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Fire Eases Imbalances of Nitrogen and Phosphorus in Woody Plants

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ABSTRACT

Fires are widespread and can result in large nutrient losses from ecosystems simultaneous with pulses in nitrogen (N) and phosphorus (P) that can increase their availability to plants. Plant growth is frequently limited by N and P, and fire has the potential to enhance or moderate the magnitude of N and P limitation in plants with important consequences for long-term net primary productivity and global carbon cycling. We used meta-analysis to explore fire effects on N and P concentrations in aboveground plant biomass among a variety of plants and plant communities worldwide. We show that across all observations, fire enhanced N concentration in plants when N/P ratios in biomass were low, and enhanced P concentration in plants when biomass N/P ratios were high. P concentration increased particularly in woody plants. Furthermore, responses of the N/P ratio in woody plants were more flexible than in herbaceous plants so that fire eased N and P imbalances only in woody plants. Our results suggest that these changes in plant N and P in response to fire may help sustain net primary productivity and persistence of woody plants in fire-affected ecosystems worldwide.

Key words: available soil nutrients; disturbance; meta-analysis; nutrient limitation; N/P stoichiometry; prescribed burn; slash-and-burn; wildfire.

INTRODUCTION

Every year between 300 and 460 million hectares of land are affected by wildfires and managed burning (prescribed burning and slash-and-burn agriculture, Giglio and others 2006; Randerson and others 2012). These fires dramatically change the structure and functioning of ecosystems (Thonicke and others 2001; Lavorel and others 2007). Fires are a critical component of woody plant encroachment (D'Antonio and Vitousek 1992; Scholes and Archer 1997), release biomass and soil carbon (C) as CO_2 into the atmosphere (Mack and others 2011), and typically enhance rates of plant growth (Goetz and others 2005). Considering the spatial scale of fires worldwide, fire effects on ecosystems have important consequences for the global climate (Randerson and others 2006; Running 2008).

The recovery of ecosystems from fire is strongly mediated by effects of fire on nitrogen (N) and phosphorus (P) availability (Wan and others 2001; Certini 2005). N and P limit plant productivity in most terrestrial ecosystems (Elser and others 2007; Harpole and others 2011) thereby influencing plant community composition (Tilman 1988). Transfers of N to the atmosphere through combustion are at least an order of magnitude larger than for P (for example, Cech and others 2010), whereas fire can also result in significant additions of N and P to the soil with significant consequences for their relative

availabilities (Boerner 1982; Wan and others 2001; Certini 2005). Fire-promoted changes in N, P, or both could therefore worsen or ease limitations of plant growth (for example, Cech and others 2008).

The N/P ratio in plant biomass has been used to indicate if growth of a plant is limited by the availability of N, P, or both nutrients (Güsewell 2004), although the use of N/P threshold ratios to predict nutrient limitation is not always clear (Craine and others 2008). Globally, plant N/P ratios decrease with latitude across a wide range of plant groups (Reich and Oleksyn 2004; Han and others 2005). Although this relationship with latitude has been associated with the effects of temperature on plant N and P physiology, variation in N and P supply from the soil likely remains a determining factor (Hedin 2004; Reich and Oleksyn 2004; Han and others 2005). Weathered soils near and in the tropics tend to be poor in P, whereas younger soils at higher latitudes are more likely to be N poor (but see Elser and others 2007). Consequently, variability in plant N/P ratios with latitude reflects, at least in part, relative availabilities of N and P in the soil. Plants have limited flexibility in regulating their biomass N/P. Nevertheless, flexible allocation of N and P can be advantageous for plant growth when the relative supply of N and P is suboptimal (Ågren and others 2012).

The availability of N and P to plants will vary widely in space and time following fire disturbance. Losses of N through combustion are much greater than those of P (Raison 1979; Cech and others 2010). Fire-promoted erosion losses are complemented by leaching losses of highly mobile inorganic N (nitrate in particular) that are large compared to those of P (Vitousek and Howarth 1991). Despite such losses, N and P availability in soil are often markedly increased directly after fire. N and P are deposited on the soil with ash while increased soil temperature and moisture content stimulate microbial mineralization of N and P (Neary and others 1999; Certini 2005). Fire may lead to redistribution of N and P from surface soils to deeper soils (Smith 1970; Turrion and others 2010). Fires also lead to horizontal redistribution of nutrients, via aeolian processes, that may counteract the nutrient concentrating effects of woody shrub encroachment in grasslands (Ravi and others 2009; Hasselquist and others 2011). These large temporal and spatial fluctuations in available N and P can have profound effects on plant performance and community structure, depending if plants are N- or P-limited.

