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Carbon and nitrogen cycling immediately following bark beetle outbreaks in southwestern ponderosa pine forests

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Abstract

Bark beetle infestation is a well-known cause of historical low-level disturbance in southwestern ponderosa pine forests, but recent fire exclusion and increased tree densities have enabled large-scale bark beetle outbreaks with unknown consequences for ecosystem function. Uninfested and beetle-infested plots ($n = 10$ pairs of plots on two aspects) of ponderosa pine were compared over one growing season in the Sierra Ancha Experimental Forest, AZ to determine whether infestation was correlated with differences in carbon (C) and nitrogen (N) pools and fluxes in aboveground biomass and soils. Infested plots had at least 80% of the overstory ponderosa pine trees attacked by bark beetles within 2 years of our measurements. Both uninfested and infested plots stored ~9 kg C m^{-2} in aboveground tree biomass, but infested plots held 60% of this aboveground tree biomass in dead trees, compared to 5% in uninfested plots. We hypothesized that decreased belowground C allocation following beetle-induced tree mortality would alter soil respiration rates, but this hypothesis was not supported; throughout the growing season, soil respiration in infested plots was similar to uninfested plots. In contrast, several results supported the hypothesis that premature needlefall from infested trees provided a pulse of low C:N needlefall that altered soil N cycling. The C:N mass ratio of pine needlefall in infested plots (~45) was lower than uninfested plots (~95) throughout the growing season. Mineral soils from infested plots had greater laboratory net nitrification rates and field resin bag ammonium accumulation than uninfested plots. As bark beetle outbreaks become increasingly prevalent in western landscapes, longer-term biogeochemical studies on interactions with other disturbances (e.g. fire, harvesting, etc.) will be required to predict changes in ecosystem structure and function.

Keywords: Ponderosa pine; Pine bark beetle; Nitrogen cycling; Soil respiration

1. Introduction

In dry forests of the western USA, fire exclusion, grazing, and harvesting have been important drivers of environmental change for over a century. These land management practices are known to alter ecosystem function (Covington and Moore, 1994; Kaye and Hart, 1998a,b; Stone et al., 1999; Kaye et al., 2005), but it is unclear how management interacts with natural disturbance regimes. For example, in ponderosa pine forests of the Southwest, one unintended consequence of fire exclusion is an increase in stand-replacing bark beetle outbreaks, especially in drought years (Kolb et al., 1998; Allen and Breshears, 1998). Interactions among fire exclusion, beetle outbreaks, and drought could induce novel and complex ecosystem changes that are not predictable from studies that focus on fire exclusion alone (Aber et al., 2001; Folke et al., 2004; Allen, 2007). A key step toward understanding these interactions is to identify changes in ecosystem structure and function that accompany beetle infestations, and in this paper, carbon (C) and nitrogen (N) pools and fluxes in uninfested and beetle-infested ponderosa pine stands in Arizona are compared.

Prior to Euro-American settlement in the late 1800s, southwestern ponderosa pine forests were open and ''park-like'', consisting of pockets of large, mature ponderosa pine interspersed in a matrix of grass (Cooper, 1960). Herbaceous vegetation was abundant, and aerial coverage of tree canopies ranged only from 17 to 30% (Pearson, 1923; Dieterich, 1980; White, 1985; Covington and Sackett, 1986). Surface fires occurred every 2–12 years prior to settlement, killing pine seedlings and maintaining this open structure (Pearson, 1923;

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Weaver, 1951; Cooper, 1960; White, 1985; Swetnam and Baisan, 1996; Kaye and Swetnam, 1999). Fire exclusion by Euro-Americans disrupted this cycle of periodic fires, allowing ponderosa pine seedlings to establish in previously open pockets of grassland. The introduction of livestock with grazing and trampling reduced herbaceous fuels that supported frequent surface fires. It is now widely accepted that grazing and fire exclusion in southwestern ponderosa pine forests lead to increasing pine densities and the subsequent risk of large-scale stand-replacing fires. More recently, ecologists have hypothesized that fire exclusion and increased pine densities have increased the likelihood of bark beetle outbreaks (Kolb et al., 1998; Samman and Logan, 2000; Fettig et al., 2007).

Bark beetles (*Ips* spp. and *Dendroctonus* spp.) are endemic to the coniferous forests of the Southwest (Samman and Logan, 2000; Fettig et al., 2007). Adult bark beetles are attracted (by aggregation pheromones from other beetles) to potential host trees. If colonization is successful, females lay eggs in the cambium layer of the targeted tree. The resulting larvae carve galleries into the cambium as they consume it during their development, which cuts off the exchange of nutrients between the crown and the roots, killing the tree. Eventually, adults emerge and seek other host trees, repeating the process. Several generations of bark beetle can occur over one season (typically April–October) and, if suitable hosts and a large enough population of beetles exist, they can infest concentrated areas of forest. Historically, bark beetles were a continual source of low-level disturbance in ponderosa pine forests (Samman and Logan, 2000). However, beetles typically reproduce in trees that are weakened by physiological stresses, such as prolonged drought (Kolb et al., 1998; Samman and Logan, 2000; Wallin et al., 2003), and outbreaks tend to occur in dense stands (Samman and Logan, 2000; Fettig et al., 2007). Thus, recent (i.e. over the past 100 years) increases in stand densities and subsequent stress on individual trees (Stone et al., 1999; Kaye et al., 2005) have lead to increased size and intensity of bark beetle outbreaks (Samman and Logan, 2000).

Forest disturbance induced by insects, specifically defoliation, has been widely investigated. Changes in nutrient dynamics, soil characteristics, dead woody debris, soil organisms, carbon allocation, and species composition have been documented across many ecosystems and types of insect disturbance (Swank et al., 1981; Schultz and Baldwin, 1982; Seastedt and Crossley, 1984; Hollinger, 1986; Scholwalter et al., 1986; Holland, 1995; Lovett and Ruesink, 1995; Webb et al., 1995; Bardgett et al., 1998; Eshleman et al., 1998; Reynolds et al., 2000; Lovett et al., 2002; Schulz, 2003; Frost and Hunter, 2004). Insect herbivores can have a pronounced impact on soil and surface water NO_3^-, especially when populations are at outbreak levels (Swank et al., 1981; Webb et al., 1995; Reynolds et al., 2000). However, prior research focused on insect herbivores that directly defoliate plants. Bark beetles differ from these well-studied foliar herbivores because trees are not directly defoliated. Bark beetles kill ponderosa pine trees by consuming cambium and disrupting phloem transport (Fettig et al., 2007). Beyond the visible structural changes (browning needles, dead trees) that follow bark beetle outbreak, and the implications of large-scale tree mortality on fire behavior and erosion (Allen, 2007), little is known about ecosystem processes that may be impacted by such a disturbance.

