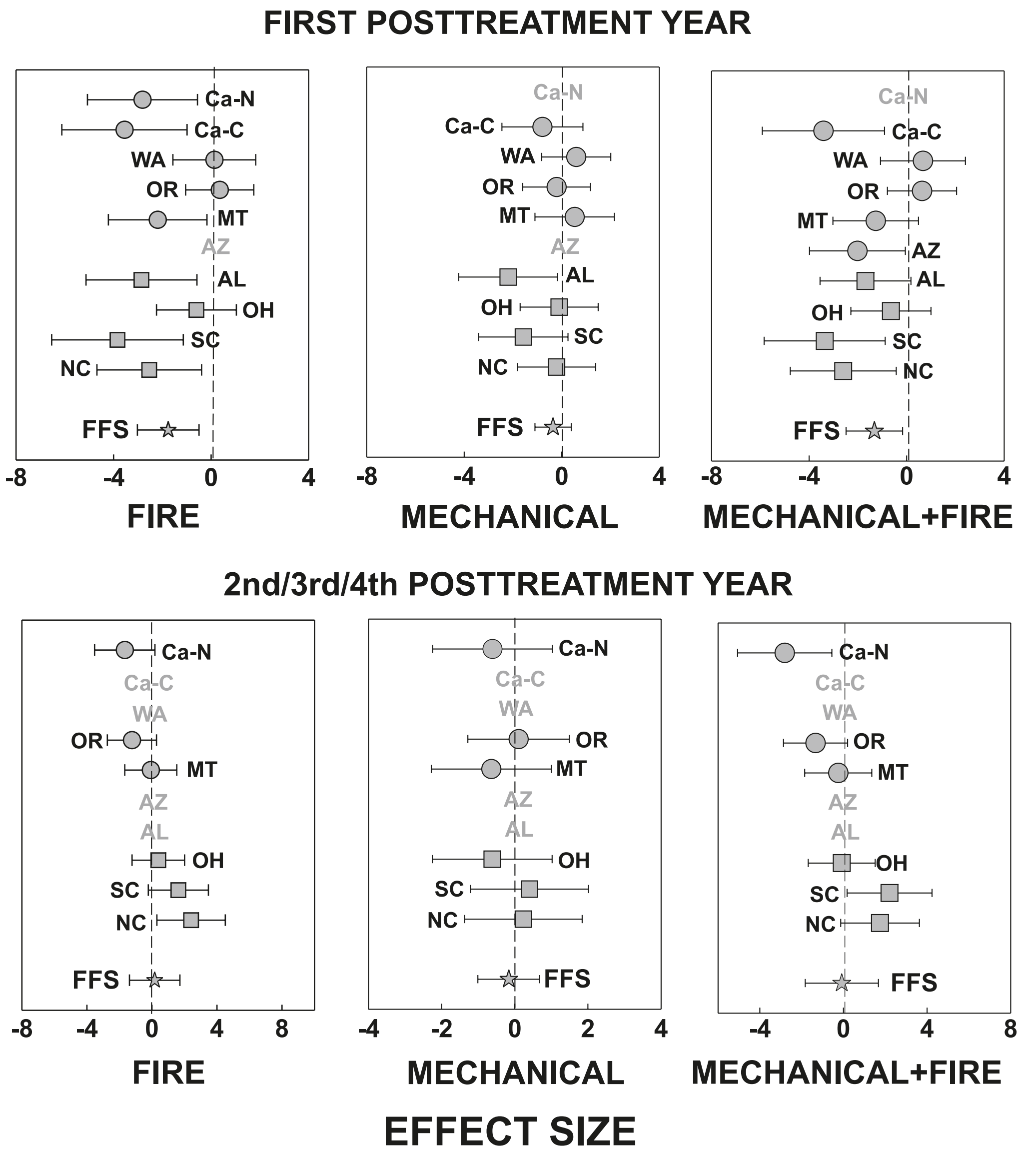


in western North America, they were considerably above previous estimates for deciduous forests of eastern North America (Table 3). Direct estimates of N stocks in deadwood are less common in the literature than are estimates of deadwood mass, and the estimates that have been published vary greatly in what suite of components they include. There appears to be little consistency in what combination of standing-dead trees (snags), fine woody debris, and coarse woody debris in various stages of decay is included in estimates. Although we considered using the available data on coarse woody debris mass to calculate a larger number of estimates of deadwood N for comparison, the relatively large range in the concentrations of C and N (and therefore C/N ratio) among species, regions, and decay classes (e.g., Lamlom and Savidge 2003) would have produced a set of calculated estimates with potentially large and unquantifiable error ranges.

