**Ecography 30: 737–748, 2007**
doi: 10.1111/j.2007.0906-7590.05080.x
© 2007 The Authors. Journal compilation © 2007 Ecography
Subject Editor: John Spence. Accepted 27 August 2007

# Host-use patterns of saproxylic phloeophagous and xylophagous Coleoptera adults and larvae along the decay gradient in standing dead black spruce and aspen

**Michel Saint-Germain, Pierre Drapeau and Christopher M. Buddle**

*M. Saint-Germain (stgermainm@sympatico.ca) Centre d'étude sur la forêt, Dépt des sciences biologiques, Univ. du Québec à Montréal, CP 8888, succ. Centre-ville, Montréal, PQ, Canada, H3C 3P8 and Dept of Natural Resource Sciences, McGill Univ., 21111 Lakeshore Road, Saint-Anne-de-Bellevue, QC, Canada, H9X 3V9. – P. Drapeau, Centre d'étude sur la forêt, Dépt des sciences biologiques, Univ. du Québec à Montréal, CP 8888, succ. Centre-ville, Montréal, PQ, Canada, H3C 3P8. – C. M. Buddle, Dept of Natural Resource Sciences, McGill Univ., 21111 Lakeshore Road, Saint-Anne-de-Bellevue, QC, Canada, H9X 3V9.*

Wood-feeding insects play important functional roles in forest ecosystems, contributing significantly to wood decay processes. However, sampling these species in a direct and quantitative way is difficult because they live most of their lives as larvae deep into the wood; knowledge of species-specific host-use patterns along the decay gradient is thus lacking in this group. To cope with these difficulties, we used a novel approach, snag dissection, to investigate occurrence patterns of such Coleoptera adults and larvae. We selected 80 snags of both black spruce and aspen along four classes of decay in five different stands distributed over the tree species' ranges within the province of Quebec, Canada, and dissected a one-meter section of each. All adults and larvae of Buprestidae, Cerambycidae and Scolytinae (Coleoptera: Curculionidae) were collected and identified to the lowest taxonomical level possible. Wood density and snag age were also calculated for each sampled snag. In black spruce, host-use was mostly concentrated at the beginning of the decay gradient. Patterns observed in aspen were opposite, as few insects were found in fresh snags, while most snags in middle to late stages of decay contained insects, often in large numbers, in some reaching densities of over 1000 cerambycid larvae $m^{-3}$. For both tree species, patterns observed were similar across regions sampled. Differences in host-use patterns between the coniferous and deciduous host species may be due to differences in secondary chemistry, mechanical defence mechanisms or the stand dynamics typically associated with each tree species.

Dead wood is a key habitat element of forest ecosystems. Among the numerous functions attributed to dead wood, it is an important pathway in geochemical cycles (Harmon et al. 1986, Krankina et al. 1999) and supports a considerable proportion of forest biodiversity. Dead wood, in its different stages of decay, harbours hundreds of species of plants, animals and fungi (Harmon et al. 1986, Berg et al. 1994, Grove 2001). Among major groups, insects are probably one of the most diverse (reviewed by Grove 2001). Siitonen (2001) estimated that saproxylic insects (i.e. species that are dependant on dead wood at least at some stage of their life cycle) represent over 25% of all known species living in boreal forests of Finland.

Several nutritional guilds are recognized within saproxylic insects (Vanderwel et al. 2006). Among them, phloeophagous and xylophagous species, which directly consume plant tissue and hereafter referred to as "wood-feeding species", play especially important functional roles. Dispersing adults act as vectors for spores of wood-decay fungi (Paine et al. 1997), and the galleries excavated by larvae structurally weaken dead wood and help fungi penetrate radially into the sapwood (Rayner and Boddy 1988). The activity of such beetles can greatly increase the rate of decay of dead wood, and hence speed up the release rate of immobilized nutrients (Edmonds and Eglitis 1989). Despite their ecological importance, knowledge on host-use patterns of wood-feeding insects is still lacking. Few studies have specifically focused on the response of this functional group to decay gradients, and some of these species' life history and behavioural traits make them difficult to sample in a direct and quantitative manner, particularly in species living in more decayed wood. Disproportionally long larval stages and particular flight behaviour may have resulted in wood-feeding species, especially in families Cerambycidae and Buprestidae, being under-represented in saproxylic insect datasets (Martikainen 2001, Sverdrup-Thygeson and Ims 2002, Hammond et al. 2004, Saint-Germain et al. 2006).