Our study investigates landscape-scale changes in ecosystem processes in a ponderosa pine forest immediately following a bark beetle infestation. Uninfested and infested plots were compared to document differences in C and N pools and to test four hypotheses regarding C and N cycling. Ponderosa pine trees typically resorb a portion of their nutrients from needles before senescence in September and October (Chapin and Kedrowski, 1983; Temple, 1995; Stone et al., 1999). Because infested trees loose their needles prior to natural senescence, it was hypothesized that needlefall N concentrations would be altered in infested plots. We predicted that N resorption would be bypassed, resulting in higher N concentrations and lower C:N ratios in needlefall of infested plots as compared to needlefall in uninfested plots. Second, it was hypothesized that a pulse of N carried in needlefall to the forest floor would alter soil N cycling processes, with the prediction being that soil available N would be higher in infested plots than uninfested plots. Soil respiration is a combination of root respiration and microbial respiration. We hypothesized that decreased belowground C allocation following tree mortality would alter soil respiration rates in infested plots compared to uninfested plots, with the prediction being that soil respiration would be lower in infested plots as compared to uninfested plots. Fourth, it was hypothesized that aspect-induced soil moisture and temperature variability might interact with ecosystem responses to beetle infestation.

2. Study site

This research was conducted in the Sierra Ancha Experimental Forest (5190 ha), on the western slope of the Sierra Ancha Mountain Range in central Arizona. Elevation ranges from 1080 to 2350 m, but we focused on ponderosa pine (*Pinus ponderosa* Laws.) forests at elevations 1400–1800 m (Pase and Johnson, 1968). Annual precipitation ranges from 45 to 125 cm/year, averaging 85 cm/year with 30% falling from June through September during the monsoon season (Pase and Johnson, 1968). Geologic formations in the area are in the Apache Group, and the soils are deeply weathered from medium to coarse-grained diabase (Pase and Johnson, 1968).

We did not identify beetle species that were active in this study area. However, Williams et al. (in press) surveyed beetle activity from 2004 to 2006 in the Tonto National Forest that surrounds our research site. The *Ips* species that they observed included *I. pini* Say, *I. lecontei* Swaine, *I. calligraphus ponderosae* Swaine, *I. latidens* LeConte, and *I. knausi* Swaine. The *Dendroctonus* species that they observed included *D. frontalis* Zimmerman, *D. brevicomis* LeConte, *D. adjunctus* Blandford, *D. approximatus* Dietz, and *D. valens* LeConte. Several species (*I. lecontei*, *I. calligraphus ponderosae*, *D. frontalis*, and *D. brevicomis*) were more abundant at low- to mid-elevation sites such as ours than they were at higher elevations. In contrast, *I. knausi*, *D. adjunctus*, *D. approx-*

imatus, and *D. valens* were less abundant at the elevations of our site compared to higher elevations. The abundance of *I. pini* and *I. latidens* did not vary with elevation.

3. Methods

To select plots, a topographic map was used to identify all areas that met the following criteria: (1) within the experimental forest, (2) within 2 km of an access road, (3) on slopes less than 30%, and (4) either on a southwest- or northeast-facing aspect. After potential sites were identified, they were listed in random order and field reconnaissance confirmed that the above criteria were met and that recently infested stands were available. From this randomized list, the first 10 sites that met the above criteria were established in May 2004. Half of these sites were on northeast and half were on southwest aspects. Each of the 10 sites was split into an uninfested plot and an infested plot, for a total of 20 plots. All plots were circular (10 m radius; 314 m^2). The uninfested and infested paired plots were at least 100 m from each other and shared similar soil and stand characteristics (Tables 1 and 2). All sampling took place from May to November 2004.

Infested plots were located where at least 80% of ponderosa pine trees showed clear signs of bark beetle infestation (both bore holes and browning needles) over a 1 ha area. We do not know exactly when the infestation began in these plots. Some trees in infested plots contained brown needles (which can be retained for 12 months following infestation), others were already needle-free, and some still had green needles. Increment cores taken from all trees (methods described below) showed that 95% of trees in both uninfested and infested plots had measurable wood growth (i.e. the tree was alive) in 1999, 2000, and 2001. In 2002, only 34% of the trees in the infested plots had measurable wood growth, compared to 96% in uninfested plots. These results suggest that the majority of trees in our infested plots died between 2002 and 2004.

Our experimental design does not attempt to explain how the forest functioned prior to infestation. These forests were infested prior to the establishment of our plots, and our study is a comparison of C and N pools and fluxes in infested and uninfested plots. To statistically test for such differences (and their interaction with aspect), a standard statistical analysis for a split-plot experimental design was used, with the main effect being aspect and the split effect being infestation status.

3.1. Trees and shrubs

For living and recently beetle-killed trees, diameter at breast height (DBH; measured 1.37 m above the ground) was recorded for all trees with DBH > 5 cm. For trees with DBH < 5 cm (called seedlings hereafter) and shrubs, stem diameter 10 cm above the base (basal diameter) was recorded. One randomly selected quarter of each circular plot was sampled for tree seedlings and shrubs due to high shrub densities.