We hypothesized that fire can reduce constraints of N and P to plant growth globally. We predicted that fire will increase plant tissue P concentration (hereafter plant [P]) more than N when the plant N/P ratio is high (P limited growth) and increase plant tissue N concentration (hereafter plant [N]) more than P when the plant N/P ratio is low (N limited growth). We further examined whether N and P in woody and herbaceous plants showed different sensitivities to fire, and whether woody and herbaceous plants showed differences in stoichiometric flexibility in N and P in response to fire. We focussed on the contrast between woody and herbaceous plants because fire often affects the relative abundance of both life forms (D'Antonio and Vitousek 1992; Scholes and Archer 1997). We used meta-analysis to examine how [N], [P] and mass ratios of N/P in green foliage of woody and herbaceous plants were affected by fire (prescribed burning, wildfire, slash-and-burn) in a total of 308 observations from 54 studies (Online Appendix A, B). We examined how fire effects on plant [N] and [P] were related to soil N and P availabilities. The studies were conducted in a wide range of ecosystems on all continents (except Antarctica) including boreal, temperate, and tropical forests, temperate and semiarid grasslands, savannas, heathlands, and shrublands (Figure 1, Online Appendix A).

MATERIALS AND METHODS

Data Collection and Extraction

We collected data from publications where both plant [N] and [P] were reported in response to fire. We screened publications that were found by searching for (fire* OR burn*) AND nitrogen AND phosphorus in Web of Knowledge (ISI), Google Scholar and Scopus, and that were cited in these publications. To be included in the meta-analysis, both plant [N] and [P] had to be reported in burned and unburned plots in green foliage or total aboveground biomass (herbaceous plants only). Fires were either a result of wildfires, prescribed burns, or slash-and-burn practices. We included one study where pre-fire measurements were used as the unburned control (Schafer and Mack 2010). Both average values and number of replication had to be reported.

To obtain an inclusive dataset of observations from a wide range of ecosystems, we included studies where plant [N] and [P] were measured in individual species (where the species was the same for the burned and unburned treatment) and in whole plant communities. We recognize that for measurements at the community level, fire effects
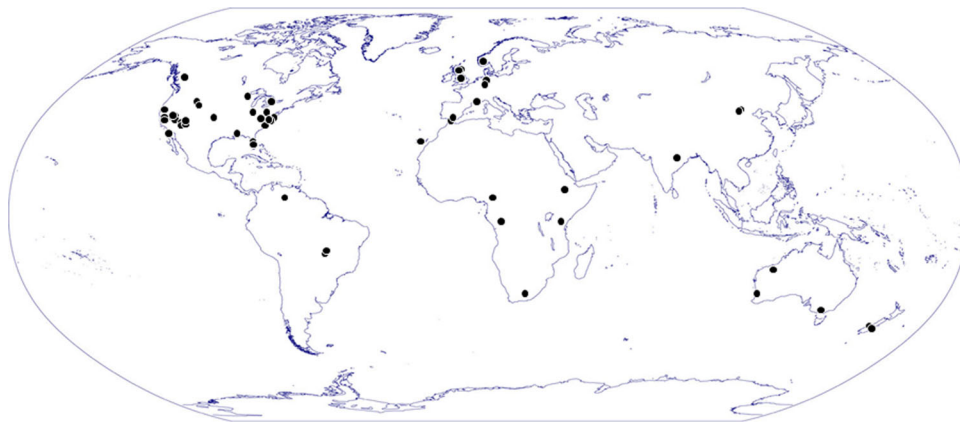
Figure 1. Map with site locations of the 54 publications used in the meta-analysis.

on plant [N] and [P] may have been caused by changes in [N] and [P] of individual species, but also by changes in species composition. However, fire effects on plant [N], [P] and mass ratios of N/P were similar for species and community level observations (see Data analysis below), suggesting that using both species and community level observations caused no bias in our results. We further recorded the life form for each observation (herbaceous or woody), ecosystem type (temperate grassland, semiarid grassland, tropical grassland, heathland, shrubland, savanna, boreal forest, temperate forest, Mediterranean forest or tropical forest), and for species level observations if the species was potentially N-fixing or a non N-fixing plant. For community level observations, life form was categorized as herbaceous or woody when it was clear from the paper that the whole community consisted of one of the two life forms. In most cases, woody plants in burned plots measured were surviving plants. In a few cases, foliar N and P were measured in new seedlings both in burned and control plots. Therefore, nutrient responses were not affected by age-related nutrient changes.

Measurements at multiple times after a fire were considered as separate observations. When fire effects were examined across other treatments (for example, fertilization, herbicide treatments), then they were also included as separate observations. Treating observations within a study as independent observations caused no bias in our results (see Data analysis below). This approach was successfully applied in other ecological meta-analyses (Liao and others 2008; Rey Benayas and others 2009; Eldridge and others 2011; García-Palacios and others 2013).

