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Charcoal and shrubs modify soil processes in ponderosa pine forests of western Montana

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Abstract Low-elevation ponderosa pine (*Pinus ponderosa* Doug. ex. laws) forests of western Montana are naturally fire maintained ecosystems. However, 80–140 years of fire-exclusion has led to the formation of dense, mixed stands of ponderosa pine and Douglas-fir (*Pseudotsuga menzesii* (Mirbel) Franco), an understory co-dominated by graminoids and ericaceous shrubs, and low N availability. Ericaceous shrubs in particular have been found to influence soil processes in boreal ecosystems and potentially exacerbate N limiting conditions. In this set of studies, we investigated the influence of graminoid and ericoid litter chemistry on soil processes and evaluated the influence of charcoal as a sorbant of C compounds and depositional product of fire. A series of experiments were performed with two common understory plants of this ecosystem, elk sedge (*Carex geyeri* Boott) and kinnikinnick (*Arctostaphylos uva-ursi* (L.) Spreng.), an ericaceous shrub. Charcoal (100 g m^{-2}) and glycine (5 g m^{-2}) were applied in factorial combination to intact litter microcosms of these species. Non-ionic resin capsules were used to monitor mobile C compounds and ionic resins were used to monitor net N mineralization and nitrification in-situ. Greenhouse studies revealed that the addition of glycine and charcoal leads to a significant increase in net nitrification in shrub litter microcosms, but not sedge litter microcosms, as measured by NO_3^- sorption to ionic resin capsules. Charcoal and glycine also resulted in a significant increase of anthrone reactive C (soluble hexose sugars, an index of bioavailable C) in shrub litter microcosms. Analysis of leaf litter leachate from these two plant communities indicated similar nutrient concentrations, but almost 20 times more phenolic compounds in shrub leaf leachates. Charcoal was shown to be extremely effective at sorbing phenols, removing over 80% of phenolic compounds from solution. These results suggest that charcoal deposition after fire may modify a nitrification interference mechanism by sorbing plant secondary metabolites. After time, charcoal loses its ability to sorb C compounds and ericaceous litter decomposition, and subsequent release of phenolics, may interfere with nitrification once again.

Keywords Allelopathy · *Arctostaphylos uva-ursi* · *Carex geyeri* · Ericoid · Ponderosa pine · Ionic resin · Sedge

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Introduction

Historically, ponderosa pine (*Pinus ponderosa* Doug. ex. laws) forests of the inland Northwest experienced low severity fires with a mean fire return interval of 20–50 years (Arno and Allison-Bunnell 2002; Arno et al. 1997; Barrett et al. 1997). However, modern forest management and fire suppression has removed this natural disturbance from the landscape and many stands in this ecosystem have not experienced fire for over 130 years (Arno and Allison-Bunnell 2002). Nitrogen (N) is the primary limiting resource in terrestrial ecosystems (Vitousek and Howarth 1991) and results show that these fire excluded ponderosa pine sites have extremely low N availability (MacKenzie et al. 2006). Little is known regarding the factors that drive changes in the nitrogen (N) cycle with increasing time since fire in these low-elevation forests.

Many studies have shown that fire increases N availability in the short-term of 1–5 years (Choromanska and DeLuca 2001; Covington and Sackett 1986; DeLuca and Zouhar 2000; Newland and DeLuca 2000; Smithwick et al. 2005). However, recent use of ionic resin capsules to monitor changing N availability with time since fire indicate that available N remains somewhat elevated for 30–40 years after fire (MacKenzie et al. 2006). This suggests that some mechanism other than the short thermal pulse associated with fire is responsible for elevated N availability in pyrogenic ecosystems. One of the primary residues remaining after fire is charcoal which has been shown to mediate plant community and sub-surface processes in boreal ecosystems (DeLuca et al. 2002; Wardle et al. 1998b; Zackrisson et al. 1996), but only recently has this idea been applied to studies in temperate forests of the inland northwest (DeLuca et al. 2006).

