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Wood-feeding beetles and soil nutrient cycling in burned forests: implications of post-fire salvage logging

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Abstract

1 Rising economic demands for boreal forest resources along with current and predicted increases in wildfire activity have increased salvage logging of burned forests. Currently, the ecological consequences of post-fire salvage logging are insufficiently understood to develop effective management guidelines or to adequately inform policy decision-makers.

2 We used both field and laboratory studies to examine the effects of post-fire salvage logging on populations of the white-spotted sawyer *Monochamus scutellatus scutellatus* (Say) (Coleoptera: Cerambycidae) and its ecological function in boreal forest.

3 *Monochamus s. scutellatus* adults were relatively abundant in both burned and clear-cut logged sites but were absent from salvage logged sites.

4 An *in situ* mesocosm experiment showed that the abundance of *M. s. scutellatus* larvae in burned white spruce bolts was linked to changes in total organic nitrogen and carbon in mineral soil.

5 Organic nutrient inputs in the form of *M. s. scutellatus* frass increased mineral soil microbial respiration rates by more than three-fold and altered the availability of nitrogen. Changes in nitrogen availability corresponded with decreased germination and growth of *Epilobium angustifolium* and *Populus* spp. but not *Calamagrostis canadensis*.

6 Although the present study focused on local scale effects, the reported findings suggest that continued economic emphasis on post-fire salvage logging may have implications beyond the local scale for biodiversity conservation, nutrient cycling and plant community composition in forest ecosystems recovering from wildfire.

Keywords Beetle frass, boreal forest, coarse woody debris, IPDM, *Monochamus s. scutellatus* (Say), nitrogen cycling, saproxylic beetles, soil microbial activity, wildfire.

Introduction

Concern over the ecological consequences of human influences on natural ecosystems continues to drive issues about biodiversity conservation and the persistence of ecosystem function to the forefront of ecological research (Ehrlich & Wilson, 1991; Pimm *et al*., 1995; Vitousek *et al*., 1997; Naeem *et al*., 1999; Chapin *et al*., 2000; Naeem, 2002; Hooper *et al*., 2005). Natural ecosystems are increasingly stressed by anthropogenic demands for marketable products and the compounding effects of global environmental change (Vitousek *et al*., 1997; Sala *et al*., 2000). Climate models predict dramatic increases (approximately 30–50%) in the occurrence of wildfires in many forest ecosystems over the next century (Overpeck *et al*., 1990; Flannigan *et al*., 1998; Li *et al*., 2000) and global economic demands for both timber and nontimber resources continue to rise. As a result, economic pressure to salvage logs from burned forests is expected to increase, and such a trend is already apparent in many North American forests (Lindenmayer *et al*., 2004; Sessions *et al*., 2004).

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At present, the ecological consequences of post-fire salvage logging are insufficiently understood to develop effective management guidelines (Lindenmayer *et al*., 2004; Lindenmayer, 2006; Schmiegelow *et al*., 2006). Despite the lack of complete scientific understanding, such policies are being developed (Lindenmayer *et al*., 2004; Nappi *et al*., 2004; Schmiegelow *et al*., 2006). Recent studies suggest that large-scale salvage operations may significantly alter post-fire bird (Morissette *et al*., 2002; Nappi *et al*., 2004) and ground beetle assemblages (Koivula *et al*., 2006; Phillips *et al*., 2006; Cobb *et al*., 2007) and also affect plant regeneration (Fraser *et al*., 2004; Donato *et al*., 2006; Greene *et al*., 2006). In addition, wildfires increase the amount of dead wood across forested landscapes, and research from Australia (Grove, 2002), Europe (Siitonen & Martikainen, 1994; Jonsell *et al*., 1998; Martikainen *et al*., 1998; Ehnström, 2001; Martikainen, 2001; Siitonen, 2001; Martikainen & Kaila, 2004) and North America (Hammond, 1997; Hammond *et al*., 2001, 2004) suggests that this resource is critical for maintaining biodiversity in forest ecosystems. For example, the loss of dead wood from intensively managed Fennoscandian forests has already resulted in the extirpation of a number of saproxylic insect species (Siitonen & Martikainen, 1994). Although most saproxylic insects are considered to be involved in wood decomposition (Speight *et al*., 2008), few direct tests of this relationship have been conducted (Edmonds & Eglitis, 1989) and the precise functional roles of most species are inadequately understood (Grove, 2002). Thus, it is difficult to predict the ecological consequences of losing saproxylic species.