The majority of observations were made directly after the fire event (83 % of the total number of observations were made within 4 years), whereas the number of observations drastically reduced

with time (Figure 2). Because of the relatively low number of long-term observations, we could not reliably analyze long-term effects of fire on plant [N] and [P]. The number of observations significantly dropped after 4 years, and we therefore
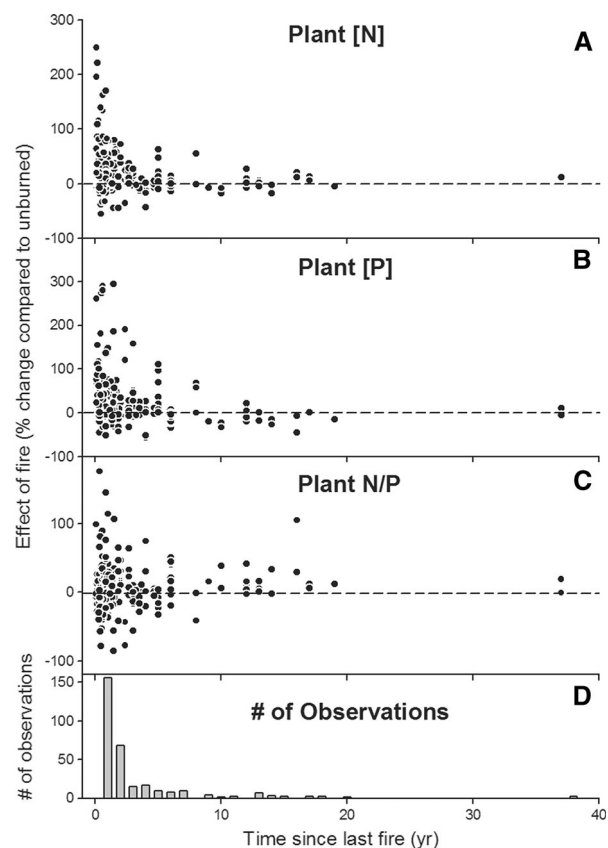

Figure 2. Fire effects on plant [N] (*A*), [P] (*B*) and N/P (*C*) as a function of time since the last fire. Fire effects are expressed as a percentage change compared to unburned or pre-burned control plots. Each data point represents one observation with a total of 308 observations. The number of observations on a yearly basis is also shown (*D*).

focused on effects caused within 4 years after fire. However, we also ran our analyses on the complete data set to test whether inclusion of long-term observations changed our results. In total, we found 54 publications with 308 observations (256 observations within 4 years after fire, Online Appendix A, B).

We recorded measures of soil available N and/or P in burned and unburned treatments when they were reported in the studies selected for plant [N] and [P]. We used these data to test how fire effects on plant [N] and [P] related to fire effects on soil available N and P. We are aware that there are more studies reporting fire effects on soil available N and P (for example, Wan and others 2001). However, our aim was to compare plant with soil data and test if the soil data could help explain the site-specific fire effects on plant [N] and [P]. We only recorded measurements that were made in the top soil layer where the largest changes are expected in response to fire. Nevertheless, sampled soil depths varied widely ranging between 2 and 20 cm among different studies. Available N and P in the soil were measured by extracting the soil with a salt solution (KCl or K_2SO_4 for N, and $NaHCO_3$, NH_4F–HCl, or H_2SO_4–HCl for P) or with deionized water. Many of these extraction methods were developed in agronomy to provide a measure of N and P availability to plants. Although there is no soil chemical assay that can measure nutrient availability precisely, extractable N and P are thought to be better indicators of available N and P after disturbance compared to total soil N and P (Binkley and Vitousek 1991). The choice of the extraction method, however, depends on soil type (for example, $NaHCO_3$ extractions are used for extracting P in neutral and basic soils and NH_4F–HCl extractions for extracting P in acid soils). There were not enough observations to analyze how the different extraction methods influenced the results. Therefore, different extraction methods used for variable soil depths may have contributed to the variability in effect sizes among the different studies. Of the 54 studies, there were 18 studies where available soil N (54 observations) and/or P (66 observations) were measured (Online Appendix A, B).

Data Analysis

For plant and soil parameters, we used the natural log of the response ratio as a metric of the effect size in the meta-analysis (Osenberg and others 1999): Ln $R = \ln(X_f/X_c)$, where X_f and X_c are the mean values for the burned and unburned treatment, respectively. The effect sizes were weighted by replication (Hungate and others 2009; van Groenigen and others 2011; Wu and others 2011; Lam and others 2012): $W_R = (n_f \times n_c)/(n_f + n_c)$ where n_f and n_c are the number of replicates in the burned and control plots respectively. In several occasions, authors' multiple replicates within burned and unburned plots were considered as pseudo-replication, and therefore here treated as one replicate. The conventional method of weighting effect sizes is by the inverse of the pooled variance (Hedges and Olkin 1985), so that studies with greater certainty are given more weight. However, standard deviations or standard errors were often not reported. We therefore decided against using the variance-based weighting because it would preclude those observations from our meta-analysis. Several authors found that replicate-based weighting, variance-based weighting, or no weighting at all gave similar results (Cardinale and others 2006; van Groenigen and others 2011; Wu and others 2011). We compared results weighted by replication (W_R) with results that were unweighted (W_U) and observed that results were qualitatively similar (Online Appendix C). Here we report results for W_R-weighted effect sizes only.