The ability of plants to drive ecosystem function and sub-surface processes has recently become more recognized in plant ecology (Bever 1994; Nilsson and Wardle 2005; Wardle 2002). Plants modify soil properties in both positive and negative ways. Allelopathy is the ability of plants to produce secondary metabolites that have a direct negative effect on other organisms. Studies have shown how plant produced chemicals can be anti-herbivory, by interfering with digestive enzymes (Wardle et al. 1998a), anti-germination, by inhibiting radicle development (Hattenschwiler and Vitousek 2000) and anti-microbial, by interfering with nutrient cycling (Bremner and McCarty 1988; Lodhi 1977; McCarty and Bremner 1989; Souto et al. 2000). Plants also have positive effects on soil microbes (Bever 1994), essentially culturing a beneficial community in their rhizosphere for the exchange of carbon (C) and nutrients. However, few studies have tried to link plant community dynamics, soil chemistry and soil biota to the natural disturbance regime. In this context, it is not clear whether the plant community is driving resource availability or whether resource availability, as mediated by the disturbance regime, is driving plant community dynamics (Wardle 2002).

A recent study showed that graminoids and shrubs become co-dominant in the understory of fire-excluded ponderosa pine stands (MacKenzie et al. 2004) and that a large percentage of the shrubs were ericoids. Plants from the Ericaceae family have been shown to produce allelopathic compounds in Boreal ecosystems (Nilsson and Wardle 2005; Nilsson et al. 2000), that interfere with tree germination when fire is not used as a silvicultural tool. Many ponderosa pine stands have missed two or more disturbance events, because fire has been excluded from this ecosystem by suppression and management (Arno and Allison-Bunnell 2002).

We hypothesize that ecosystem function and sub-surface processes in fire-excluded stands reflect plant litter decomposition characteristics more so than the effect of past disturbance, because the remnant charcoal is no longer active. We also hypothesize that allelopathic interactions may exist in fire-excluded stands and that fresh charcoal may mediate the allelopathic effect of certain plant types. The purpose of the work reported here was to examine the soil chemistry created by two different plant litter types. To do this we choose two species commonly found in the late secondary succession of low-elevation forests in western Montana; kinnikinnick (*Arctostaphylos uva-ursi* (L.) Spreng.), representing ericoids and woody shrubs in general, and elk sedge (*Carex geyeri* Boott), representing graminoids. The specific objectives of this study were to investigate: (1) if charcoal serves an interceding influence on net N mineralization and nitrification under these two common plant types; and (2) what are the differences in litter chemistry associated with graminoid and ericoid plant communities.

Materials and methods

Site description

Litter samples were collected as intact 'microcosms' from a site in the Sapphire mountains of the Bitterroot valley (N 46°17′37.9″, W 113°55′59.7″), of western Montana, in 2001. This stand had not burned since before 1880 and therefore experienced approximately 120 years of fire exclusion according to the local USDA Forest Service inventory maps (Bitterroot Ranger district, Hamilton, MT, USA). Microcosm samples were collected from locations that were not exposed to recent fire as verified by a dense understory and lack of fire scars. The soil subgroup is Lithic Dystrustept, formed on granitic parent material, with a slope of 33°, elevation of 1590–1668 m, a predominantly southern aspect and an average pH of 6.41 (n = 4, standard deviation = 0.40). The sandy texture and overall uniformity of this site makes it ideal for collecting intact microcosms of forest floor and mineral soil for potted greenhouse trials.

Experimental design

Microcosms were collected at the end of the growing season from two common understory plants, *Arctostaphylos uva-ursi* (L.) Spreng. and *Carex geyeri* Boott. As much as possible, only residual plant litter was collected for each plant type and any living tissue was left to desiccate for 1 week after collection. Soil microcosms were excavated from the forest floor by using a sharp, flat spade wherein the surface litter and mineral soil were cut out at the dimensions of 15 cm × 15 cm by 5 cm deep (of mineral soil) removing the whole layer intact, and placing them into square, plastic gardening pots (15 cm × 15 cm × 10 cm) with drainage holes on the bottom. Each sample had variable litter depth with an average depth and standard deviation of 3.6 ± 0.92 cm. Twenty microcosms were collected for both plant types and returned to a greenhouse facility at the University of Montana.