The white-spotted sawyer *Monochamus scutellatus scutellatus* (Say) (Coleoptera: Cerambycidae) is a pyrophilous ('fire-loving'), saproxylic beetle found throughout most of North America (Yanega, 1996). It is common in coniferous forests with abundant recently killed, weakened or dying trees, especially after fire (Rose, 1957; Wilson, 1962). The primary host tree species is considered to be eastern white pine (*Pinus strobus* L.) but females readily oviposit in, and larvae feed on, freshly cut or otherwise weakened jack pine (*Pinus banksiana* Lamb.), red pine (*Pinus resinosa* Ait.), balsam fir (*Abies balsamea* [L.] P.Mill.), white spruce (*Picea glauca* [Moench] Voss), black spruce (*Picea mariana* [P.Mill.] B.S.P.) and red spruce (*Picea rubens* Sarg.) (Wilson, 1962). Adults eat needles and twig bark, causing minor damage to the tips of branches (Wilson, 1962). After mating (Hughes, 1979), eggs are deposited singly in scars in the bark made by the female's mandibles and larvae hatch within 9–14 days (Rose, 1957; Peddle *et al*., 2002). Larvae feed primarily in the phloem and sapwood but burrow into the heartwood to pupate, thereby causing significant economic degradation in standing dead trees and log decks (Richmond & Lejeune, 1945; Rose, 1957; Ross, 1960). Larval development generally requires 2 years but may be shorter in southern extremes of the species' range (Wilson, 1962; Yanega, 1996). In addition to the galleries under bark, evidence of larval feeding activity is visible on the ground, in that wood chips and frass (faecal material) frequently build up around the base of the tree.

We investigated the effects of post-fire salvage logging on *M. s. scutellatus* and the role of this beetle in altering soil processes by recycling nutrients and organic matter from burned coniferous trees. Using a series of field and laboratory studies, we determined: (i) the effect of post-fire salvage logging on populations of adult *M. s. scutellatus*; (ii) the relationship between larval abundance and soil nutrients at the base of burned white spruce trees; (iii) the effect of organic nutrient inputs in the form of larval frass on soil microbial activity and nitrogen availability; and (iv) the effect of such frass on germination and growth of plant species that colonize recently burned forests.

Materials and methods

Field studies

Beetle survey. Populations of adult *M. s. scutellatus* were surveyed in and around a severe, large-scale wildfire (approximately 120 000 ha) that occurred from 23 May to 4 June 2001 near the hamlet of Chisholm, Alberta, Canada (54° 55′N, 114° 10′W). The study area was in the mid-boreal upland ecoregion, which is characterized by well-drained and gray luvisolic soils (Strong & Leggat, 1981). During the data collection periods (April to September 2002 and 2003), mean daily temperature was 18.5°C (2002) and 16.8°C (2003), and the mean monthly precipitation was 19.5 mm (2002) and 33.5 mm (2003). Before the fire, the study area was dominated by pure and mixed stands of white spruce (*P. glauca* [Moench] Voss), black spruce (*P. mariana* [P. Mill.] B.S.P.), trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.) and jack pine (*P. banksiana* Lamb.), with minor elements of balsam fir (*A. balsamea* [L.] P.Mill.), larch (*Larix laricina* [Du Roi] K. Koch) and paper birch (*Betula papyrifera* Marsh).

The present study focused on mixed stands of white spruce (approximately 60% of canopy composition) and trembling aspen (approximately 40%). Specifically, we selected sites in one of four categories: (i) GRN: 'green', reference sites that had not been burned or harvested in >100 years; (ii) BRN: sites that were 'burned' by the Chisholm fire; (iii) HAR: unburned, 'harvested' sites that were clear-cut logged in 2001; and (iv) SAL: sites that were burned by the Chisholm fire and then 'salvaged' during the winter of 2001/2002 (after the fire). Sites were individual stands of trees (3–30 ha) selected on the basis of pre-disturbance stand characteristics (age, tree species composition, stem density, soil characteristics) and accessibility, as determined initially from forest inventory maps (Alberta Sustainable Resource Development) and then verified on the ground. Six sites were selected for each stand category (total 24 sites). The minimum distance between any two sites was 1 km.

Adult beetles were sampled using flight-intercept traps (Kaila, 1993; Hammond, 1997) attached to white spruce trees and stumps. These traps consisted of a thin (0.3 cm) piece of clear plastic (20 cm × 30 cm) connected below to a heavy cloth funnel and a plastic sample cup (100 mL) that was charged with approximately 30 mL of silicate-free ethylene glycol. A total of 120 traps were deployed in the study and formed part of a general saproxylic beetle survey (Cobb, 2007). In GRN and BRN sites, four traps per site were attached to standing white spruce trees at approximately 1.5 m above the ground, whereas, in the HAR and SAL sites, the traps (four per site) were attached to stumps because trees were scarce. To account for the possible confounding effect of trap height, an additional two traps per site were placed at the base of the standing trees in the GRN and BRN sites. All traps were serviced biweekly during the frost-free months (April to September) of 2002 and 2003 to remove all beetles and replace the ethylene glycol.