Nitrogen stocks in mineral soil varied by less than a factor of three across the network and averaged approximately 3206 ± 437 kg·ha^{-1} (Fig. 1). The N stocks in soils underlying our western coniferous forests (mean of approximately 3171 ± 316 kg·ha^{-1}) and eastern forests (mean of approximately 4128 ± 883 kg·ha^{-1}) fell well within the ranges reported for similar ecosystems (Table 3) once the differences in soil depths among studies were taken into account.

The comparison of the distribution of N among ecosystem

Fig. 5. Summary of the meta-analysis of the effects of the three Fire and Fire Surrogates study treatments on forest floor nitrogen. Format follows Fig. 4.



components presented here contrasts strongly with our previously published estimates for C (Boerner et al. 2008). Whereas aboveground vegetation and soil organic matter contained approximately equal proportions of total ecosystem C (45% vegetation, 40% mineral soil), there was approximately ninefold more N stored in mineral soil than in aboveground vegetation. Thus, a considerably greater proportion of ecosystem C than N is subject to impact from both fire and mechanical treatments.

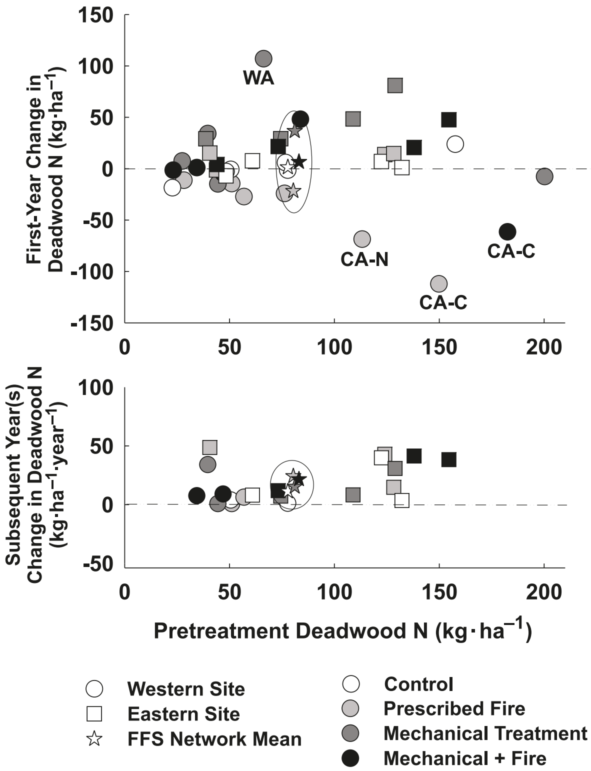
Treatment effects on N pools

First-year losses of vegetation N at the network scale in response to all three manipulative treatments were statistically significant (Fig. 2), though aboveground vegetation N stocks changed more as the result of the mechanical and combined mechanical and fire treatments than of the fire-only treatment (Fig. 2).

At the network scale, the loss of aboveground vegetation N to fire averaged 25 ± 11 kg·ha^{-1} (compared with a network-wide mean of 3 ± 7 kg·ha^{-1} in the controls, with the 95% confidence limits of –10 and 16 kg·ha^{-1}; Fig. 2). Only two individual sites exhibited significant losses of aboveground vegetation N as a result of prescribed fire alone (NC, MT) (Fig. 4).

The modest change in vegetation N stocks resulting from prescribed fire was not unexpected. Prescribed fire is often applied during the dormant season, thereby minimizing loss of green tissue, and given the long history of frequent low-severity fire in these ecosystem types, many of the woody species have resistant or resilient responses to such fire. For instance, Hubbard et al. (2004) conducted prescribed burns to remove understory and advanced regeneration in a Georgia oak–pine (*Quercus–Pinus*) forest. Although fire caused an average of 13% tree mortality, this value was not statistically significantly different from an average of zero mortality because of high spatial variability in fire severity. Similarly, Boerner (1983) observed no significant loss of biomass of overstory or understory vegetation following

Fig. 6. Net changes in nitrogen (N) storage in the deadwood during the first posttreatment year (top) and change from posttreatment year 1 to the next sampling period divided by years elapsed (bottom) resulting from the Fire and Fire Surrogates study treatments. Points specifically mentioned in the text are labeled with their site code. Format follows Fig. 3.



low-severity prescribed fire in a New Jersey Pine Barrens pine–oak forest.