Glycine and charcoal were applied to the samples with a 2 × 2 factorial design and five replicates per treatment located randomly along the greenhouse bench. The treatments consisted of 0 or 5 g glycine m^{-2} and 0 or 100 g charcoal m^{-2}, roughly equal to 50 kg glycine ha^{-1} and 1,000 kg charcoal ha^{-1}, which are representative values of organic N and charcoal deposition following fire (DeLuca et al. 2002; Zackrisson et al. 1996). To implement these treatments, 5 ml of a 0.32 M solution of glycine and 5 ml of a 7.5% (w/v) charcoal suspension were injected by syringe at the organic/mineral interface of each microcosm, at six different spots, for a total of 30 ml of each solution. Natural charcoal was collected from charred ponderosa pine trees on a similar site in the Sapphire Mountains that burned in 2000. The charcoal was ground to pass a-100 μm sieve, and never came in contact with the mineral soil until it was injected into the samples.

Ionic and non-ionic resin capsules were installed in the microcosms just below the organic matter/mineral soil interface and left to incubate for 1 month (Kjønaas 1999; Morse et al. 2000) with weekly watering to field capacity. Commercial polyester mesh capsules were used that contained approximately 10 ml (approximately 1 g dry weight) of mixed anionic, cationic resins (PST-2, Unibest, Bozeman, MT, USA). Non-ionic resins were encased in the same polyester capsules (Unibest, Bozeman, MT, USA), but were filled with approximately 1 g dry weight (about 1,100 m^2 of surface area) of XAD-7 resin (Rohm and Hass Inc., Philadelphia, PA). Fishing line and flagging tape were attached to each capsule to aid in recovery. Microcosms were watered to field capacity once a week and left in the greenhouse under ambient conditions (approximately 14 h of light and day time temperature of 25°C). After 1 month, the resin capsules were recovered and frozen until they could be analyzed.

Resin capsule analysis

Ionic resins were extracted by using successive rinses in 2 M KCl (DeLuca et al. 2002). Resin capsules were placed into a 200 ml French square bottle and shaken in 10 ml of 2 M KCl for 30 min, and the solution decanted into a centrifuge tube, the process repeated two times (three rinses) and the extractant centrifuged at 3000 RPM (rotor diameter 30 cm) for 10 min to remove any remaining soil particles. The extracts were analyzed for NH_4^+–N and NO_3^-–N on a segmented flow Autoanalyzer II (Bran and Luebbe, Chicago, IL, USA). We used the salicilate–nitroprusside method for NH_4^+ and the cadmium reduction method for NO_3^- (Mulvaney 1996).

Non-ionic resins were extracted with two different eluents in succession (deionized water followed by 50% aqueous methanol). Non-ionic resin capsules were placed on top of 200 ml French square bottles under a partitioning pump that delivered 0.8 ml of extractant per minute for 35 min to create a total of 30 ml of extractant. The first extractant (deionized water) was analyzed for anthrone reactive C (AR-C) and the second extractant (50% methanol) was analyzed for soluble phenols. Anthrone reactive C was measured by reacting the water samples with anthrone reagent and measuring absorbance at 625 nm, against a glucose standard (DeLuca 1998). Total phenols were measured by the Prussian Blue method (Stern et al. 1996), where potassium ferric cyanide and ammonium ferrous sulfate are used to develop a blue color for each phenol group and absorption is measured at 720 nm, against a (+)-catechin standard curve. Studies in our lab have shown that distilled water only removes approximately 10% of the total phenols, while 50% methanol removes 90% of the remaining phenolic compounds adsorbed to the XAD-7 material (DeLuca, unpublished data).

Leaf leachate analysis

A leaf leachate was produced from the fresh leaf tissue of each species collected from the study site by placing 100 g of finely chopped tissue into 1 l of deionized water. The suspension was then shaken for 24 h and filtered through 0.20 μm filters to exclude microbes. Leaf leachates were diluted to 1% (v/v) of the original concentration with deionized water and analyzed for NH_4^+ and NO_3^- as outlined above. Phosphorus concentrations were measured on a segmented flow Technicon Autoanalyzer II by the ascorbic acid–molybdate method (Bray and Kurtz 1945). Total phenols were measured as outlined above.