Host-use patterns of wood-feeding insects have seldom been studied on extended portions of the decay gradient. Fragmentary information shows that the occurrence of coniferophagous wood-feeding species varies along the decay gradient. Some studies looking at the whole saproxylic community report shifts in dominance of the different trophic guilds along the decay gradient (Savely 1939, Howden and Vogt 1951, Vanderwel et al. 2006). A diverse and abundant wood-feeding guild usually dominates in the first stages of decay, to be eventually replaced by fungivores, saprophages and predators as predominant groups. Other studies exclusively focusing on fresh coniferous snags also report abundant and species-rich wood-feeding assemblages (Schroeder and Eidmann 1993, Schroeder et al. 1999). We found no recent comprehensive studies focusing on wood-feeding assemblages in coniferous snags or logs of more advanced decay. Information from deciduous host species is even scarcer. Lindhe and Lindelöw (2004) report wood-feeding species found in four species of deciduous trees sampled using ecclector traps, but do not present the data according to sampling year following tree death.

Hanks (1999) classified cerambycid wood-feeders according to the physiological status of their hosts. Among these behavioural guilds, two can be found in succession in dead wood. Stressed-host species will attack hosts that are stressed to the point that death is imminent, or are recently dead. Host-selection in this guild is strongly driven by host volatiles (Brattli et al. 1998, Allison et al. 2004), and most species feed in the nutrient-rich but ephemeral phloem and cambium, at least in their first larval stages. Only one generation of these species will usually develop on a specific host (Hanks 1999), and thus are expected to be found only in the very first stages of decay. Dead-host species are insects which oviposit on hosts that are no longer green, and feed mostly in the sapwood or heartwood. In such species several successive generations usually develop in the same host (Hanks 1999).

Because of the importance of dead wood as a support for biodiversity, modern forestry practices are moving towards leaving legacies (e.g. high stumps, partial cutting, green tree retention) in the managed landscape in an effort to insure spatial and temporal connectivity between habitat elements (Larsson and Danell 2001, Jonsson et al. 2005). However, we know relatively little about diversity patterns of saproxylic organisms among dead wood of different tree species and along the decay gradient, or about the mechanisms driving these patterns. This lack of knowledge limits our conservation efforts to coarse filter approaches when dealing with organisms dependent on dead wood, i.e. a context-dependent maximization of dead wood volume regardless of specialization patterns between host species or along the wood decay gradient.

The main objective of this study was to characterize species occurrence of wood-feeding Coleoptera along the decay gradient, snag stages only, on two tree species of the boreal mixed-wood forest of eastern North America, aspen *Populus tremuloides* and black spruce *Picea mariana*. These species were chosen for their ecological and economical prevalence in North American boreal forests. To characterize insect species assemblages and to determine whether observed patterns were dependant on landscape context (i.e. relative forest cover tree species composition), we sampled snags in five different sites distributed across the range of each tree species within the province of Quebec, Canada. Within each site, we dissected snags of all available stages of decay and collected both larvae and adults. Wood dissection is extremely useful to maximize the number of individuals collected and gives an instant portrait of the community using the sampled snag, with absolute estimates of density. It does not suffer from time constraints and excessive mortality seen in in-situ or ex-situ rearing or from severe biases inherent to trunk-window trapping when used to sample at tree level (Saint-Germain et al. 2006).

## Methods

### Snag selection and sampling

Early during the summer of 2004, one site was selected for each tree species in western Quebec: Lake Duparquet teaching and research forest (LDTRF) for aspen and Selbaie 1 for black spruce (Table 1, Fig. 1). Both sites were mature forests and had high volumes of dead standing trees in diverse stages of decay. In each of these sites, transects distanced 40 m apart were set up perpendicular to the road, along which 24 snags over 15 cm in diameter were selected arbitrarily, equally distributed in numbers among 4 decay classes based on visual appearance. Decay classes were based on the criteria described in Maser et al. (1979), in addition to wood texture, presence of insect entry or exit holes and presence of polypore fungi.