We calculated mean effect sizes and generated 95 % bootstrapped confidence intervals (CI) using the random-effects model in MetaWin 2.1 (Rosenberg and others 1999). For bootstrapping, we used 4999 iterations. Fire effects were considered significant if the 95 % CI did not overlap with zero. The LnR mean effect sizes were back transformed and fire effects were reported as a percentage change compared to unburned controls $(100(R - 1))$.

Measurements at multiple times after a fire and across other treatments were considered as separate observations. In the strict sense, multiple measurements from one study are not independent. This lack of independence of observations within a study is a common problem in ecological meta-analyses (Hedges and others 2010). We tested whether this resulted in biased mean effect size estimates. We performed a separate analysis where we considered only one randomly chosen observation for each study and compared the results with the results obtained from the whole dataset (Vilà and others 2011; García-Palacios and others 2013). Because the mean effect size estimates were similar for both analyses (Online Appendix D), we assumed that multiple measurements from one study did not bias our results, and that all observations can be included in the analysis. Another approach is to reduce the weight of each observa-

tion by the number of observations within a study so that studies with a large number of observations do not have a dominating effect on the mean effect size (van Groenigen and others 2011). We also used this weighting approach and found that results were similar compared to results without using this weighting. Recently, another approach was developed to minimize potential bias with non-independent observations using a generalized least squares model to pool within-study effects (Lajeunesse 2011; Curtis and Queenborough 2012). We decided not to use this approach because standard deviations need to be known for each observation; for 37 % of all our observations standard deviation (or standard error) was not reported.

A potential problem with meta-analysis is the possibility of publication bias. However, we observed no correlation between effect sizes and sample size ($r = 0.06$, $P = 0.35$ for plant [N], $r = 0.03$, $P = 0.68$ for plant [P], and $r = 0.02$, $P = 0.72$ for plant N/P), whereas the scatter plots of effect size versus sample size showed the typical funnel-shape, suggesting there was no under-representation of observations with both low sample size and low effect size (Palmer 1999; Cardinale and others 2006; Borenstein and others 2009).

First we tested whether effect sizes were related to time since last fire (for all observations and for observations made within 4 years after the last fire) using the continuous random-effects model with time since last fire as the continuous variable. We used P_{random} values associated with $Q_{regression}$ (heterogeneity accounted for by the continuous variable time since last fire) to identify if relationships were significant.

We tested whether the magnitude and direction of fire effects on plant [N], [P], and N/P depended on plant N/P ratios measured in unburned control plants, where all N/P ratios are expressed as a mass ratio. We used the plant N/P ratio in unburned control plots as an indicator for nutrient limitation of plant growth (Koerselman and Meuleman 1996; Güsewell 2004). For instance, the threshold N/P ratios of 14 and 16 were suggested for N and P limitation respectively across a wide range of plant communities (Koerselman and Meuleman 1996). Because plant N/P ratios are species dependent and are affected by plant part, age, growth rate, and type of photosynthesis (Elser and others 2000; Cech and others 2008; Zhang and others 2013), we used the more conservative threshold ratios of 10 and 20 (Güsewell 2004). The ability of N/P threshold ratios to predict nutrient limitation is sometimes limited (Craine and others 2008). Nevertheless, N/P thresholds remain valuable in

assessing how different plants across different landscapes are potentially constrained by N or P. We therefore grouped observations into the following categories: plant N/P below 10, N/P between 10 and 20, and N/P above 20. We calculated mean effect sizes and bootstrapped CIs for each category. We did this for all observations and for observations with herbaceous and woody plants separately, the latter to test whether the magnitude and direction of fire effects differed between herbaceous and woody plants. Because no consistent differences in foliar N/P ratios were found between herbaceous and woody plants worldwide (Reich and Oleksyn 2004), we assumed no bias when the two life forms were grouped into the three different nutrient limitation categories. We further examined if fire effects differed among fire types (wildfire, prescribed fire, and slash-and-burn), ecosystem types (temperate grassland, semiarid grassland, tropical grassland, heathland, shrubland, savanna, boreal forest, temperate forest, Mediterranean forest and tropical forest) between plant level (species vs. community), and between N-fixing and non N-fixing plants (for species level observations only). We used $Q_{between}$ (heterogeneity in effect sizes associated to differences between categories) to test if fire effects differed between categories. Differences between categories were considered significant at $P_{random} < 0.05$. Means and standard deviation of plant [N], [P] and N/P for different categories in control and burned plots are reported in Online Appendix E.