Mesocosm experiment. We conducted an *in situ* mesocosm experiment to examine the relationship between the abundance of larval *M. s. scutellatus* feeding on burned white spruce stems and changes in soil nutrients. This experiment was designed as a one-factor (larval abundance) analysis of variance (ANOVA) with five levels (0, 2, 5, 8 and 10 larvae) and four replicates. Larval abundance levels were selected to span the natural range of densities observed in the surrounding area. Twenty enclosures (0.22 m^3) were placed on the ground at one of the burned (BRN) sites (54°54.3′N, 114°6.8′W) described above. Enclosures were open-bottomed but screened on the top and sides (mesh size = 1 mm) to prevent colonization by additional beetles and predation by woodpeckers and parasitoid wasps. In the centre of each enclosure, we placed a single bolt of wood vertically so that one end remained in contact with the ground. Bolts were obtained by felling three healthy (unburned) white spruce trees and then cutting the stems into 50-cm lengths. Each bolt was scorched over a wood fire in a fire pit to simulate the action of wildfire and to kill any existing fauna. The top end of each bolt was sealed with paraffin wax to reduce the rate of moisture loss. Bolts were numbered and then randomly assigned to a particular enclosure position and larval abundance treatment.

Monochamus s. scutellatus larvae (second instar) were collected from nearby burned white spruce trees and placed in notches (2.5 cm in length) cut into the sapwood of the bolts with an ethanol-sterilized chisel. We used second-instar larvae exclusively because this stage was most readily available at the start of the experiment. Larvae that did not immediately burrow under the bark and begin feeding in the bolts were discarded and replaced. In accordance with the rate of development expected in the northern portion of the beetle's range, larvae were allowed to feed for 24 months. Enclosures were monitored biweekly and any germinating plants were removed to reduce the influence of germination on soil chemistry. At the end of July 2003 and 2004 (i.e. 1 and 2 years post-treatment), we determined the mass (± 0.1 kg) of each log using a digital scale (Siltec™ GS-1) and collected mineral soil samples (0–3 cm in depth) from each enclosure. For each soil sample, we determined pH, total carbon, nitrogen and phosphorous using standard methods (Kalra and Maynard, 1991). Specifically, pH was determined on a 1:2 (by mass) soil : 0.01 M $CaCl_2$ suspension, total carbon by combustion, total nitrogen by the Kjeldahl method and total extractable phosphorous by the Bray 1 method.

Laboratory studies

Frass collection. For all laboratory experiments, *M. s. scutellatus* frass was obtained from individuals reared in captivity on scorched (as above) white spruce logs. Rearing cages were maintained in an environmental growth chamber at 20°C, 30–60% relative humidity (RH) and a constant photoperiod (LD 16:8 h) for 2 years. Frass that accumulated in the bottom of each cage was periodically collected, manually sorted into its two components (chewing dust and faecal pellets) and air-dried at 20°C.

Microbial activity and nitrogen availability. The effect of *M. s. scutellatus* larvae frass on soil microbial activity was examined in a laboratory experiment that compared CO_2 evolution and changes in nitrogen availability in mineral soil samples with and without the addition of frass. Ten flat-bottomed, glass test tubes (150 mL) were filled with 50 g of air-dried (20°C) mineral soil and 15 mL of de-ionized water. Mineral soil (0–3 cm in depth) for this experiment was collected from three available, recently burned (< 30 days) mixedwood sites (white spruce and trembling aspen) in northern Saskatchewan, Canada (site 1: 56°16.0′N, 108°54.1′W; site 2: 55°29.1′N, 104°51.1′; site 3: 53°13.2′N 105°58.3′W). Soil from all three sites was combined, sieved (mesh size = 0.5 cm) to remove as much of the debris and vegetative propagules as possible and air-dried for several weeks at 20°C.

We augmented frass experimentally by adding both faecal pellets (1.2 mg/g soil) and chewing dust (20.8 mg/g soil). Concentrations of frass components were derived from ten samples collected from the soil surface, which averaged a 1:17 ratio (faecal pellets : chewing dust) by mass. The contents of all test tubes were thoroughly mixed, covered with gas permeable film and allowed to settle for 6 days at 20°C. Microbial activity was assessed by monitoring CO_2 evolution after the test tubes were covered with rubber stoppers for 1 h. Headspace CO_2 samples were collected using a needle inserted through the rubber stoppers and CO_2 concentrations were determined using a Hewlett-Packard 5890 Series II gas chromatograph (Hewlett-Packard, Palo Alto, California) equipped with a 1-m Porapak Q column (Supelco, Bellefonte, Pennsylvania), HP3396 Series II integrator and helium as the carrier gas.

We examined changes in nitrogen availability by incubating all the test tubes described above for an additional 13 days at 20°C. After this incubation, water extracts of the soil (45 mL of water to 3.0 g fresh mass) were analysed for concentrations of total soluble carbon and nitrogen (Shimadzu Carbon and Nitrogen Analyzer, Mandel Scientific Co. Inc., Canada), NH_4^+-N and NO_3^--N (Technician Auto Analyzer II, Technician Industrial Systems, Tarrytown, New York) and soluble organic nitrogen (by difference).