A simple experiment was conducted to test the ability of charcoal to adsorb phenols from the leaf leachates of *A. uva-ursi* and *C. geryii*. Instead of performing a bioassay with charcoal purified solutions (Keech et al. 2005), we measured the concentration both before and after charcoal filtration of phenols as a proxy for allelopathic compounds. Four replicate samples of the diluted leaf leachate for each plant species were created by measuring 25 ml of solution in 100 ml centrifuge tubes. The same wildfire-collected charcoal that was used for the greenhouse treatments was added to each replicate at a rate of 1% (w/v). The solution plus charcoal slurries were shaken for 30 min and filtered on a vacuum manifold with Buchner funnels and Whatman 2 filter papers, and total phenols were measured on the extracts as outlined above.

Statistical analysis

Analysis of variance (ANOVA) was used to determine if differences existed between treatments in the microcosm experiment. A paired *t*-test was used to determine if there were differences before and after treatment with charcoal for the leaf leachate experiment. In each case, we tested the error terms to ensure that the assumptions of heterogeneity, random variance and normal distribution were met, and transformed the data as needed (Underwood 1997; Wilkinson 1999). We used an α of 0.10 to determine significant differences among all statistical results. The statistical package used for these analyses was Systat 9.0 (Wilkinson 1999).

Results

Greenhouse experiment

Factorial applications of glycine and charcoal had a significant effect on net N mineralization as measured by sorption of NH_4^+ and NO_3^- to ionic resin capsules (Fig. 1). Charcoal without glycine added had no effect on resin sorbed NH_4^+ or NO_3^- concentrations for either plant type. The addition of glycine alone, as a labile organic N source, stimulated a significant amount of ammonification for soil under *A. uva-ursi*, but not nitrification and had the opposite effect on soil under *C. geryii* samples. The application of both glycine and charcoal significantly increased NO_3^- on resins for *A. uva-ursi* (Fig. 1). *Carex geyeri* microcosms had increased nitrification in the presence of glycine alone and there was no effect of charcoal and glycine on net nitrification.

The addition of glycine and charcoal also significantly affected labile C pools (Fig. 2). Non-ionic resin collected AR-C was significantly greater for glycine and charcoal amended shrub microcosms as compared to the control (Fig. 2). There was no treatment effect for resin collected AR-C for *C. geyeri* microcosms. Non-ionic resin