The mechanical and combined mechanical and fire treatments resulted in a network-wide mean N loss from aboveground vegetation of approximately 133 ± 21 and 145 ± 19 kg·ha^{-1}, respectively, during the first growing season following treatment (Fig. 2). Together, the mechanical and mechanical plus fire treatments resulted in a mean N loss from aboveground vegetation of 158 ± 21 kg·ha^{-1} in western coniferous forest sites and 110 ± 14 kg·ha^{-1} in the eastern sites. Eight of 10 individual sites had significant reductions in vegetation N as a result of mechanical treatment, and six sites experienced significant reductions from the combined mechanical and fire treatment (Fig. 3). The greatest losses of vegetation N were in the mechanical and mechanical and fire treatments at CA-C and CA-N (Fig. 3).

The FFS mechanical treatments removed 14%–46% of the tree biomass (Table 2). The amount of N removed from aboveground vegetation from those treatments (mean of 103 ± 9 kg·ha^{-1} without the two relatively extreme sites, CA-C and CA-N) was about 30%–50% of the amounts reported after clear-cutting in western coniferous and eastern deciduous forests (260 and 177 kg·ha^{-1}, respectively; Mann et al. 1988) and in a mixed deciduous–coniferous forest in Tennessee (296 kg·ha^{-1}; Clinton et al. 1996).

At the network scale, N storage in aboveground vegetation changed little between the first posttreatment growing season and the last sampling period (hereafter referred to as "subsequent growing seasons"), regardless of treatment applied (Fig. 2). There were no significant changes in vegetation N during the subsequent sampling years at either the network or site levels (Fig. 3).

Network-wide losses of forest floor N to fire and combined mechanical and fire treatments averaged 215 ± 36 and 183 ± 45 kg·ha^{-1}, respectively (Fig. 4), and meta-analysis indicated that the first-year losses of forest floor N as a result of the fire and combined fire and mechanical treatments were statistically significant (Fig. 5). Six of the nine sites for which posttreatment forest floor N data were available had significant losses of forest floor N due to fire, and four of the nine had significant losses as the result of the combined mechanical and fire treatment (Fig. 5). Extreme values occurred with the fire and the combined mechanical and fire treatments at CA-C, which lost 610 and 766 kg·ha^{-1} during the initial posttreatment year, respectively (Fig. 4). On average, the western sites lost somewhat more forest floor N to the fire and combined mechanical and fire treatments (264 ± 52 and 217 ± 74 kg·ha^{-1}, respectively) than did the eastern sites (154 ± 43 and 140 ± 31 kg·ha^{-1}, respectively).