Plant germination and growth. Effects of larval frass on plant germination and growth were examined experimentally in a culture chamber (22°C, 60–70% RH, LD 16:8 h). This experiment was designed as a one-factor ANOVA with three levels ('+ Frass', '−Frass' and 'germination control') and ten replicates. A total of 30 plastic pots (10 cm in diameter, closed-bottom) were filled with 240 g of soil collected and prepared as described for the microbial activity study above. The '+ Frass' treatment (n = 10 pots) was established, as above, by adding 4.992 g of chewing dust (20.8 mg/g soil) and 0.288 g of faecal pellets (1.2 mg/g soil), whereas the '−Frass' treatment (n = 10 pots) contained only unamended soil. These 20 pots were each seeded with 20 field-collected seeds of each of the species: trembling aspen (*P. tremuloides* Michx.), balsam poplar (*P. balsamifera* L.), fireweed (*Epilobium angustifolium* L.) and bluejoint grass (*Calamagrostis canadensis* [Michx.]). Plant species were chosen to represent common early colonizers in the region and final selection was based on seed availability. An additional ten pots were established as a 'germination control' to examine natural germination levels. All pots were watered weekly with de-ionized water at a rate of 65 mL/week during the 180 days of the experiment. At each watering, the number of germinants was recorded and, at the end of the experiment, shoot and root biomass for each germinant was determined. Biomass values for all plant tissues were assessed after thorough washing with de-ionized water and drying them to a constant mass (70°C). At the end of the experiment, water extracts of the soil were analysed for concentrations of total soluble carbon and nitrogen, soluble organic-N, NH_4^+-N and NO_3^--N by the same methods as described for the microbial study above.

Statistical analysis

To account for variability in sampling effort arising from trap disturbance, catches of adult *M. s. scutellatus* were standardized (number of individuals/functioning trap-days) prior to analysis. Differences in mean catch rates across stand treatments were evaluated using one-factor ANOVA followed by Tukey's honestly significant difference (HSD) post-hoc tests when the overall analysis was significant. Repeated measures analysis of variance (RM-ANOVA) was employed to examine year-to-year changes in the mass of the wood bolts used in the mesocosm experiment. Linear regression was used to examine relationships between larval abundance and soil nutrient parameters in the mesocosm experiment. Student's t-tests were used to compare the effect of frass addition on mean microbial CO_2 evolution as well as post-incubation nutrient parameters. Finally, to evaluate the effects of frass on plant germination, growth and soil nutrient parameters (at the end of the experiment), we again used one-factor ANOVA. For all tests, data were transformed [$\log_{10(x+1)}$] prior to analysis when necessary to meet the assumptions of normality (Kolmogorov–Smirnov) and homoscedasticity (Levene 's test) (Zar, 1996). These analyses were performed using SPSS for Windows, version 11.5 (SPSS, Inc., Chicago, Illinois).

Results

Field studies

Beetle survey. Sampling effort (traps × days) for the field survey was 28 207 trap days and resulted in a total collection of 157 adult *M. s. scutellatus*. The effect of stand treatment on standardized mean catch rates (individuals/trap-day) was significant (ANOVA; $F_{3,20} = 19.695$, $P < 0.001$) (Fig. 1) because catch rates were higher in BRN sites than in HAR sites; no specimens were collected in either GRN or SAL sites (Tukey's HSD; $P < 0.05$). Trap height (high vs. low) had no statistically significant effect on *M. s. scutellatus* catch rates (Student's t-test: $t = 1.630$, $P = 0.106$).

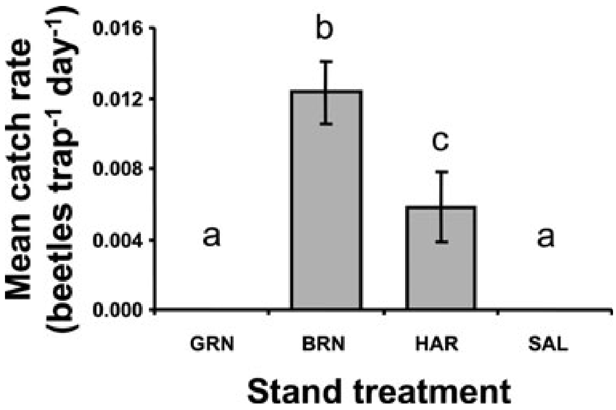

Figure 1 Standardized mean catch rate of adult white-spotted sawyer beetles across the four stand treatments (GRN = green, control; BRN = burned; HAR = harvested; SAL = salvage logged). Different lower case letters indicate significant differences between stand treatments (Tukey's honestly significant difference, $P < 0.05$). Bars represent the mean ± SE for $n = 6$ sites.

Table 1 Summary of carbon and nitrogen concentrations of white-spotted sawyer beetle frass components (faecal pellets and chewing dust) obtained from laboratory cultures (250 beetles) reared on burned white spruce bolts

Parameter	Faecal pellets	Chewing dust
Total carbon (% dry weight)	49.6	48.4
Total nitrogen (% dry weight)	0.6	0.6
Carbon : nitrogen	84.7	83.8
Total soluble carbon (μg/g)	60 036.4	11 214.6
Total soluble nitrogen (μg/g)	425.7	95.1
Soluble organic nitrogen (μg/g)	423.3	88.6
Soluble inorganic nitrogen (μg/g)	2.4	6.5
NH_4^+-N (μg/g)	0.0	0.3
NO_3^--N (μg/g)	2.4	6.2

Values for both materials are from a composite sample.