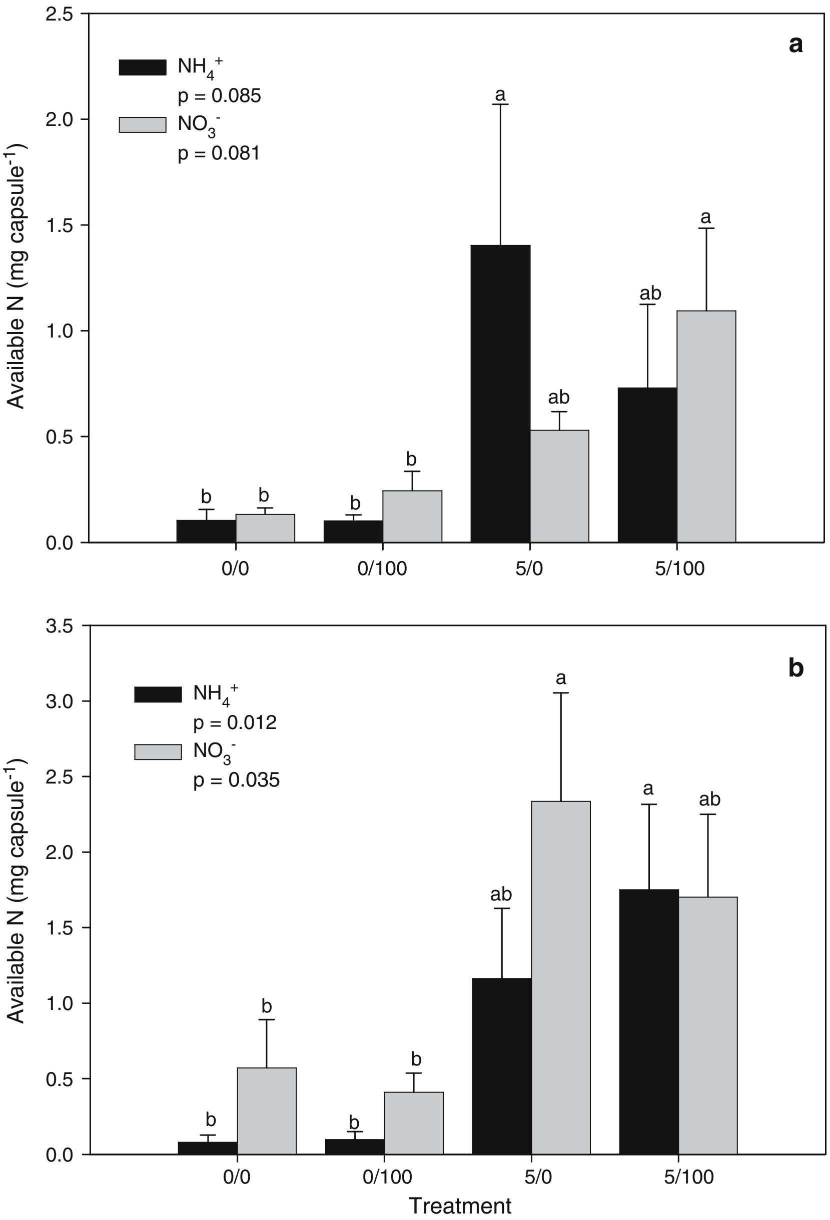

Fig. 1 Available NH_4^+ and NO_3^- (mg capsule^{-1}) measured with ionic resin capsules from factorial applications of glycine (5 g m^{-2}) and charcoal (100 g m^{-2}) to greenhouse incubated litter samples of two different plant types, (**a**) *Arctostaphylos uva-ursi* (shrub) and (**b**) *Carex geyeri* (sedge), found in the understory of ponderosa pine forests of western Montana. The control (0/0) represents conditions on fire-excluded sites. Different letters indicate significant differences with ANOVA and Tukey LSD post-hoc comparisons