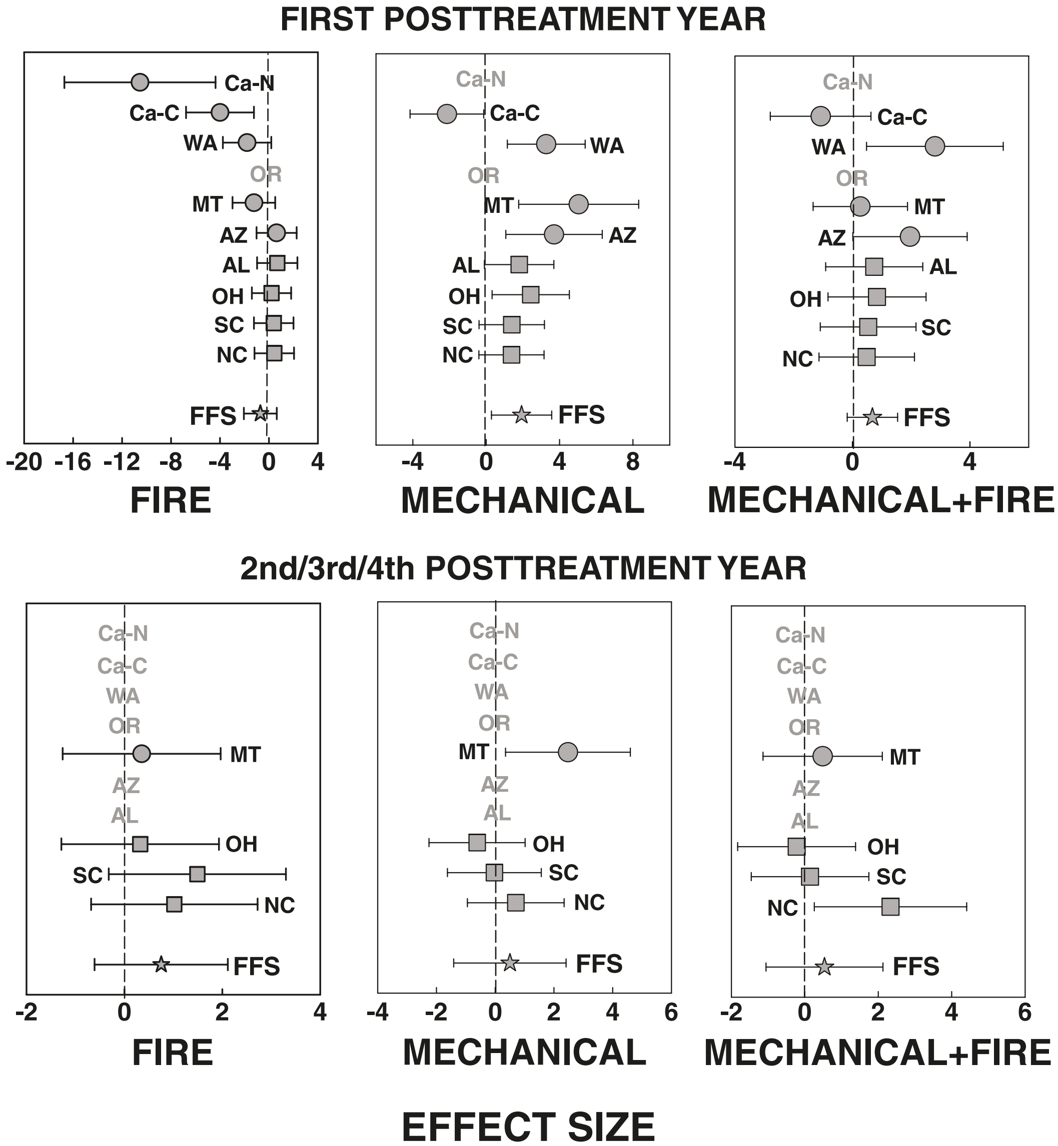
Combustion of forest floor fuels consistently accounts for the bulk of the N loss during prescribed fire. Losses of forest floor N from one or more prescribed fires have ranged from <20 kg·ha^{-1} (Schoch and Binkley 1986; Clinton et al. 1996; Vose et al. 1999) to >300 kg·ha^{-1} (Debyle 1980; Little and Ohmann 1988), with such losses accounting for 12%–84% of the prefire forest floor N stock. Losses of forest floor N as the result of the FFS prescribed fires (with or without mechanical treatment) averaged 36%–55% of the initial forest floor N and fell well within the range reported by Wan et al. (2001) in their meta-analysis of forest fire effects.

At the network scale, the mechanical treatment resulted in a decrease of 21 ± 24 kg·ha^{-1} in forest floor N (Fig. 4), but meta-analysis indicated that these losses were not statistically significant (Fig. 5). Only the Gulf Coastal Plain (AL) site exhibited a significant first-year loss of forest floor N as the result of mechanical treatment (Fig. 5).

As logging residues contain significant quantities of N, we had expected that forest floor N stocks would increase after mechanical treatment; however, harvesting intensity and residue treatment are both important in determining additions of N from logging residues. For example, bole-only clear-cutting of mature *Pinus ponderosa* added 309 kg·ha^{-1} of N to the forest floor, whereas thinning of a young, dense stand resulted in a net N addition of only 38–40 kg·ha^{-1} (Strahm et al. 2005). Similarly, Olsson et al. (1996) found that leaving branches and needles on site after conifer harvesting in Sweden added 171 kg·ha^{-1} of N , with an average C to N (C/N) mass ratio of 105, while leaving only needles (with an average C/N ratio of 50) added 45 kg·ha^{-1} of N.