We tested whether plant responses followed changes in N and P availability in the soil. We used linear regressions (using JMP, version 4.0.4, SAS Institute, Cary, NC, USA) to relate LnR calculated for plant [N], [P] and N/P with LnR calculated for available soil N, P, and N/P. We also tested for fire effects on available soil N, P, and N/P using the random-effects model as was done for plant [N], [P], and N/P. Because the depth of the top soil layers varied among studies (ranging between 2 and 20 cm), we tested whether fire effects differed between shallow (sampled to less than 10 cm soil depth) and deep soil sampling (sampled to 10 cm and deeper), using $Q_{between}$ and P_{random}.

RESULTS

We first examined how fire-affected plant [N] and [P] as a function of time since the last fire for all individual observations ($n = 308$). We observed a variety of responses immediately after fire. Plant [N] and [P] increased up to 249 and 294 % respectively, but decreases of more than 50 % were
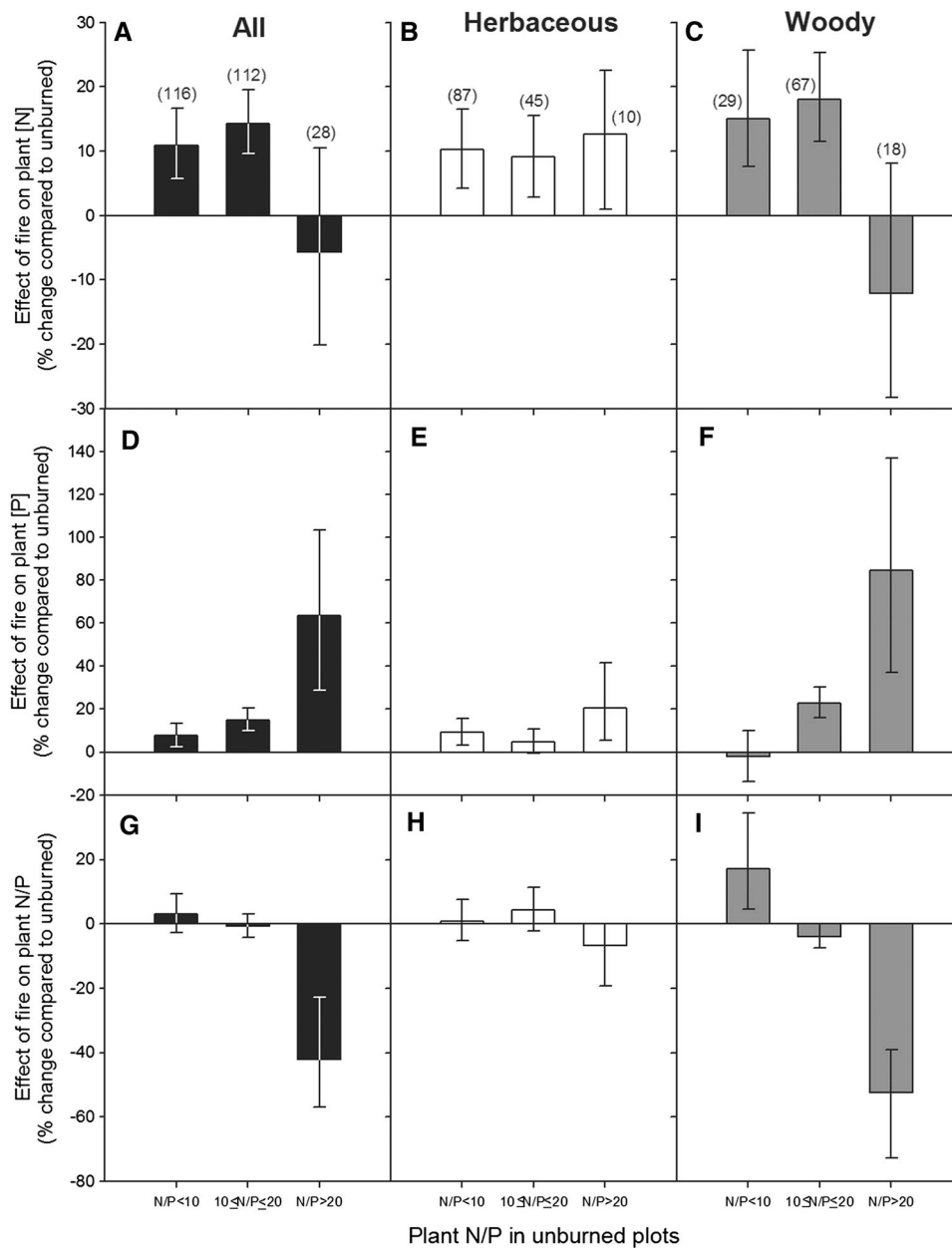
Figure 3. Meta-analysis results of the response of plant [N], [P] and N/P to fire. Fire effects on plant [N] (*A–C*), plant [P] (*D–F*) and plant N/P (*G–I*) are shown for observations where plant N/P in unburned or pre-burned control plots were smaller than 10, between 10 and 20, and larger than 20. Results are shown for all observations (*A, D, G*), herbaceous plants (*B, E, H*) and woody plants (*C, F, I*). Effect sizes were weighted by replication. *Error bars* indicate bootstrapped 95 % confidence intervals. The number of observations for each category is shown in *brackets*.