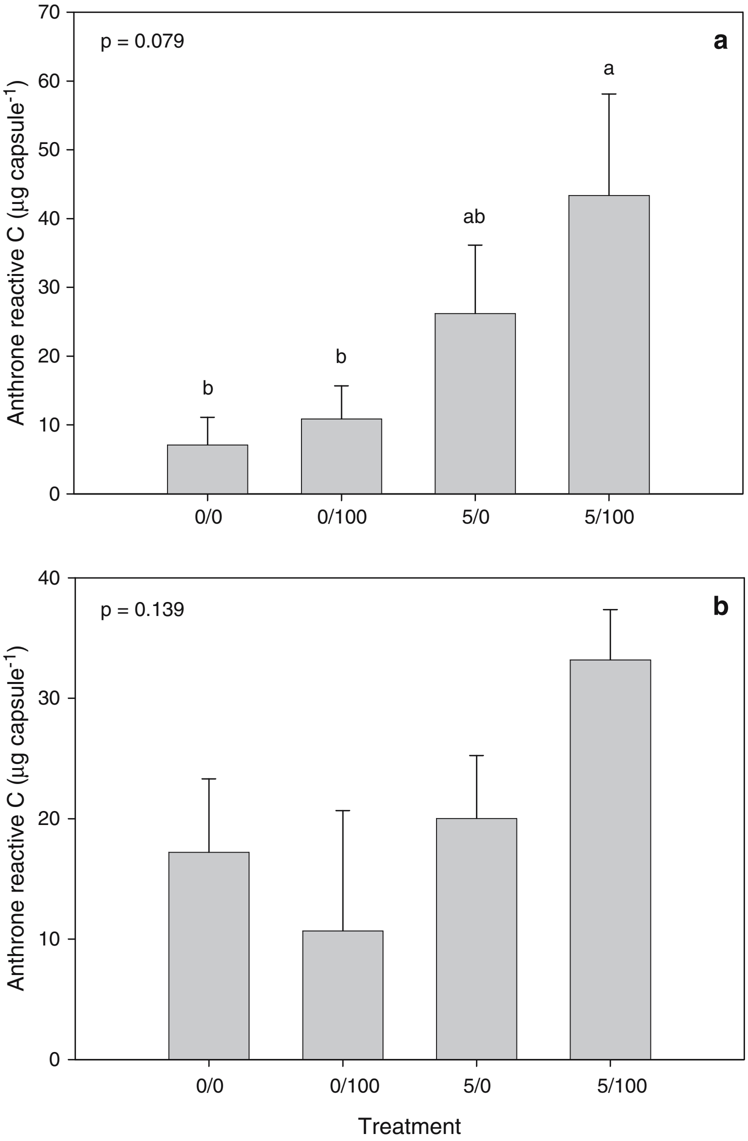

Fig. 2 Anthrone reactive C (mg capsule^{-1}) measured with ionic resin capsules from factorial applications of glycine (5 g m^{-2}) and charcoal (100 g m^{-2}) to greenhouse incubated litter samples of two different plant types, (**a**) *Arctostaphylos uva-ursi* (shrub) and (**b**) *Carex geyeri* (sedge), found in the understory of ponderosa pine forests of western Montana. The control (0/0) represents conditions on fire-excluded sites. Different letters indicate significant differences with ANOVA and Tukey LSD post-hoc comparisons

collected phenols did not exhibit any significant trend for either plant litter type (data not shown).

Leaf leachates

Analysis of leaf leachates revealed similar concentrations of nutrients for both plant types (Table 1), however *A. uva-ursi* had a concentration of total phenols that was almost 20 times greater than that of *C. geyeri*. When leaf leachates from both plant types were shaken with field-collected charcoal, the total phenol concentration was significantly reduced for *A. uva-ursi* extracts, but not for *C. geyeri* extracts (Fig. 3).

Discussion

Nitrogen availability is typically very low in fire-excluded stands of ponderosa pine, however, this may in part be a function of methodological limitations. Our recent studies using ionic resin capsules suggest that inorganic N remains elevated for longer than previously expected

Table 1 Nutrient and phenol concentrations (µg g^{-1}) in leaf leachates produced from two different plant types, *Artostaphylos uva-ursi* (shrub) and *Carex geyeri* (sedge), found in the understory of ponderosa pine-Douglas-fir forests of western Montana

Plant type	Nutrient (µg g^{-1})			Total phenol (µg g^{-1})
	NH_4^+	NO_3^-	PO_4^-	
1% Sedge	0.49	0.09	1.26	10.7
1% Shrub	0.24	0.10	1.60	200.5

(DeLuca et al. 2002; MacKenzie et al. 2006). Results from MacKenzie et al. (2006) showed that resin sorbed and therefore plant available NH_4^+ and NO_3^- stay elevated in ponderosa pine forests for a period of 30–40 years after fire, whereas most fire effects studies suggest that N mineralization increases last for 1–3 years after fire (see Smithwick et al. 2005). In this current study, we observed low resin sorbed NO_3^- levels in the untreated litter microcosms of both species. Adding glycine to the system is a surrogate for the portion of labile C and N added in the natural environment by annual litter deposition and tests the ability of the microbial community cultured in the rhizosphere of each different plant type to mineralize C and N. The fact that ammonification increased with the addition of glycine alone (5/0) for both litter types indicates that microbial activity is substrate limited, and probably water limited as well, in these dry forest ecosystems. The nitrifying community supported by the sedge was readily stimulated by glycine additions, as NO_3^- levels also increased significantly in the sedge microcosms with the addition of glycine alone. The charcoal alone (0/100) treatment had no effect on ammonification or nitrification for either plant type, but the addition of glycine and charcoal (5/100) stimulated significant nitrification in shrubs. This indicates that ericoid shrubs interfere with nitrification and that adding fresh charcoal, a surrogate for fire, removes the mechanism of inhibition.