None of the treatments resulted in significant net change in forest floor N at the network scale over the later and subsequent sampling years. Only two individual sites exhibited a change in N >100 kg·ha^{-1}·year^{-1} during the subsequent sampling period: NC control and mechanical treatments lost 136 and 117 kg·ha^{-1}·year^{-1} of N, respectively, and OR control and mechanical treatments gained 133 and 145 kg·ha^{-1}·year^{-1} of

Fig. 7. Summary of the meta-analysis of the effects of the three Fire and Fire Surrogates study treatments on deadwood nitrogen. Format follows Fig. 4.

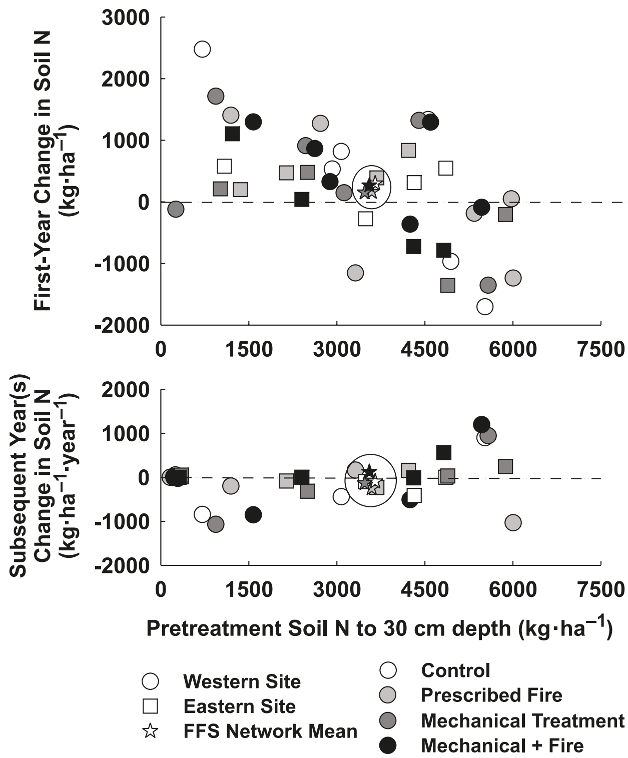


N, respectively (Figs. 4, 5). We had anticipated that forest floor N would decrease between the first posttreatment year and later samplings, as decomposition and leaching rates commonly increase after fire (Covington and Sackett 1984; Schoch and Binkley 1986); however, we did not observe decreases in forest floor N in the fire or combined mechanical and fire treatments, and we have no mechanistic explanations for the four cases in which we did observe significant changes in forest floor N.

In most cases, N storage in deadwood changed little as a result of the treatments (Fig. 6), and there was no significant meta-analytical effect of either the fire or the combined mechanical and fire treatment during the first posttreatment year at the network scale (Fig. 7). In contrast, meta-analysis revealed a significant network-wide increase in deadwood N following mechanical treatment (Fig. 7), averaging 29 ± 8 kg·ha^{-1} across the network, 22 ± 13 kg·ha^{-1} among the western sites, and 38 ± 10 kg·ha^{-1} among the eastern sites (Fig. 6). There were two notable exceptions to the network pattern of deadwood N. The first was the significant increase of 107 and 48 kg·ha^{-1} in deadwood N at WA after the mechanical and combined mechanical and fire treatments, respectively; these results are presumably due to the helicopter logging used at this site (Fig. 6). The second was the significant N losses >60 kg·ha^{-1} after fire at CA-N and after both fire and mechanical thinning plus fire at CA-C; these two sites had the greatest fire intensity (Figs. 6, 7). There were no significant network-wide effects of any of the treatments on deadwood N storage during the subsequent sampling years, and there were few significant site-level effects (Fig. 7).