Mesocosm experiment. In the mesocosm experiment, frass production was visible in individual enclosures within 2 days of larval introduction. Based on a visual inspection of emergence holes and larval galleries in each bolt at the end of the experiment, larval mortality was estimated at approximately 5–10% across all replicates. However, it was not possible to accurately determine when mortality occurred, so nutrient values were averaged across years to reduce the effect of year-to-year variation within replicates. Soil chemistry analyses were highly variable but revealed significant positive relationships between larval abundance and total carbon, total nitrogen, nitrogen : phosphorous and carbon : phosphorous (Fig. 2). No significant relationship was detected between larval abundance and total phosphorous or carbon : nitrogen (Fig. 2). Soil pH levels ranged from 4.9 to 6.2 over all samples but did not vary significantly with changing larval abundance (linear regression: $r^2 = 0.010$, $P = 0.6712$). Bolt masses declined gradually during this study (RM-ANOVA, effect of year: $F_{1,15} = 25.42$, $P < 0.001$) but the decline did not vary across treatments

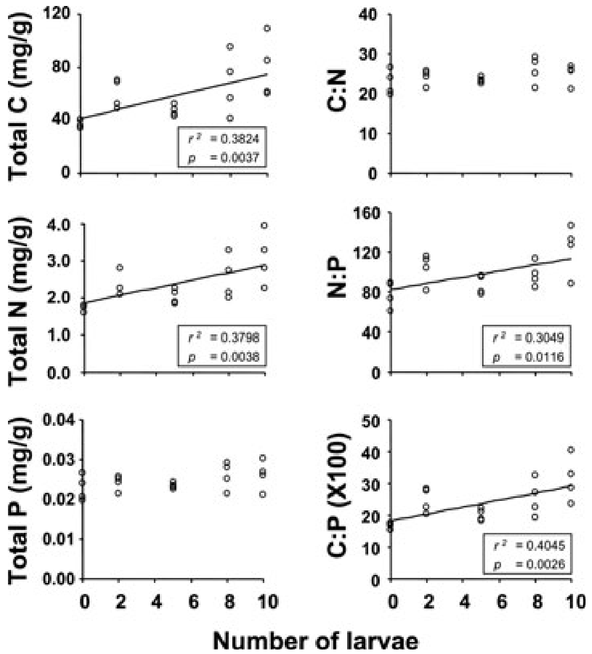

Figure 2 Summary of mesocosm experiment results showing the effect of varying larval white-spotted sawyer beetle abundance on nutrient parameters in the top 0–3 cm of mineral soil. Trend lines indicate significant relationships (linear regression).

(RM-ANOVA, effect of larval abundance: $F_{4,15} = 1.80$, $P = 0.1819$).

Laboratory studies

Microbial activity and nitrogen availability. Monochamus s. scutellatus frass that accumulates at the base of burned trees is comprised of faecal pellets and chewing dust that can be readily separated under a dissecting microscope. Chemical analysis of composite samples of both faecal pellets and chewing dust from individuals reared in captivity on burned white spruce bolts indicated similar carbon : nitrogen values in both types of material (Table 1). Further analysis revealed that soluble forms of carbon and nitrogen in both faecal pellets and chewing dust were largely organic. However, the faecal pellets also contained a small amount of soluble inorganic-N as NO_3^--N and the chewing dust contained a small amount of both NO_3^--N and NH_4^+-N (Table 1).

The addition of *M. s. scutellatus* frass (faecal pellets and chewing dust) to mineral soil samples significantly increased microbial respiration rates (Fig. 3). Compared with controls, headspace CO_2 evolution was more than three times greater in frass-augmented samples. After a 13-day incubation of these samples, we found that water extracts of frass-augmented soil contained significantly greater concentrations of soluble organic carbon, soluble organic nitrogen and NH_4^+-N but significantly lower total soluble nitrogen and NO_3^--N concentrations than those of the frass-free soil (Table 2).

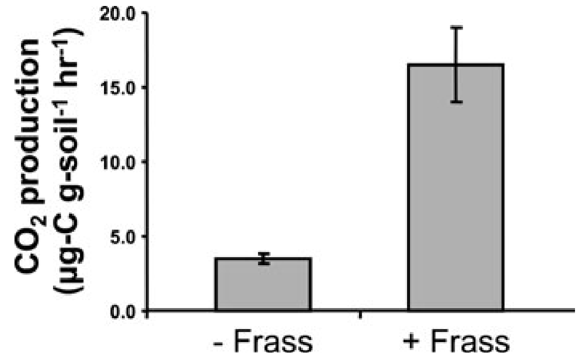

Figure 3 Microbial activity, as measured by microbial CO_2 production (at 20°C), in samples with and without the addition of white-spotted sawyer beetle frass. Bars are the mean ± SE for $n = 5$ samples of mineral soil.