also observed, while in many cases little or no changes were observed in response to fire (Figure 2). Changes in plant [N] and [P] were not always in parallel, resulting in variable responses in plant N/P ranging between −86 and 177 %. Fire effects on plant [N], [P], and N/P strongly decreased with time since the last fire. However, because fire effects showed both positive and negative effects on plant [N], [P] and N/P, effect sizes were not related to time since last fire ($P_{random} > 0.1$). Because of the limited number of long-term observations, we focused our meta-analysis on observations that were made within 4 years (256 observations or 83 % of the total number of observations, see

''Methods'' section). For these observations, effect sizes for plant [N], [P], and N/P were also not related to time since the last fire ($P_{random} > 0.1$).

We grouped the 256 observations into three categories: control plant N/P less than 10 (suggesting N limitation), control plant N/P between 10 and 20, and control plant N/P greater than 20 (suggesting P limitation, see ''Methods'' section). Across all 256 observations made within 4 years, fire caused a significant increase in plant [N] when control plant N/P ratios were smaller than 10 or between 10 and 20 (on average by 11 and 14 % respectively, Figure 3A), whereas largest increases in plant [P] occurred when control plant N/P ratios were larger

Table 1. Summary of Results from the Meta-analyses on Plant [N], [P] and N/P Categorized by Fire Type and Plant Level

Nutrient	Category	# Observations	LnR (%)	95 % CI	
				Min	Max
N	Prescribed burn	200	**10.5**	6.4	14.9
	Wildfire	53	**10.3**	1.5	22.2
	Slash-and-burn	3	**13.6**	9.6	16.2
	$Q_{between}$ ($df = 2$)		0.0047		
	P_{random}		0.98		
	Species	196	**10.9**	6.5	15.6
	Community	60	**9.6**	2.0	17.5
	$Q_{between}$ ($df = 1$)		0.014		
	P_{random}		0.76		
	N-fixing	18	5.2	−0.4	13.0
	Non N-fixing	178	**11.4**	6.7	16.3
	$Q_{between}$ ($df = 1$)		0.062		
	P_{random}		0.48		
P	Prescribed burn	200	**13.6**	8.7	19.1
	Wildfire	53	**22.1**	10.4	35.5
	Slash-and-burn	3	**18.1**	15.4	21.1
	$Q_{between}$ ($df = 2$)		0.21		
	P_{random}		0.55		
	Species	196	**16.8**	11.4	22.8
	Community	60	**9.2**	1.2	18.3
	$Q_{between}$ ($df = 1$)		0.40		
	P_{random}		0.16		
	N-fixing	18	5.6	−2.3	15.3
	Non N-fixing	178	**17.6**	4.7	32.2
	$Q_{between}$ ($df = 1$)		0.22		
	P_{random}		0.28		
N/P	Prescribed burn	200	−2.8	−8.3	2.5
	Wildfire	53	**−9.6**	−16.3	−1.8
	Slash-and-burn	3	**−3.8**	−9.5	−0.1
	$Q_{between}$ ($df = 2$)		0.21		
	P_{random}		0.59		
	Species	196	−5.0	−10.8	0.6
	Community	60	0.4	−7.5	9.1
	$Q_{between}$ ($df = 1$)		0.27		
	P_{random}		0.31		
	N-fixing	18	−0.4	−5.6	7.4
	Non N-fixing	178	−5.3	−11.5	0.4
	$Q_{between}$ ($df = 1$)		0.05		
	P_{random}		0.66		

Bold, when 95 % bootstrapped confidence intervals, 95 % CI, did not overlap with 0. Effects sizes (LnR) were weighted by W_R. Differences among fire type categories and between plant level categories are indicated by $Q_{between}$ and P_{random}.

than 20 (average increase by 63 %, Figure 3D). Plant [N] and [P] increased across all three categories in herbaceous plants so that plant N/P was not affected by fire (Figure 3B, E, H). On the other hand, when control plant N/P ratios were larger than 20, the [N] in woody plants was not affected by fire whereas woody plant [P] showed the largest increase in response to fire (by 85 %, Figure 3C, F).