At the network scale, changes in mineral soil N averaged <10% of pretreatment stocks during both the initial posttreatment year and the subsequent sampling years (Fig. 8). However, individual site-by-treatment combinations exhibited considerably larger changes during the first posttreatment year, especially in the western sites. There was an apparent negative relationship between pretreatment mineral

Fig. 8. Net changes in nitrogen (N) storage in mineral soil to a 30 cm depth during the first posttreatment year (top) and change from posttreatment year 1 to the next sampling period divided by years elapsed (bottom) resulting from the Fire and Fire Surrogates study treatments. Format follows Fig. 3.



soil N and the magnitude of change during the first posttreatment year; however, this apparent relationship existed among all treatments (including the controls) and was therefore unrelated to the treatments applied. Meta-analysis demonstrated that there was no significant network-wide effect of any of the FFS treatments on mineral soil N during either sampling period (Fig. 9). In addition, significant site-level effects were uncommon and appeared to be idiosyncratic (Fig. 9). The lack of significant effects of prescribed fire on mineral soil N we observed was consistent with the meta-analyses of Johnson and Curtis (2001) and Wan et al. (2001).

Although most of the total ecosystem N was in mineral soil, this N is relatively unresponsive to single management treatments at the intensity applied in the FFS study (Johnson and Curtis 2001; Wan et al. 2001). We therefore summed the N contained in vegetation, forest floor, and deadwood to obtain an estimate of total aboveground N, so that overall changes resulting from the FFS treatments could be compared. In the controls, total aboveground N did not change significantly (mean of –22 ± 42 kg·ha^{-1}) from the pretreatment to the first posttreatment growing season (Fig. 10), while the three treatments resulted in mean network-wide decreases in N of –235 ± 39 kg·ha^{-1} from prescribed fire, –162 ± 46 kg·ha^{-1} from mechanical treatment, and –294 ± 61 kg·ha^{-1} from mechanical treatment followed by prescribed fire (Fig. 10). An average of 84% of the N loss from fire was from the forest floor; in contrast, an average of 92% of the loss due to mechanical treatment came from vegetation (principally wood). Of the loss of N from the combined mechanical and fire treatment, an average of 45% was from vegetation and 55% was from the forest floor (Fig. 10). The total aboveground N losses for each treatment were consistently greater in the western coniferous forest sites than in the eastern forest sites (Fig. 10), primarily as a result of greater losses of forest floor N in the western sites (Fig. 10). On average, western sites lost ∼100 kg·ha^{-1} more forest floor N as the result of fire or mechanical treatment and ∼60 kg·ha^{-1} forest floor N as the result of the combined mechanical and fire treatment (Fig. 10). Though neither eastern nor western sites lost significant vegetation N through prescribed fire, western sites also lost considerably more vegetation N than did the eastern sites as the result of mechanical or combined mechanical and fire treatment (Fig. 10).