Plant germination and growth. In the culture chamber, germination began in all pots 21 days after the initial seeding. The addition of *M. s. scutellatus* frass significantly altered the germination and growth of two of the three plant taxa investigated (Table 3). Seeded pots contained more germinants than the unseeded control ('germination control') pots, and the mean number of germinants was significantly lower in frass-augmented pots than in those without frass. Germinants of the two *Populus* spp. were combined because they could not be readily distinguished at this early stage of development. Analysis of final biomass values indicated that addition of frass reduced the above-ground biomass accumulation (shoot growth) of *E. angustifolium* and *Populus* spp. but had no significant effect on *C. canadensis*. Composite values (all plant taxa combined) for total shoot mass, root mass and root : shoot ratios were not significantly affected by the addition of frass. Chemical analysis of water extracts of the soil from each pot at the end of the 180-day plant growth period (Table 4) showed that total soluble carbon and NH_4^+-N did not vary significantly between treatments but that frass-augmented pots contained significantly greater concentrations of soluble organic nitrogen and significantly lower concentrations of total soluble nitrogen and NO_3^--N.

Discussion

The results obtained in the present study demonstrate that removal of dead wood from burned forests by post-fire salvage logging may potentially alter naturally-occurring links between wood-feeding insects and nutrient dynamics in forests after wildfire (Fig. 4). A number of pyrophilous, wood-boring beetles are among the first organisms to colonize recently burned forests (Gardiner, 1957b; Evans, 1971; Hart, 1998; Schmitz & Bleckmann, 1998; Wikars, 2002) and the data obtained in the present study show that the abundance of at least one of these species was clearly linked to nutrient cycling. By feeding on burned dead wood, *M. s. scutellatus* larvae help to begin the process of gradually returning organic materials from standing burned coniferous trees to the soil. The data also show that this feeding activity was linked to changes in soil microbial

Table 2 Post-incubation soluble carbon and nitrogen results showing the effect of adding white-spotted sawyer beetle frass to mineral soil

Parameter	− Frass	+ Frass	d.f.	t	P
Total soluble carbon (µg/g soil)	147.88 ± 8.59	234.73 ± 9.73	8	−6.732	< 0.001
Total soluble nitrogen (µg/g soil)	34.21 ± 2.40	10.95 ± 0.48	8	9.573	< 0.001
Soluble organic nitrogen (µg/g soil)	1.26 ± 0.43	9.17 ± 0.68	8	−9.851	< 0.001
NH_4^+-N (µg/g soil)	0.02 ± 0.01	1.68 ± 0.71	8	−2.464	0.039
NO_3^--N (µg/g soil)	33.61 ± 2.95	0.18 ± 0.11	8	11.486	< 0.001

Values are the mean ± SE for $n = 5$ samples. Incubation was 13 days at 20°C.

Table 3 Summary of laboratory plant study results showing the effects of white-spotted sawyer beetle frass on germination and growth (after 180 days) of three plant taxa, *Calamagrostis canadensis, Epilobium angustifolium*, and *Populus* spp

Parameter	Germination control	− Frass	+ Frass	$F_{2,27}$	P
Number of germinants	0.7 ± 0.7[a]	10.3 ± 1.3[b]	6.3 ± 1.7[c]	75.510	< 0.001
All shoots (µg/plant)	118.4 ± 34.6	27.4 ± 2.6	18.3 ± 2.7	0.180	0.837
Calamagrostis (µg/plant)	118.4 ± 34.6	44.6 ± 19.2	29.3 ± 12.8	1.040	0.367
Epilobium (µg/plant)	0.0 ± 0.0[a]	20.6 ± 2.4[b]	11.2 ± 3.1[c]	20.860	< 0.001
Populus (µg/plant)	0.0 ± 0.0[a]	37.9 ± 9.4[b]	15.3 ± 3.6[c]	10.743	< 0.001
All roots (µg/plant)	450.6 ± 171.1	34.9 ± 14.0	29.2 ± 12.8	0.993	0.384
Root : shoot	2.4 ± 0.9	1.2 ± 0.3	1.4 ± 0.5	1.159	0.329

Biomass values are for oven-dried (70°C) tissues standardized by the number of plants. Values are the mean ± SE for $n = 10$ replicates. Different superscript letters indicate significant differences (Tukey's honestly significant difference; $P < 0.05$) within each parameter.