Plant N/P ratios in woody plants were also more flexible than herbaceous plants in response to fire showing an increase in plant N/P when control plant N/P ratios were smaller than 10 (by 17 %) and a decrease in plant N/P when control plant N/P ratios were larger than 20 (by 52 %, Figure 3C, F, I). When we did the same analyses for all 308 observations (including observations made beyond
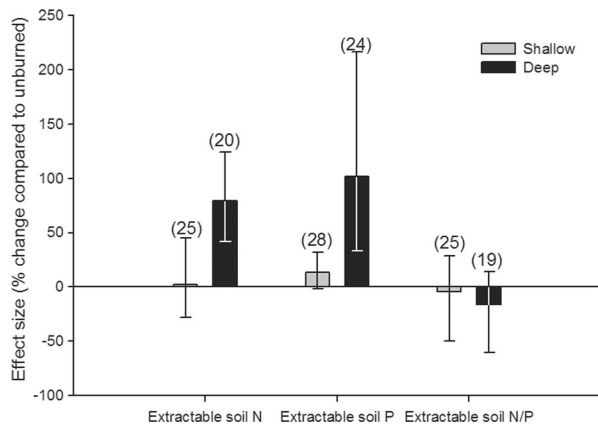
Figure 4. Meta-analysis results of the response of extractable soil N, P and N/P to fire measured at shallow and deep soil depth. Observations were separated into measurements made to less than 10 cm (shallow soil) and to 10–20 cm soil depth (deep soil). Effect sizes were weighted by replication. *Error bars* indicate bootstrapped 95 % confidence intervals. The number of observations for each category is shown in *brackets.*

DISCUSSION

Our meta-analysis supports our hypothesis that at the global scale and in the short-term, fire is important for improving plant [N] and [P] thereby potentially reducing constraints on plant growth. Plant [N] and [P] increased in response to fire across a wide range of N/P ratios in unburned herbaceous plants (on average by 11 and 12 % for N and P, respectively, across all three N/P categories), but plant [P] showed the largest increases in response to fire in woody plants (by 85 %) when unburned plant N/P ratios were larger than 20 (implying N sufficiency, and possibly limitation by P or other nutrients). These results suggest that fire may be particularly important for easing P constraints of growth of woody plants in P poor systems.

4 years), results did not change (Online Appendix F).

Fire effects on plant [N], [P] and N/P were not affected by fire type (prescribed burning, wildfire, slash-and-burn), plant level (species and community level) or ability to fix N (N-fixing and non N-fixing, Table 1). Although prescribed burn, wildfire, and slash-and-burn all increased plant [N] and [P], no differences were observed among the three fire types ($P_{random} > 0.1$). Likewise, plant [N] and [P] increased for measurements made at the species and the community level, but no differences were found between levels. Plant [N] and [P] responses to fire were larger for non N-fixers than for N-fixers, although the two groups were not significantly different. Fire effects on plant [N], [P], and N/P were also not significantly different among ecosystem types (Online Appendix G).

We observed no relationship between fire effects on available N and P in the soil and fire effects on plant [N] and [P], respectively (Online Appendix H). Fire significantly increased available N by 32 % and P by 50 % across all observations although the N:P ratios of available pools were unaffected by fire. However, when we separated observations into measurements made to less than 10 cm (shallow soils) and measurements made to 10 cm or deeper (deep soils), fire only increased the available N and P in the deep soils ($Q_{between} = 3.3$, $df = 1$, $P_{random} = 0.02$ for N and $Q_{between} = 4.1$, $df = 1$, $P_{random} = 0.03$ for P, Figure 4).

Our meta-analysis further indicates N/P flexibility in woody plants in response to fire, with increases in N/P when plant N/P in control plants was low, and decreases in N/P when plant N/P in control plants was high. In contrast, plant N/P in herbaceous plants was not affected by fire. Stoichiometric flexibility in plants is a major force structuring ecological responses to disturbances (Sistla and Schimel 2012). When the supply of N and P becomes imbalanced (that is, when one nutrient becomes more limiting to growth compared to the other nutrient), plants may allocate more resources to acquire the nutrient that becomes most limiting thereby maintaining a homeostatic N/P (Ågren and others 2012). However, because of the energetic costs involved in maintaining stoichiometric homeostasis, growth of plants showing flexible N:P stoichiometry may be favored when N and P supply vary in space and time (Sardans and others 2012). Therefore, the flexibility in N/P of woody plants that we observed in our meta-analysis may benefit woody plant growth and persistence in fire-prone systems.