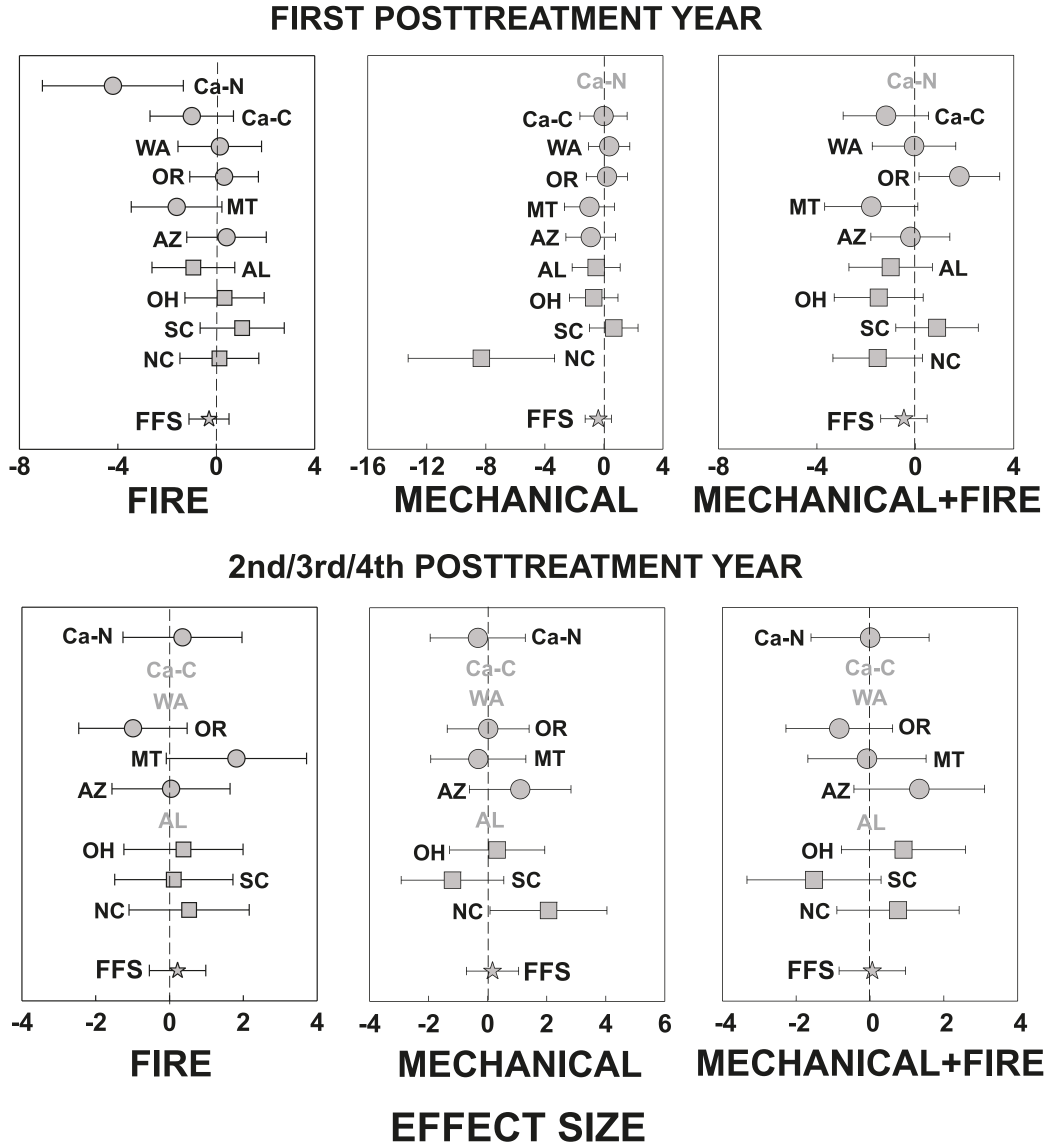
Although at each of the five eastern sites some of the parameters were measured during a second posttreatment year, only three sites (OH, NC, SC) underwent a complete second posttreatment sampling from which total aboveground N pools could be estimated. In these three sites, there were no significant changes in aboveground N stocks in the controls (mean: 3 ± 20 kg·ha^{-1}·year^{-1}) or in the mechanical treatments (35 ± 23 kg·ha^{-1}·year^{-1}) during the subsequent sampling years. In contrast, the fire treatments (110 ± 19 kg·ha^{-1}·year^{-1}) and the combined mechanical and fire treatments (111 ± 20 kg·ha^{-1}·year^{-1}) both showed significant net gains in aboveground N (Fig. 10).

Only two of the seven western sites (OR, MT) underwent a complete second sampling. That sparse data base, indicated that aboveground N increased significantly in both the controls (289 ± 57 kg·ha^{-1}·year^{-1}) and the mechanical treatments (mean of 245 ± 20 kg·ha^{-1}·year^{-1}). However, increased forest floor N at MT accounted for 78%–87% of that apparent increase, and we remain uncertain about whether this large increase in forest floor N at that site (especially in the controls) was real. In contrast, the aboveground N pools of neither the fire (36 ± 72 kg·ha^{-1}·year^{-1}) nor the combined mechanical and fire (–57 ± 115 kg·ha^{-1}·year^{-1}) treatments in the two western sites changed significantly during the latter sampling interval (Fig. 10).

None of the manipulative FFS treatments impacted more than 10%–15% of the total N capital of these ecosystems. As at least 80% of the total N resides in the mineral soil, and these treatments rarely impact the soil to depths greater than 5–10 cm (e.g., Raison 1979; Johnson and Curtis 2001); therefore the N economy of these forests appears to be well buffered against the effects of prescribed fire, thinning of the canopy or subcanopy, or their combination. Many previous studies confirm this. Johnson et al. (1982) compared whole-tree harvest to sawlog harvest in oak–hickory forests in Tennessee. Both harvesting regimes removed only a small fraction of the total ecosystem N, and the authors concluded that reserves in the soil plus atmospheric inputs would be sufficient to replace these losses quickly. Similarly, Hubbard et al. (2004) reported a total ecosystem N loss of 55 kg·ha^{-1} in a prescribed fire in an eastern mixed forest in Tennessee and noted that this loss was equivalent to approximately 5 years of atmospheric N deposition in that region.