Table 4 Summary of soluble carbon and nitrogen concentrations of mineral soil showing the effect of white-spotted sawyer beetle frass after 180 days of plant growth

Parameter	Germination control	− Frass	+ Frass	$F_{2,27}$	P
Total soluble carbon (µg/g soil)	1.12 ± 0.17	1.03 ± 0.14	1.43 ± 0.27	1.064	0.359
Total soluble nitrogen (µg/g soil)	0.24 ± 0.03[ab]	0.30 ± 0.02[a]	0.15 ± 0.08[b]	7.258	0.003
Soluble organic nitrogen (µg/g soil)	0.07 ± 0.02[ab]	0.04 ± 0.01[a]	0.11 ± 0.02[b]	4.366	0.023
NH_4^+-N (µg/g soil)	0.04 ± 0.01	0.05 ± 0.01	0.03 ± 0.01	0.999	0.381
NO_3^--N (µg/g soil)	0.13 ± 0.04[a]	0.21 ± 0.03[a]	0.01 ± 0.01[b]	15.138	< 0.001

Values are the mean ± SE for $n = 10$ replicates. Different superscript letters indicate significant differences (Tukey's honestly significant difference; $P < 0.05$) for each parameter.

activity, nitrogen availability and the germination and growth of colonizing plants in early post-fire ecosystems.

Our survey of adult *M. s. scutellatus* populations across a range of boreal mixed wood stand treatments, showed that this species was present in both recently burned and recently harvested sites but was either absent or below our detection limits in undisturbed and salvage logged sites (Fig. 1). Previous studies have demonstrated that populations of this species increase sharply in the first 1–2 years after a wildfire (Richmond & Lejeune, 1945; Rose, 1957; Ross, 1960; Saint-Germain *et al*., 2004), leading to the recommendation that salvage operations be conducted as soon as possible after a fire to minimize damage to timber and maximize economic recovery (Richmond & Lejeune, 1945; Ross, 1960; Sessions *et al*., 2004). The abundance of *M. s. scutellatus* in stands with a profusion of fire-killed or freshly cut coniferous trees and stumps, similar to the BRN and HAR sites in our study, has been attributed to attraction of adults to volatile compounds such as ethanol and terpenes in conifer oleoresin and smoke (Gardiner, 1957a, b; Chénier & Philogène, 1989; Allison *et al*., 2001). Several studies have reported increased catches of this and related cerambycid taxa in traps baited with ethanol and blends of monoterpenes including (±) − α-pinene, (−) -β-pinene, (±)-camphene and myrcene (Chénier & Philogène, 1989; Peddle, 2000; de Groot & Nott, 2001, 2004). However, no specimens were collected in salvage logged sites in the present study, despite an abundance of burned and freshly cut stumps, suggesting that post-fire salvage logging negatively affects populations of this species. Data from studies conducted at mill sites (Richmond & Lejeune, 1945; Allison *et al*., 2001; Morewood *et al*., 2002), as well as our own observations of salvaged logs on trucks and at the mill, suggest that post-fire salvage logging does not hinder oviposition but rather that the larvae are simply being removed from field sites in salvaged stems. Interestingly, this pattern did not appear to be the same in the HAR sites because *Monochamus* activity (galleries and frass) was readily apparent in the unburned stumps.

The results obtained in the mesocosm experiment suggest that the larval abundance of *M. s. scutellatus* can affect soil chemistry, at least at a local scale. For example, we found a positive relationship between larval abundance and both total carbon and total nitrogen of mineral soil samples taken from

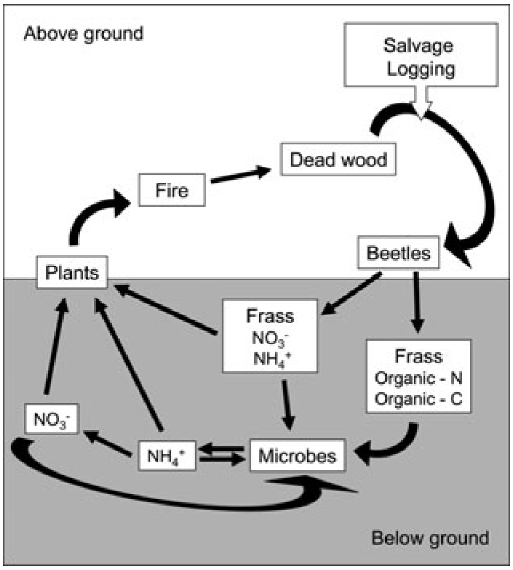

Figure 4 A conceptual model illustrating the ecological linkages between saproxylic beetles and nutrient cycling in forest ecosystems. Post-fire salvage logging (top right) may upset this pathway by severing the link between dead wood and saproxylic beetles in forests recovering from wildfire.

around the base of burned white spruce bolts (Fig. 2). From our mesocosm data, it is difficult to discern whether or not modified larval densities could affect soil chemistry beyond the local scale. However, assuming an average stem diameter of 0.18 m (Cobb, 2007), an average stem density of 1273.2 stems/ha (Cobb, 2007) and our observation that substantial frass deposits were visible up to 1 m from the base of each tree stem, we estimate that approximately 47.2% of the forest floor surface would receive direct inputs of frass. We also observed that frass accumulations around the base of burned trees are readily moved by wind throughout the stand, suggesting that the area influenced by frass deposits from this beetle species may be even larger. Given that large quantities of carbon can be lost from forest soils during intense wildfires (Certini, 2005), frass inputs may be one way in which soil organic matter recovers after a fire.