In contrast to what Reich and Oleksyn (2004) found, plant N/P in control plants did not relate to latitude of the site. We also found no relationship between effect size and latitude, which is consistent with observations by Elser and others (2007) who also found no clear pattern between type of nutrient limitation and latitude, Possibly, our number of observations was too small to detect significant relationships with latitude (308 observations compared to 5087 observations by Reich and Oleksyn 2004). However, the relationship with latitude found by Reich and Oleksyn (2004) was observed for relatively undisturbed sites. Our results suggest that fire disturbance can change plant N/P of

woody plants, which may confound the relationship between plant N/P and latitude at the global scale.

The greater increase in plant [P] and greater flexibility in N/P of woody plants in response to fire may be a consequence of woody plants generally being larger than herbaceous plants. Woody plants may, therefore, take greater advantage of nutrient pulses after fire, for instance by taking up different nutrients from shallow and deep soil layers (Jackson and others 2000). Different plant [N] and [P] responses to fire could also have been caused by luxury nutrient consumption. Woody plants tend to have lower relative growth rates compared to herbaceous plants (Houghton and others 2013; Hunt and Cornelissen 1997), and therefore have a greater proficiency to store nutrients that are not directly needed for growth (Cornelissen and others 1997). However, fire particularly increased the concentration of the plant nutrient that was least available before the fire (according to the control plant N/P ratio), suggesting that fire mostly relieves nutrient limitation rather than causing luxury nutrient consumption.

Plant [N] and [P] were not related to available pools of N and P in the soil, suggesting that fire effects on available soil N and P are poor predictors for plant responses. It should be noted, however, that available forms of N and P in the soil were determined with different extraction methods. Therefore, effect sizes may have been influenced by the extraction method used, and this may have obscured relationships with plant [N] and [P]. Further, increased supply of N and P in the soil does not necessarily increase plant [N] and [P], but may only stimulate plant growth. Nevertheless, fire increased both available soil N and P. These increases could have been a result of increased supply of N and P directly after fire, but also because of reduced uptake due to a reduction in plant biomass directly after fire. Similar results were observed for available soil N in a larger data set (Wan and others 2001). Soil N and P in response to fire particularly increased when sampled to a greater soil depth, which may have favored N and P uptake by deeper-rooted woody plants compared to more shallow rooted herbaceous plants. Increases in available N and P after fire when sampled to a greater soil depth may have been a result of more favorable conditions for microbial release of N and P in the deep soil, because of leaching of N (and less so of P) into deeper soil layers (Boerner 1982; Certini 2005), or because of more rapid plant uptake of N and P in the surface soil directly after fire. However, we note that the soil depth results came from a relatively small number of observations. Further investigation of fire effects on redistribution of N and P in soil is warranted.

Because of a lack of long-term observations, we were only able to reliably analyze short-term effects of fire on plant [N] and [P] (observations less than 4 years since the fire event). Fire events may have to reoccur to maintain supplies of N and P in the long-term to prevent nutrient limitation, particularly in systems where substantial N and P are locked in slowly cycling humus (Wardle and others 2004). Even so, short-term increases in plant [N] and/or [P] may play crucial roles in plant productivity directly after fire (Boerner 1982; Grogan and others 2000). On the other hand, when fires recur too frequently, processes replacing one or both nutrients may be insufficient to prevent development of nutrient impoverished, low-productivity systems (Peterson and Reich 2001; Cech and others 2008).

For our analysis, we used observations made at the species and community level. For community level observations, fire effects on plant [N], [P], and N/P could have arisen because of fire-induced changes in species abundance and composition (for example, McKenzie and Tinker 2012). However, fire effects on plant [N], [P], and N/P were similar for species and community level observations (Table 1), suggesting that fire effects did not depend on and were not biased by species and community level observations. On the other hand, at the species level, fire effects significantly increased plant [N] and [P] for non N-fixers, but not for N-fixers (although responses to fire were not significantly different between these two groups, Table 1). The result for plant [N] is not surprising because non N-fixing plants may rely more on pulses of available N in the soil after fire compared to N-fixers (Cui and others 2010).

The majority of studies were prescribed burns that tend to be less intense than wildfires or slash-and-burn fires, which may have influenced our results. However, there were no significant differences in plant [N], [P], and N/P responses among fire types, whereas fire effects on plant [N] and [P] were significant for all three fire types (Table 1) suggesting that our results are broadly applicable.

The data presented here highlight that as N and P become more limiting to plant growth, so does the importance of fire to relieving that limitation, particularly for woody plants. With ongoing climate change, fires are predicted to change in frequency and likely in severity in many ecosystems, with important consequences for vegetation structure and productivity (Wardle and others 2004; Kraw-

chuk and others 2009). Our results indicate the need to include fire-induced changes in N and P biogeochemistry if we are to improve predictions about how altered fire regimes worldwide will affect plant community structure, primary productivity, and carbon cycling. Increased knowledge of long-term effects of frequent fire events on the type of nutrient limitation is required.

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