Table 1
Summary of aboveground site characteristics

Component	Beetle status		Aspect	
	Uninfested	Infested	Northeast	Southwest
Basal area (m^2 ha^{-1})				
Live ponderosa pine	28.7 (11.0) a	7.5 (5.8) b	18.5 (4.6)	17.7 (4.4)
Dead ponderosa pine	0.3 (0.4) a	27.5 (9.8) b	16.5 (5.7)	12.2 (4.1)
Oak species[a]	7.7 (7.6)	11.1 (6.5)	5.7 (1.8)	8.9 (2.1)
Other tree species	5.5 (10.5)	6.2 (11.8)	6.0 (3.9)	5.7 (3.2)
Shrubs	1.4 (0.4)	2.9 (0.9)	2.5 (0.8)	1.8 (0.6)
Stem density (stems ha^{-1})				
Live ponderosa pine	376 (92) a	127 (23) b	261 (74)	242 (83)
Dead ponderosa pine	19 (13) a	290 (38) b	153 (56)	156 (50)
Oak species[a]	403 (132)	446 (91)	226 (68)	659 (112)
Other tree species	105 (43)	111 (23)	110 (26)	107 (41)
Litterfall (g dry mass m^{-2})				
Summer	51.1 (6.1)	57.9 (5.6)	45.9 (5.0) a	63.1 (5.4) b
Fall	105.7 (15.9)	127.1 (29.0)	135.0 (26.2)	98.7 (18.8)
Needlefall (g dry mass m^{-2})				
Summer	59.6 (12.1)	50.4 (8.1)	51.6 (9.5)	58.5 (11.2)
Fall	270.9 (46.8) a	128.7 (28.9) b	220.9 (37.5)	178.7 (51.4)
PAR (% full sunlight)	33.7 (37.8) a	51.6 (27.9) b	42.3 (33.1)	43.0 (35.8)

Values are means ($n = 10$) and 1S.E. in parentheses. Differing letters within a row indicate whether the means are significantly different from one another ($p < 0.05$) in a two-way split-plot ANOVA.

[a] This category includes all live and dead stems of evergreen and deciduous oak species.

Table 2
Summary of soil characteristics at the sites

Component	Beetle status		Aspect	
	Uninfested	Infested	Northeast	Southwest
Surface rock cover (m^2 ha^{-1})[a]	108.6	48.9	41.5	116.0
Soil texture (mass%)				
Sand	46.8	46.4	47.0	46.2
Silt	22.5	22.7	23.6	21.5
Clay	30.7	31	29.4	32.3
Soil bulk density (g cm^{-3})	1.00	0.97	0.94	1.03
pH				
Organic soil	5.3 (0.2)	5.2 (0.1)	5.1 (0.07)	5.4 (0.2)
Mineral soil (0–15 cm)	6.5 (0.08)	6.4 (0.12)	6.2 (0.07) a	6.6 (0.08) b
C to N mass ratio				
Organic soil	42.7 (3.8)	39.5 (2.3)	42.4 (3.9)	39.8 (2.3)
Mineral soil (0–15 cm)	19.9 (0.8)	19.2 (0.6)	20.1 (0.6)	19.1 (0.8)

Values are means ($n = 10$) and 1S.E. in parentheses. Differing letters within a row indicate whether the means are significantly different from one another ($p < 0.05$) in a two-way split-plot ANOVA.
[a] Surface area of rocks with at least one dimension >10 cm long visible at the soil surface.

Species-specific allometric equations were applied to our field-identified trees (standing and dead) and shrubs to convert measured diameters to aboveground biomass. Equations for ponderosa pine trees were from Kaye et al. (2005). Silverleaf oak (*Quercus hypoleucoides*), mountain mahogany (*Cercocarpus montanus*) and manzanita (*Arctostaphylos* spp.) equations were from Whittaker and Niering (1975). Douglas-fir (*Pseudotsuga menziesii*) and alligator juniper (*Juniperus deppeana*) equations were from Jenkins et al. (2004). For several species and all tree seedlings, allometric equations were unavailable. Silverleaf oak equations were applied to all oak species (evergreen and deciduous) and New Mexican locust (*Robinia neomexicana*). For shrubs, manzanita equations were applied to smooth sumac (*Rhus glabra*), all oak seedlings, and tree of heaven (*Ailianthus altissima*). Mountain mahogany equations were applied to Arizona madrone (*Arbutus arizonica*), and New Mexican locust seedlings. Equations for palo verde (*Parkinsonia microphylla*) were applied to alligator juniper seedlings, Douglas fir seedlings, and ponderosa pine seedlings. Biomass in trees, shrubs, and tree seedlings using an equation from another species amounted to <1.3% of total plot biomass in all cases.

The biomass of dead ponderosa pine trees that were either standing or recently fallen were determined on a case-by-case basis using the field-determined decay class of the tree. For instance, when beetle-killed ponderosa pine trees were intact with no foliage, all components of tree biomass were included in calculations except foliage. Designations of decay class follow Maser et al. (1979).

All ponderosa pine trees were cored with and increment borer (4 mm diameter) at breast height (1.37 m) and bark thickness was measured. The samples were stored in paper straws, mounted onto wooden trays, and sanded to maximize the visibility of ring boundaries. Cores were crossdated (Stokes and Smiley, 1996) and annual rings from 1950 to 2003 were measured to the nearest 0.01 mm with a sliding-stage micrometer. Growth increment was summed in decadal time periods. Current basal area of each tree was calculated from field-measured DBH and past basal area was calculated by decrementing current basal area by decadal growth increments from 2000 to 1950 assuming that bark thickness did not change over time. Approximately 11% of the trees could not be crossdated due to suppressed tree growth and wood decay and were excluded from the analysis.

3.2. Coarse and fine woody debris and herbaceous vegetation

Coarse woody debris (CWD) was defined as any down and dead woody vegetation within the plot that was not killed by the current beetle outbreak. Three forms of CWD 10 cm in diameter or greater (Harmon et al., 1999) were defined: (1) logs, (2) snags and (3) stumps. Logs that extended beyond the boundaries of the plot were measured only on dimensions occurring within the plot. Log diameter was measured at each end and at the midpoint of the log along with length. Species and decay class were also recorded. For snags, DBH and, if the snag is broken, height of snag were recorded. For stumps, height and diameter at half stump height were recorded. Volume was calculated as in Harmon and Sexton (1996) for all three classes of CWD.