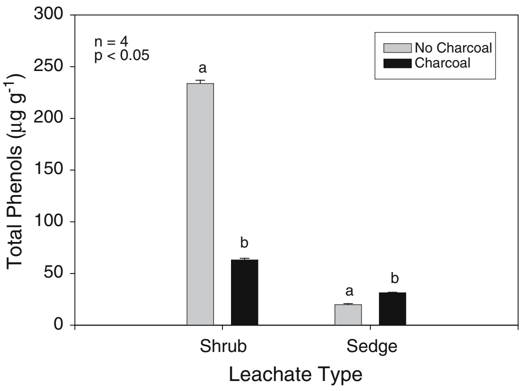

Fig. 3 Total phenols (µg g^{-1}) from leaf water extracts (diluted to 1% v/v) of two different plant tissue types, remaining in solution after shaking with and without charcoal (1% w/v). The plants are common in the understory of ponderosa pine stands in western Montana and were *Arctostaphylos uva-ursi* (shrub) and *Carex geyeri* (sedge), respectively

Charcoal is a significant component of pyrogenic ecosystems and has been shown to sorb organic compounds (DeLuca et al. 2002; Wardle et al. 1998b; Zackrisson et al. 1996). It represents the long-term 'foot-print' of the wildfire disturbance regime, but has an activity shelf-life of 100 years in boreal systems (Zackrisson et al. 1996), a period similar to the natural fire return interval in that environment. This period of activity may be shorter (~50 years) in the dry inland Northwest (MacKenzie et al. 2006). During the active phase, charcoal has been found to increase nitrification as shown above and previously (DeLuca et al. 2006). However, it is not clear if this is the result of charcoal adsorption of compounds that inhibit microbes (White 1994), initiate immobilization (Schimel et al. 1998), that bind proteins (Hattenschwiler and Vitousek 2000), are hydrophobic and notoriously low in N (Piccolo et al. 1999) or by providing microbes a protected site with adequate resources and away from predation (Pietikainen et al. 2000a, b). Phenols are a broad class of C compounds, but some phenols, including Batatasin III (Nilsson and Wardle 2005) have been implicated in allelopathy. Results from the experiment that combined leaf leachates and charcoal showed that charcoal adsorbs total phenols from solution very effectively. This may be evidence for adsorption of compounds that inhibit microbes as a mechanism for increased nitrification on fire-excluded forest soils in the presence of charcoal.

Soluble anthrone reactive C (AR-C) has been reported to be positively correlated with microbial biomass and respiration (DeLuca 1998). The low AR-C concentrations point to low levels of biologically available C in the *A. uva-ursi* litter and implies a mechanism of interference with microbially mediated mineralization of soil organic matter that is alleviated by adding charcoal. It does not tell us if the interference is direct (allelopathic) or indirect, where polyphenol protein complexes reduce N availability (MacKenzie et al. 2006). It is also not clear if bacteria are using charcoal as a protected site (Pietikainen et al. 2000a, b). In our previous work, we observed that the microbial biomass remained constant with increasing time since fire, (MacKenzie et al. 2006). If the nitrifying community experienced direct inhibition we might expect microbial biomass to decrease, which may have been the case for nitrifier biomass, but the fumigation-extraction method does not allow us to differentiate between microbe functional types. The rapid 24 h response of the nitrifier community to added charcoal as observed by DeLuca et al. (2006) suggests that the nitrifier community is intact, but not active, supporting indirect inhibition.

There is evidence that certain plant functional groups prefer one form of inorganic N over another (Kronzucker et al. 1997). Graminoids are fast growing species that may prefer NO_3^- due to the increased mobility of this ion in the soil matrix (e.g., Jones et al. 2005; Persson et al. 2003). The apparent inhibition of the nitrifier community by ericoid shrub litter could have evolved as a means of N conservation in N limited systems, where NO_3^- may be subject to loss by leaching and denitrification during periods of heavy rain, such as in the spring and fall.