Logging residues contain significant quantities of nutrients, particularly N, and the mass of N in the logging slash may be equivalent to the amount removed during con-

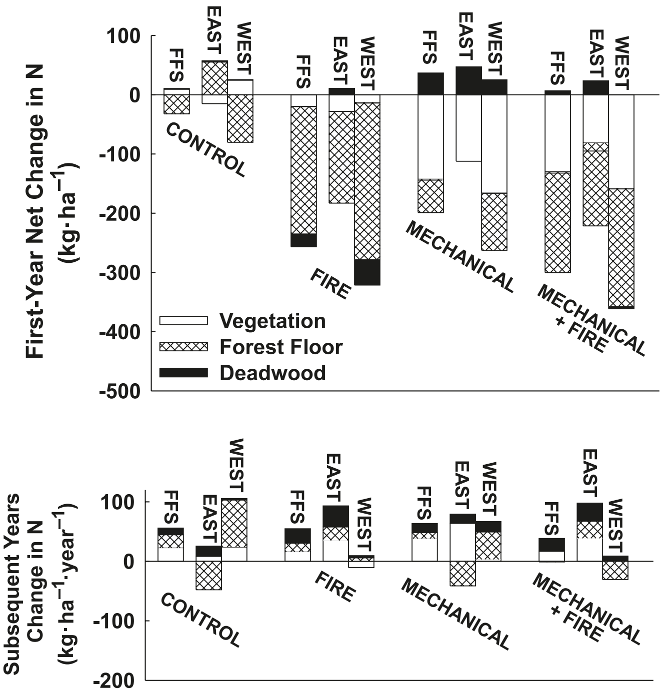
Fig. 9. Summary of the meta-analysis of the effects of the three Fire and Fire Surrogates study treatments on mineral soil nitrogen to a 30 cm depth. Format follows Fig. 4.



ventional bole-only harvesting (Bigger and Cole 1983). This retention of N after harvesting is of particular importance to postharvesting regrowth in the western portion of North America, as the forests of that region are still considered N limited (Gessel et al. 1973; Johnson et al. 1997; Hart et al. 2006). Björkroth (1983) reported that 27%–73% of the N in original logging residues in a Swedish spruce forest was recovered 18 years later in tree biomass, soil, and remaining woody residues, with the importance of the residue N being greatest in sites with the lowest N availability.

In the forest types of eastern North America addressed in this study (i.e., those with a lengthy history of frequent low-severity fire but with elevated rates of atmospheric N deposition), the N in logging residues or the N made available by the increases in net N mineralization commonly observed after prescribed fire (Wan et al. 2001; Hart et al. 2005; Boerner 2006) may be of less importance for sustaining future forest productivity than it is in western forests. For example, in deciduous forests in eastern Tennessee, Clinton et al. (1996) found that 2 years of regrowth following clear-cutting and burning produced 18 $kg \cdot ha^{-1}$ of N in new above-ground vegetation, while atmospheric deposition of N over that time period was 25 $kg \cdot ha^{-1}$. In evaluating long-term changes in N cycling in the Coweeta Long-Term Ecological Research site , Swank and Vose (1997) found that prescribed fire had little effect on N retention by these forested ecosystems. They noted that most Coweeta watersheds are beginning to show higher nitrate export and greater amplitude of nitrate fluctuations in stream water than in previous decades, and suggested that these forests are beginning the transition from strong N sinks to net N sources. Similarly, Boerner et al. (2004) found strong increases in net nitrification in Ohio deciduous forests between 1984 and 2003 that were independent of prescribed fire, up to five fires over 8 years, and Peterjohn et al. (1999) have documented widespread net nitrate export from forested watersheds in West Virginia. Thus, designing management strategies that maximize posttreatment C gain by minimizing loss of potentially

Fig. 10. Net gain or loss of total ecosystem nitrogen (N) from Fire and Fire Surrogates (FFS) network sites in relation to FFS treatments and sampling interval.



plant-growth-limiting N should be a focus in western forests as well as in eastern forests where fire has historically been less frequent or where atmospheric N deposition rates are low (e.g., Gough et al. 2007), as these are ecosystems where C and N cycling are still tightly linked. In contrast, such management strategies may be inappropriate in those eastern forests where chronic atmospheric N deposition has decoupled the C and N cycles.

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