Rarely was there any CWD not identified as ponderosa pine or oak. In these rare cases, equations from one of the two trees that most closely resembled that species in form and wood density were applied. Equations for ponderosa pine were applied to ponderosa pine CWD. Equations for oak species were applied to oaks as well as New Mexican locust, manzanita, and alligator juniper. Volume in ponderosa pine was converted to mass by using mean density estimates (Harmon and Sexton, 1996). Volume in oaks was converted to mass using specific gravity values from Adams and Owens (2001), who specify three decay classes as opposed to our five. Therefore, any oak

given a decay class in our dataset above 3 was given the specific gravity value for decay class 3.

The center of each plot was marked along with points 4 and 8 m from the center in the four cardinal directions, for a total of nine points within a plot. At each point, fine woody debris (FWD) was sampled in a 1 m^2 frame. Any FWD extending beyond the framed area was clipped at the frame boundary. The FWD was stored in a paper bag, oven-dried at 65 °C for 48 h, and weighed. In the same 1 m^2 frames, herbaceous biomass was clipped, then bagged, oven-dried at 65 °C for 48 h, and weighed.

3.3. Litterfall and needlefall

Litter traps were placed at five points within each plot (plot center and 6 m from center in each cardinal direction). Needlefall and litterfall (non-needle material in the traps) were collected once from May to August 2004 (called ''summer'') and once from August to November 2004 (called ''fall''). To obtain a spring sample, freshly fallen needles were collected from the forest floor immediately after plot set-up (May 2004). The freshly fallen needles were determined qualitatively by collecting needles on the forest floor surface that were not discolored from decomposition or UV-damaged (needles that overwinter or spend months on the forest floor are grey or mottled grey while freshly fallen needles are reddish-brown). In the laboratory, samples were oven-dried at 65 °C for 48 h, weighed, composited by plot, ground, and analyzed for C and N concentrations as described below for O horizon soil.

3.4. Organic and mineral soil carbon and nitrogen

A smaller (10 cm^2) frame was nested within each of the 1 m^2 frames to sample the entire organic (O) soil horizon. A serrated knife was used to cut into the O horizon and the entire horizon could be collected down to the organic–mineral soil interface. The O soil samples were air-dried until they were transported back to the laboratory. In the laboratory, the samples were oven-dried at 65 °C for 48 h, weighed, composited by plot, ground, and analyzed for C and N concentrations using a PerkinElmer® 2400 Series II CHNS/O Analyzer (PerkinElmer Instruments, Shelton, CT, USA). C and N concentrations were converted to g m^{-2} using the area of the sampling frame and mean dry mass of the O horizon samples.

Directly beneath the O soil horizon sampling area, mineral soil was collected using a manual soil corer (5 cm diameter) to a depth of 15 cm. If more than one-third of the core volume was occupied by rocks, a second mineral soil sample was collected at an adjacent (within 10 cm if possible) location. This approach overestimates soil C storage but it is unlikely to impact our comparisons of uninfested and infested plots because there were not differences in surface rockiness among plots (Table 2). Mineral soil samples were air-dried until they were transported back to the laboratory. In the laboratory, these samples were oven-dried at 105 °C for 48 h and then weighed, composited by plot, ground, and analyzed for C and N concentrations as described above for the O horizon. C and N concentrations were converted to g m^{-2} using the mean rock-free dry mass of soil, core volume, and core depth. Rock cover was collected at the whole-plot scale by recording the length and width of any rocks greater than 10 cm on their longest dimension. Soil surface area displaced by rock area, tree and shrub basal area were used to scale mineral and organic soil carbon values to the plot level.

3.5. Inorganic N in soils and resin bags

Our study site exhibits a pronounced wet season during the monsoons that is known to be time of concentrated soil microbial activity and nutrient cycling compared to the dry seasons before and after the monsoons (Boyle et al., 2005). Therefore, resin bags were deployed in June of 2004, before the monsoon rains began, and collected 87 days later at the end of the summer monsoon season. To make the resin bags, nylon bags were filled with two tablespoons of mixed bed ion-exchange resin beads (Binkley and Hart, 1989), acid-washed overnight, rinsed thoroughly with deinoized water, dried until slightly damp, and stored in a refrigerator.

Five resin bags were buried in each plot at a fixed distance from litter traps using a trowel inserted into the ground at a slight angle and then tilted to create a slit in the soil. The resin bag was placed in the slit at about 5 cm depth and flattened horizontally. After removal from the soil, resin bags were placed in separate plastic bags, stored in a cooler for transport back to the laboratory and air-dried. Once dried, the loose soil was brushed off of the bags, and the resin beads were removed and extracted with 100 ml 2 M potassium chloride (KCl) and analyzed for total inorganic N (NH_4^+ and $NO_3^- + NO_2^-$) on a Lachat QuickChem® 8500 (Milwaukee, WI, USA).

Composited samples of soil were analyzed for potential net ammonification and nitrification rates in November 2004 using a 24-day laboratory incubation. Two sets of each soil composite were weighed (10 g) in specimen cups. One set of samples was extracted immediately (time-zero sample) using 50 ml of 2 M potassium chloride (KCl), 1 h of shaking, and gravity filtration through preleached Whatman #4 filter papers. Extracts were frozen until analysis for nitrate and ammonium concentrations as described above for the resin extracts. The second set of samples were wetted to field capacity and incubated in an aerobic, dark environment at room temperature for 24 days. The potential net N transformation rate was calculated from the difference in NH_4^+-N (net ammonification) or NO_3^--N (net nitrification) between the incubated and time-zero samples. These samples were monitored frequently and their water content was adjusted to ensure they were at field capacity.