Net nitrification in the graminoid microcosms was similar in magnitude to that induced by the addition of charcoal and glycine in the ericoid microcosms. These results are remarkably similar to those of DeLuca et al. (2006) which showed that nitrification potentials in forest soils amended with charcoal and glycine were close to those found in natural grassland soils. Also similar to that study, we found that charcoal had no effect on net nitrification in the graminoid microcosms. The results from the greenhouse incubations indicate that *A. uva-ursi* interferes with nitrification, which may be a means of competitive nutrient acquisition. It is not clear however, if this is a unique trait of *A. uva-ursi* or something representative of the woody shrub functional group, a group that has increasing understory coverage after disturbance. The noted difference in phenol concentrations of the litter extracts of *A. uva-ursi* vs. *C. geryii* are consistent with the work of Almendros et al. (2000) who demonstrate uniquely high leaf tissue concentrations of phenols in *A. uva-ursi* compared to numerous other Mediterranean plant species. In general, woody plants exhibit slow growth and tolerate low nutrient environments (Lambers et al. 1998). Inhibiting or reducing net nitrification could be a mechanism by which plants reduce N loses to leaching and denitrification, resulting in a predominance of slowly available N. Leaching and denitrification may be a problem in this environment where snow melt and spring rains saturate the soils of this otherwise dry ecosystem (NCDC 2005; Nimlos 1986).

In a similar study in the boreal forests of Sweden, DeLuca et al. (2002) showed that resin sorbed NO_3^- remained elevated for a period of 80–100 years and that charcoal had the capacity to stimulate nitrification in the fire-excluded stands. This period of elevated N availability is similar to the natural fire return interval of boreal systems, as is the period of elevated N availability in ponderosa pine systems (30–50 years as mentioned above). It seems that there are distinct similarities between the way fire and charcoal are linked to soil resource availability and therefore ecosystem function in these two very different forest types. The fire-excluded boreal systems studied by DeLuca et al (2002) have shrub dominated understories that lack a significant grass component in late secondary succession. In western Montana, grasses are a distinct part of understory vegetation, are adapted to nutrient pulses (Bardgett et al. 1999) and do not directly inhibit nitrification as seen in previous studies (DeLuca et al. 2006), and given the data from experiments conducted above. However, there seems to be a similar pattern for N cycling after disturbance, which is modified by charcoal and vegetation, as shown by this study and others (Berglund et al. 2004; Keech et al. 2005). The data seem to indicate a theoretical framework, where beyond the natural disturbance induced N

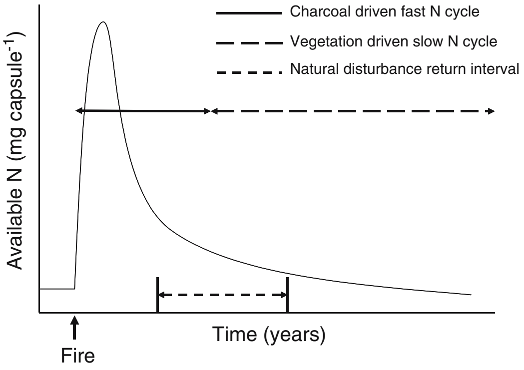

Fig. 4 A theoretical framework for changing N availability with increasing time since fire in any pyrogenic forest ecosystem. Disturbance driven N availability dominates during the natural fire return interval and vegetation driven N availability dominates beyond the natural fire return interval (adapted from DeLuca et al. 2002; MacKenzie et al. 2006)

cycle, there is a plant community induced N cycle that will exhibit spatial heterogeneity depending on the type of understory community that develops in late secondary succession (Fig. 4).

In many ecosystems it is not clear whether plant community dynamics are driving resource availability or whether resource availability is driving plant community dynamics (Wardle 2002). In fire prone ecosystems, we suggest that both processes are active at different temporal and spatial scales. In the presence of active charcoal, we would argue that it is the disturbance regime that drives N mineralization, a top down control. In the absence of active charcoal and beyond the natural disturbance interval, it seems that the plant community drives N mineralization with the quality of organic inputs, a bottom up control (Wardle 2002). This shift in ecosystem function is potentially an important one in contemporary forest management given that fire exclusion has greatly altered natural ecosystem processes over the last 80–140 years in the dry, low elevation forests of the Inland Northwest.

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