Published estimates of nitrogen concentration in conifer phloem tissue (Mattson, 1980), along with our data on nitrogen concentration in larval *M. s. scutellatus* frass (Table 1), suggest that nutrient absorption by these beetles is inefficient, requiring individuals to process a relatively large volume of plant material during their development. Although there is a small amount of NO_3^--N (0.56% of total nitrogen) in the faecal pellets of this species (Table 1), most of the nitrogen being returned to the soil is organic and not immediately available to plants. However, we found that addition of *M. s. scutellatus* frass to mineral soils led to a significant increase in microbial activity, a decrease in total soluble nitrogen and a shift in the dominant mineral nitrogen form from NO_3^--N to NH_4^+-N . Immobilization of mineral nitrogen by microbes may help to reduce leaching of nitrogen from early post-fire forests soils (Smithwick *et al*., 2005), which can exhibit elevated nitrate and ammonium concentrations for at least 3 years after burning (Wan *et al*., 2001). Indeed, the mineral soils used in our laboratory experiment, collected from recently burned stands, exhibited much higher mineral nitrogen concentrations than those reported for similar unburned forests (Jerabkova *et al*., 2006). The influence of frass deposition on soil nutrient dynamics may last for a number of years, given the relatively gradual 1–2-year development time for *M. s. scutellatus* (Rose, 1957; Wilson, 1962).

In nitrogen-limited boreal forests, competition for nitrogen between plants and microbes and among plant species is one of many factors that may influence primary productivity and plant species composition (Schimel & Bennett, 2004; Smithwick *et al*., 2005; Luzuriaga & Escudero, 2008). In our plant growth experiment, we found that the addition of *M. s. scutellatus* frass to mineral soil from recently burned forests reduced the germination and growth of *Populus* spp. and *E. angustifolium*, which are common colonizers of early post-fire boreal forests in our study area. Altered nutrient dynamics in frass-augmented soils may partially explain this result because these soils contained significantly lower NO_3^--N and total soluble nitrogen and higher soluble organic nitrogen concentrations at the end of our plant growth study (Table 4). By contrast, *C. canadensis* was not significantly affected by frass addition in the present study, suggesting that this species may also remain unaffected by frass inputs in the field. In a hydroponic study, Hangs *et al*. (2003) noted that *C. canadensis* has a greater uptake capacity for nitrate and ammonium than either *Populus* spp. or *E. angustifolium*.

A number of studies have reported changes in the composition of plant communities related to salvage logging of burned boreal mixedwood stands (Purdon *et al*., 2004; MacDonald, 2006; Kurulok & MacDonald, 2007). Although we did not examine the effects of *M. s. scutellatus* frass on conifer germination, there is some evidence to indicate that plant communities in burned conifer-dominated boreal mixedwood stands may be particularly sensitive to salvage logging (Purdon *et al*., 2004). Several mechanisms have been proposed to explain the effect of salvage logging on plant communities, including mechanical soil disturbance (Fraser *et al*., 2004; Purdon *et al*., 2004; Donato *et al*., 2006; MacDonald, 2006; Kurulok & MacDonald, 2007), altered soil microclimate (Purdon *et al*., 2004; MacDonald, 2006; Kurulok & MacDonald, 2007) and poor seedling recruitment due to loss of cones (Greene *et al*., 2006). Our findings suggest that effects on populations of *M. s. scutellatus* (and possibly many other saproxylic species) and associated soil nutrient dynamics may also play a role.

Conclusions

The scale of the present study was limited to permit a close investigation of the complex above- and below-ground relationships between the feeding activity of *M. s. scutellatus* and soil nutrient dynamics in forests recovering from fire. However, as is the case with many such studies, the findings obtained have implications that go beyond the local scale. Collectively, our results suggest that reduced densities of *M. s. scutellatus* larvae resulting from post-fire salvage logging not only alter soil nutrient dynamics, but also influence growth of colonizing plant species. Although *M. s. scutellatus* and other wood-feeding beetle species may be viewed as 'pests' that rapidly reduce the economic value of salvaged timber (Ross, 1960; Sessions *et al*., 2004), their role in nutrient cycling and food web dynamics (Hoyt & Hannon, 2002) in burned forests should not be overlooked in the development of guidelines for post-fire management. By removing fire-killed trees, post-fire salvage logging in North American boreal ecosystems may be as damaging to saproxylic insect diversity as is intensive forestry and fire suppression in Europe (Siitonen, 2001; Grove, 2002). Although functional roles of most beetle species have not been investigated, the results obtained in the present study support the idea that the effects of post-fire salvage are not limited to biodiversity loss. Therefore, in burned boreal forests, long-term persistence of natural ecological functions may require the retention of at least some burned timber. Questions about the quantity and quality of burned timber needed to maintain populations of *M. s. scutellatus* and other saproxylic species require further study. However, given the projected increases in the occurrence of wildfire, especially in parts of North American forests (Overpeck *et al*., 1990; Flannigan *et al*., 1998; Stocks *et al*., 1998; Li *et al*., 2000), wise policies and effective guidelines for the management of post-fire salvage logging will be required to balance ecological and economic considerations.

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