3.6. Soil respiration and microclimate

The flux of carbon dioxide (CO_2) from soils to the atmosphere (soil respiration) was measured using an Infra-Red Gas Analyzer (IRGA) (PP Systems®, Amesbury, MA, USA). Soil respiration was collected in the spring (27 May–11 June 2004), summer (2–11 August 2004) and fall-winter (20 November–16 December 2004) of 2004 at five points in each plot. This seasonal sampling scheme was designed to capture

periods of high and low soil temperatures coupled with high and low soil moisture values to assess how beetle outbreaks alter soil respiration under common environmental conditions. Due to travel time, samples from all sites could not be collected on the same day, however, paired plots that constitute a site (i.e. the paired infested and uninfested plots that were compared statistically) were always sampled on the same day. The IRGA was calibrated in the field with a CO_2 standard (392 ppmv). Any herbaceous vegetation within the sampling area was clipped prior to data collection. Concurrent with soil respiration sampling, soil temperature, gravimetric soil moisture content (drying at 105 °C for 48 h), and time of day were recorded. The coarse litter layer on the forest floor allowed air to flow in from sides of the IRGA chamber. To avoid mixing of atmospheric air with chamber air, three PVC collars were constructed of different lengths, which attached snugly to the base of the IRGA chamber. The length of the collar used was determined by the depth of the forest floor. To insert the IRGA chamber into the soil, a serrated knife was used to cut around the area of the PVC collar into the soil to avoid soil disturbance during readings. The chamber with the collar attachment was then inserted in the cut ring of forest floor for a reading. In these forests, O horizons do not contain roots, so our procedure should not have disturbed root respiration.

HOBO® temperature data loggers were deployed in four plots: two plots with northeast aspects and two plots in southwest aspects. In each of these plots, three data loggers recorded soil temperature and one data logger recorded air temperature. The soil temperature data loggers were buried in the mineral soil at 2 cm below the surface. The air temperature data logger was hung at breast height (1.37 m) in a ventilated and capped PVC pipe, which prevented the sensor from being exposed to direct sunlight. Data loggers collected temperature from May to December 2004. A ceptometer (Decagon Devices, Inc.®, Pullman, WA, USA) was used to measure photosynthetically active radiation (PAR). Readings were taken between 1000 and 1400 h in direct sunlight and at five points within each plot.

3.7. Statistical analyses

The effect of aspect (northeast vs. southwest) and infestation (uninfested vs. infested) on the variables measured was compared using a two-way split-plot ANOVA ($\alpha = 0.05$ for all tests). A repeated-measures ANOVA was used to assess the overall effect of season (time) on variables that were sampled several times. The analyses were performed using Systat® 10 software (Point Richmond, CA, USA). Additionally, soil respiration data were analyzed for possible covariates of soil temperature and soil moisture using repeated-measures ANCOVA with SAS® 9.1.3 software (Cary, NC, USA).

4. Results

4.1. Basic ecosystem characteristics

As expected, infested plots had greater density and basal area of dead ponderosa pine trees than uninfested plots. There was no difference ($p > 0.05$) among plots in basal area or stem density for other tree species, shrubs, or combined (live plus dead) ponderosa pine trees. In addition, there were no treatment or aspect differences in ponderosa pine basal area between 1950 and 2004 (Fig. 1). No differences were found in rock-free mineral soil bulk density or soil texture among treatments (Table 2). Soil pH and PAR differed between uninfested and infested plots (Tables 1 and 2). Microclimatic conditions differed as well, with infested plots having higher air and soil temperatures than uninfested plots (Fig. 2). Soil moisture (Fig. 3A) was higher in infested plots during the summer ($p = 0.018$), but not in the spring or fall ($p = 0.4$ and 0.1, respectively).

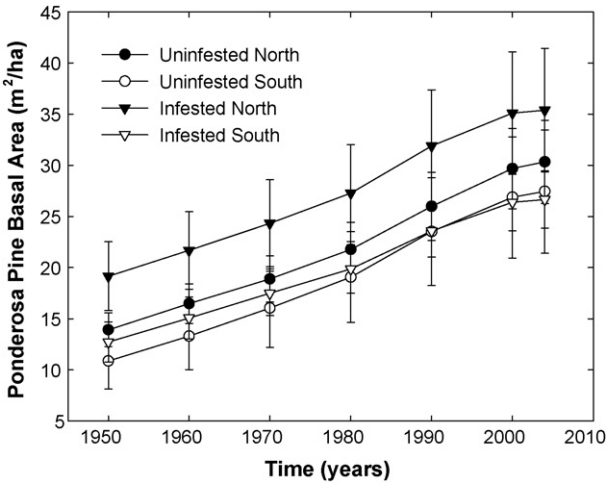

Fig. 1. Changes in the basal area of ponderosa pine trees over time. Data from 1950 to 2000 are reconstructed from tree rings, while values from 2004 were directly measured. There were no differences between aspects ($p = 0.4$) or with beetle infestation ($p = 0.2$), and there were no significant interactions between these factors and time ($p > 0.17$). These data are means of all trees (live and dead) that could be crossdated. Because it was not possible to cross date some trees (see Section 3) the means here are not identical to values in Table 1.

Infestation altered the biomass C (Table 3) of both live and dead trees ($p = 0.002$ and <0.000, respectively). Uninfested plots had more live biomass C and infested plots had more dead biomass C, despite having similar total biomass C. Independent analyses of other categories of biomass C, such as CWD, FWD and soil carbon, were similar across treatments. There were no significant effects of infestation status or aspect on total ecosystem C (Table 3), which is similar across plots ($p = 0.4$).

4.2. Inorganic nitrogen

Laboratory net N transformation rates (both NH_4^+-N and NO_3^--N) in the organic soil horizon (Fig. 4A) did not differ among treatments ($p = 0.7$ and 0.6, respectively). In mineral soils (Fig. 4B), net nitrification (net NO_3^--N accumulation during the laboratory incubation) rates were greater in infested plots than uninfested plots ($p = 0.006$), but net ammonification was similar among plots ($p = 0.2$). There was no difference in the time-zero samples of organic or mineral soil horizons for either NH_4^+ or NO_3^- (data not shown). Resin

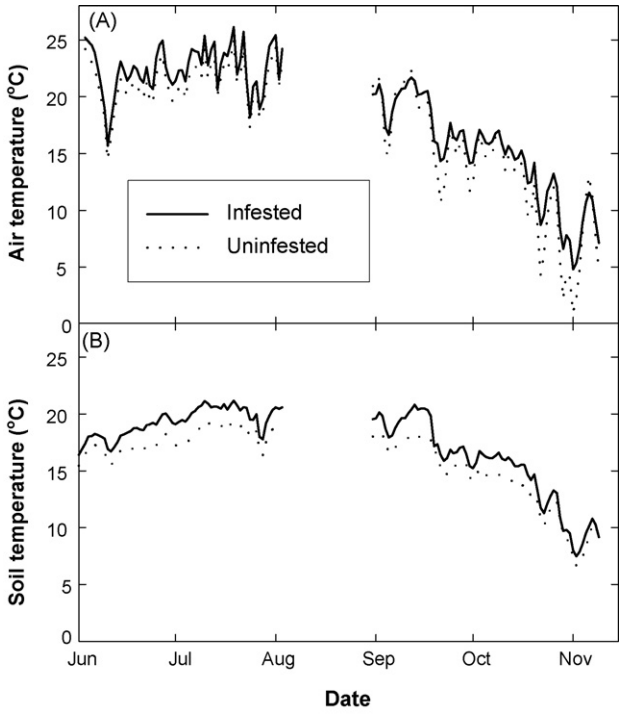

Fig. 2. Air (A) and soil (B) temperature in infested and uninfested stands. Lines are the means of two plots. Data from August 4 to 30 were not collected.

bags deployed in the field accumulated more NH_4^+ in soils of infested plots compared to soils of uninfested plots ($p = 0.04$) (Fig. 4C). However, resin NO_3^- did not differ among treatments ($p = 0.3$).

4.3. Carbon to nitrogen mass ratios

Ponderosa pine needles showed a consistent pattern of lower C:N in infested plots (Fig. 5) within a sampling date and across all three seasons ($p < 0.0001$). The effect of aspect was significant ($p = 0.05$), with plots on northeast aspects having higher C:N ratios than plots on southwest aspects (data not shown). The difference in C:N ratios was due exclusively to changes in N concentration because C concentration (~50% by mass) of needles did not vary among treatments. The mean nitrogen concentration of needles from infested plots was 1.2, 1.1, and 0.9% (mass basis) in the spring, summer, and fall, compared to 0.6, 0.7, and 0.5% in the uninfested plots from the same time periods. In both the organic soil horizon and the mineral soil horizon, C:N was similar among plots ($p = 0.5$ and 0.2, respectively) (Table 2).

4.4. Soil respiration and litterfall

Spring soil respiration was higher on northeast aspects than southwest aspects ($p = 0.03$) (Fig. 3C). There were no infestation or aspect effects on soil respiration rates for summer or fall ($p = 0.8$ and 1.0, respectively). When all three seasons were analyzed together, only season had a significant impact on soil respiration rates ($p < 0.0001$); neither soil

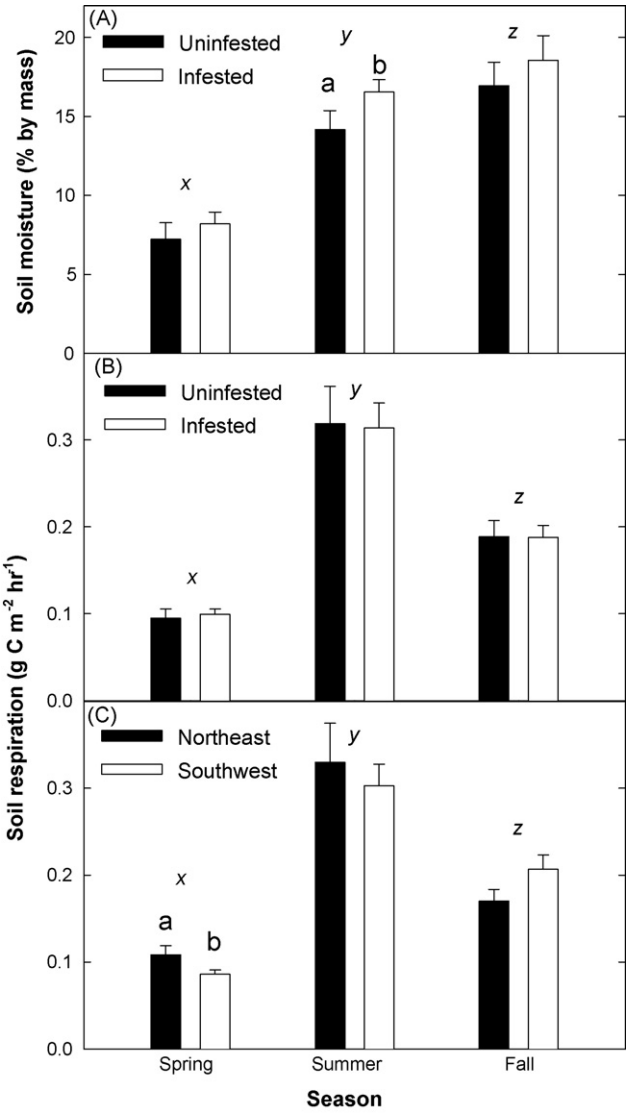

Fig. 3. Seasonal variation in soil moisture (A) and soil respiration (B) in uninfested and infested plots, and soil respiration compared between aspects (C). Bars are means and 1S.E. Lowercase letters (a, b, c) indicate whether values within a season are significantly ($p < 0.05$) different, lowercase italic letters (*x*, *y*, *z*) indicate whether seasons are significantly different ($p < 0.05$).

temperature ($p = 0.6$) nor soil moisture ($p = 0.08$) were significant covariates in the analysis.

Needlefall mass collected from May to August 2004 (summer) showed a significant ($p = 0.05$) interaction between aspect and infestation status, with uninfested, southwest aspects having higher mass (Table 1). Other litterfall (non-needle material in the litter traps) collected during this same time was higher in southwest-facing plots compared to northeast-facing plots ($p = 0.04$). Needlefall collected from August to November (fall) had higher mass values in uninfested plots compared to infested plots ($p = 0.01$). This is expected, as the majority of ponderosa pines in infested plots were dead and had few needles remaining on them by the beginning of the fall litterfall sampling period. There was no significant trend in the data overall in total litterfall from August to November ($p = 0.6$).

Table 3
Ecosystem carbon (C) pools

Component	Beetle status		Aspect	
	Uninfested (kg C m^{-2})	Infested (kg C m^{-2})	Northeast (kg C m^{-2})	Southwest (kg C m^{-2})
Live trees	7.9 (0.7) a	3.6 (0.6) b	5.4 (0.9) a	6.2 (1.0) a
Dead trees	1.2 (0.3) a	6.5 (0.6) b	4.7 (1.1) a	3.0 (0.8) a
Shrubs	0.05 (0.02) a	0.1 (0.07) a	0.1 (0.07) a	0.06 (0.01) a
Coarse woody debris	0.5 (0.1) a	0.4 (0.2) a	0.7 (0.2) a	0.2 (0.09) a
Fine woody debris	0.3 (0.02) a	0.3 (0.1) a	0.3 (0.1) a	0.2 (0.02) a
Herbaceous vegetation	0.002 (0.002) a	0.002 (0.001) a	0.003 (0.002) a	0.001 (0.001) a
Mineral soil (0–15 cm)	7.1 (0.7) a	6.9 (0.6) a	6.9 (0.7) a	7.1 (0.5) a
Organic soil horizon	5.7 (0.6) a	5.5 (0.6) a	5.5 (0.8) a	5.7 (0.4) a
Total	24.4 (2.1) a	22.5 (1.0) a	25.0 (2.0) a	21.9 (1.1) a

Values are means ($n = 10$) and 1S.E. in parentheses. Differing letters within a row indicate whether the means are significantly different from one another ($p < 0.05$) in a one-way ANOVA. There was an interaction between aspect and infestation status in dead trees (the effect of aspect depends on infestation).

5. Discussion

5.1. Ecosystem structure

The main goal of our research was to test hypotheses regarding ecosystem function (next section), but we also quantified ecosystem structure to describe the context in which the hypotheses were tested. Basic soil characteristics (texture, bulk density, and C pools) were similar in uninfested and infested plots (Tables 2 and 3). Measurements of current and past (using tree rings) tree diameters suggest that infested and uninfested plots had similar tree densities, basal area, and decadal basal area increments (Fig. 1) prior to the bark beetle outbreak. Thus, based on the soil and plant pools that we measured, there were no major differences in ecosystem structure among the plots prior to infestation. Beetles altered ecosystem structure in several expected ways; a large fraction of tree C shifted from live to dead biomass pools following infestation, and the mortality of canopy trees increased PAR reaching the forest floor.

5.2. Ecosystem function: nitrogen cycling

Our initial hypothesis was that tree mortality induced by bark beetles would affect needle N concentration, with the prediction being that premature needlefall would result in increased needle N concentration. This hypothesis was supported. Needle N concentrations were higher in infested plots over all three seasons. Our results indicate that soils beneath beetle-killed trees received less litterfall than uninfested plots overall, but the litter has a higher N concentration. Thus, bark beetle infestation greatly altered the quantity and quality of litter falling to the forest floor. Our second hypothesis, that the pulse of high-N litter would alter soil N cycling, was also supported. The higher levels of resin bag NH_4^+ detected in infested plots in the field could be attributed to at least four N cycling pathways: (1) reduced plant uptake, (2) increased gross microbial mineralization, (3) decreased gross microbial immobilization of NH_4^+ (including the nitrification pathway), or (4) increased inputs of N from the O horizon (by leaching or microfaunal activity) resulting from high-N litterfall. Our data do not enable us to determine the cause for increased NH_4^+ availability in mineral soils, but some of these pathways are more likely than others. In our laboratory incubations, infested plots had higher mineral soil net nitrification rates than uninfested plots. High NH_4^+ accumulation can occur in soils with high net nitrification rates when (1) gross mineralization rates are high (pathway #2) or (2) gross nitrification rates are low (pathway #3), but gross nitrate immobilization rates are substantially lower. The laboratory incubations also show that NH_4^+ is immobilized in the O horizon, suggesting that downward leaching of NH_4^+ from fresh litter inputs (pathway #4) may not occur under conditions of adequate soil moisture in the field. Lovett and Ruesink (1995) found immobilization of N to be an important component in ecosystem N retention in gypsy moth defoliation experiments.

We are unaware of any other studies of N cycling in beetle-infested forests in North America. In Germany, Huber et al. (2004) and Huber (2005) measured N fluxes in chronosequence of mesic (160–200 cm precipitation/year) spruce forests that were killed by bark beetles 0–20 years in the past. They found that throughfall N inputs to soils declined from 1.2 to 1.6 g N m^{-2} $year^{-1}$ in an uninfested forest to <0.5 g N m^{-2} $year^{-1}$ following the infestation. Throughfall remained low for at least 6 years but had returned to pre-infestation levels within 16 years (Huber et al., 2004). In the soil, N flux through the O horizon (measured with zero tension lysimeters) increased immediately following the infestation, and remained elevated for 4 years, after which nitrate fluxes through humus began to increase to a peak ~6 years after the outbreak (Huber et al., 2004). Nitrate concentrations measured 40 cm below the soil surface (tension lysimeters) did not change during the year of the outbreak, but in the growing season following the outbreak, concentrations increased dramatically and stayed elevated for at least 5 years (Huber, 2005). Huber (2005) suggested that the lack of plant uptake was an important factor allowing high nitrate leaching following the outbreak, but our results suggest that a large pulse of N rich litter inputs may also play a role.

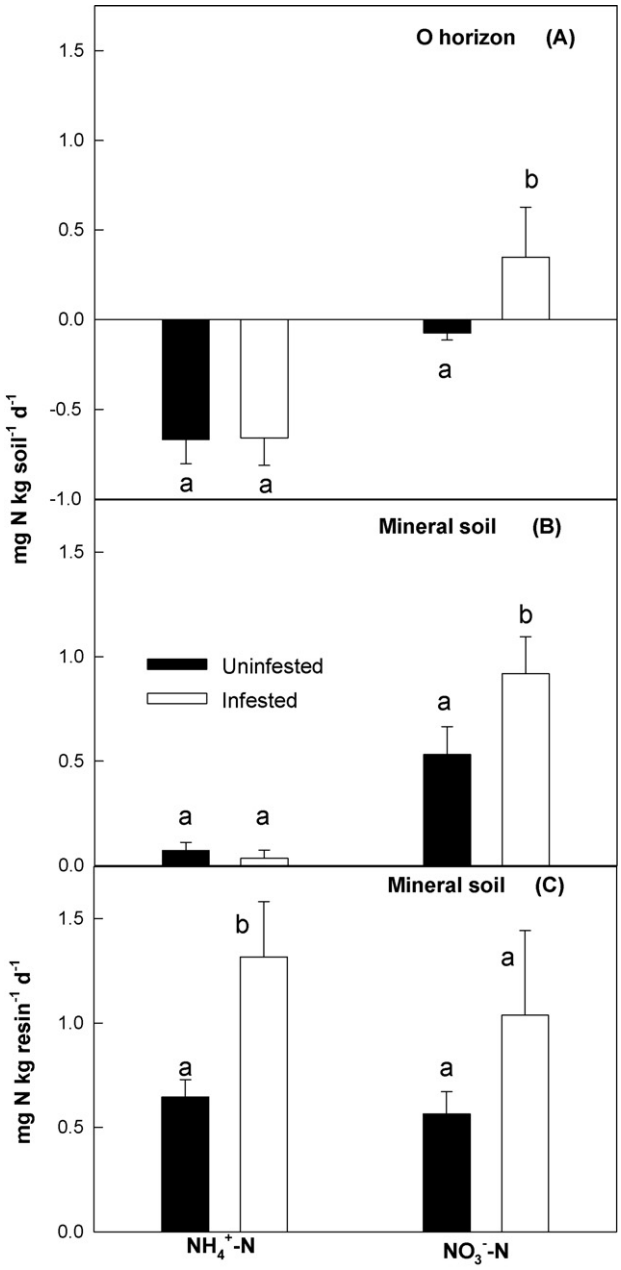

Fig. 4. Rates of extractable inorganic N accumulation in O horizon and mineral (0–15 cm) soils during laboratory incubations (A and B), and on resin bags incubated in the field 5 cm below the top of the mineral soil (C). Bars are means and 1S.E. Different lowercase letters indicate statistically significant ($p < 0.05$) differences in values between infested and uninfested plots for a given N species.

5.3. Ecosystem function: soil respiration

The third hypothesis explored, that the decrease in below-ground C allocation following tree mortality would alter soil respiration, was not supported. Despite pronounced vegetation mortality in infested plots, a decrease in soil respiration rates was not observed. Although an effect of aspect in soil respiration rates in the spring was found, this trend was not observed in subsequent seasons, and so the hypothesis that aspect would interact with infestation to impact soil respiration

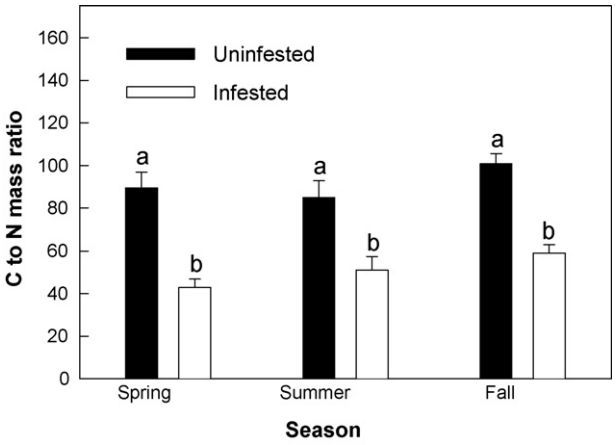

Fig. 5. The C to N mass ratio of ponderosa pine needlefall. Bars are means ($n = 10$) and 1S.E. Differering lowercase letters indicate statistically significant ($p < 0.05$) differences between ratio values in uninfested and infested plots.

was not supported. Similar soil respiration in uninfested and infested plots suggests that in beetle-infested plots: (1) fine roots continue to respire stored carbohydrate reserves, (2) heterotrophic soil microorganisms increase respiration by decomposing recently dead roots, or (3) increased soil temperature (Fig. 2) and soil moisture (Fig. 3) increase respiration rates. Support for #1 and #2 come from forest stand girdling experiments (Edwards and Ross-Todd, 1979; Hogberg et al., 2001; Bhupinderpal-Singh et al., 2003; Binkley et al., 2006). It seems likely that both of these factors maintain soil respiration (though to highly variable degrees) following girdling. We suspect that in our semi-arid forests, microclimatic effects (#3) also influence soil respiration in infested stands that have greater radiation supply to the forest floor (Table 1) and higher soil temperatures (Fig. 2). Support for this hypothesis comes from thinning experiments in other ponderosa pine forests where decreased canopy shading results in higher soil temperatures and respiration rates than in unthinned forests (Kaye and Hart, 1998b; Boyle et al., 2005).

6. Conclusions

Prior studies of bark beetle outbreaks in ponderosa pine forests have focused on individual tree physiology (Kolb et al., 1998) or landscape-scale ecotonal shifts (Allen and Breshears, 1998) but not on ecosystem biogeochemical changes. Our research showed that bark beetle outbreaks result in a pulse of high-N needlefall within 2 years of the outbreak. During this period, soil N cycling differs among infested and uninfested plots, suggesting that research is warranted to assess bark beetle effects on nutrient export and N availability following disturbance. We also documented a large shift in aboveground tree C in infested plots from live to dead pools, but it was unclear how tree death and soil respiration were linked (or apparently not linked in our data).

Short-term responses of the ecosystem to bark beetle infestation were investigated in this study, but the long-term effects, or the effects of larger-scale (e.g. whole watershed) outbreaks are difficult to predict. Allen and Breshears (1998)

investigated large-scale ponderosa pine tree mortality that occurred in the 1950s due to drought and beetle infestation and noted that a large shift in ponderosa pine distribution due to mortality had persisted for over 40 years. Savage and Mast (2005) conducted a regional survey of stand-replacing fires in ponderosa pine forests throughout the Southwest and observed two distinct trajectories, some areas regenerated back to forests while others persisted as grasslands or shrublands for decades. These studies, and the research by Huber (2005), illustrate the fact that our single year observations within 1–2 years of the initial beetle outbreak are insufficient to document the full suite of interactions that may occur between beetle outbreaks and biogeochemistry over longer time scales. Our short-term observations suggest that future research could illuminate the longevity of altered soil N cycling in beetle infested stands and the impact of altered N cycling on watershed N export. Likewise, our soil respiration results suggest that research is needed to understand how changes in belowground C allocation alter the long-term C balance of soils.

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