Table 1. Characteristics of all sites sampled for both tree species, including number of snags sampled, geographic coordinates and information on the landscape context around each site (forest cover).

| Sites | # Snags | Coordinates | | Landscape context |
|---|---|---|---|---|
| Black spruce | | | | |
| Selbaie 1 | 24 | 49°25′N′ | 79°00′W | Black spruce-dominated |
| Selbaie 2 | 12 | 49°33′N′ | 78°59′W | Black spruce-dominated |
| Selbaie 3 | 12 | 49°48′N′ | 78°55′W | Black spruce-dominated |
| Chauvin | 16 | 48°26′N′ | 70°05′W | White spruce/balsam fir-dominated; black spruce <10% |
| Grands-Jardins | 16 | 47°41′N′ | 70°51′W | Balsam fir/black spruce co-dominants |
| Aspen | | | | |
| LDRTF | 24 | 48°28′N′ | 79°16′W | Aspen-dominated, some spruce and birch |
| Magusi 1 | 12 | 48°24′N′ | 79°27′W | Aspen-dominated, some jack pine |
| Magusi 2 | 12 | 48°26′N′ | 79°24′W | Aspen-dominated, some jack pine |
| Chauvin | 16 | 48°26′N′ | 70°05′W | White spruce/balsam fir-dominated, aspen <10% |
| Oka | 16 | 45°29′N′ | 74°01′W | Beech/maple-dominated, aspen marginal <2% |

At the end of July 2004, the selected snags were cut down and a 1-m section, taken in average between 0.5 and 1.5 m in height, was sealed and taken to the laboratory for insect sampling (dissection). Wood samples were also taken to determine the time of death of the tree and to measure wood density (see below). Bark was removed and examined, and every larvae and adult beetles were collected. Then, the bole segments were cut into ca 20-cm long sections, and these were dissected with axes and hatchets, following galleries or other signs of use, and all insects were collected. Large cerambycid larvae were boiled in water before being put in 70% ethanol for preservation. Cerambycid larvae were identified to species using Craighead (1923), Gardiner (1953, 1957) and Švácha and Danilevsky (1986, 1987, 1988). Buprestid larvae were identified to genus using Bright (1987). Adult Scolytinae (representing the vast majority of scolytid specimens) were identified to species. Identifications of larvae were cross-checked by V. Grebennikov at the Canadian National Collection of Insects, Arachnids and Nematodes (Ottawa, Canada).

We replicated our characterization of host-use patterns by sampling additional sites in 2005 to test whether patterns were similar between stands and across regions. For each species, we selected 4 additional sites, 2 within the same region near the location of the main sites, in which we sampled 12 snags each, and 2 others distributed throughout the tree species' distribution within the province, in which we sampled 16 snags each (Table 1, Fig. 1). Snags were felled between the end of July and early September 2005 depending on the sites. The same snag selection and sampling procedures as in 2004 were used. For each tree species we sampled a total of 80 snags (24 in main sites, 56 in supplementary sites) over two years. The average diameters (±1 SD) were of 20.6±4.0 cm (range 15.1–30.4 cm) for black spruce snags and 23.3±5.8 cm (range 14.9–40.1 cm) for aspen snags.

## Assessing degree of decay

Assessment of decay classes based on visual appearance sometimes gives inaccurate results as most of the criteria used are subjective in their appraisal and some, like a broken top, can occur in different contexts. Also, decay does not necessarily proceed in the same manner in different tree species (e.g. some species might retain their bark longer than others). Therefore, we also measured wood density for all 160 snags, and we estimated the time of death of the 48 snags from the main sites using dendrochronology. Wood density was measured by averaging density (dry weight/volume) of three ca 50 ml wood samples taken systematically at 120° around the bole from a wood disk taken at ca 1.5 m from the ground. Volume was measured by water displacement. To age tree death, we measured growth rings from the 48 snags from LDRTF and Selbaie 1 on 4 radii from two wood disks taken at 1.5 and 5 m above ground, respectively. Measurements were crossdated using the software COFECHA (Grissino-Mayer 2001) with master chronologies previously produced for the same sites (Bergeron et al. 2002, Lecomte et al. 2005). Most class 6 and some class 5 spruce snags could not be dated because growth rings were no longer discernable. In the light of the results given by each technique, we opted to use wood density to represent the decay gradient in the presentation of our results and in our analyses, mainly because we could not measure the age of all 160 snags sampled and also because of some problems we had at precisely aging spruce (see below).

## Statistical analyses

To determine to what extent results from the different methods used to quantify decay were similar, we first compared the wood density of the different decay classes using a one-way analysis of variance, followed

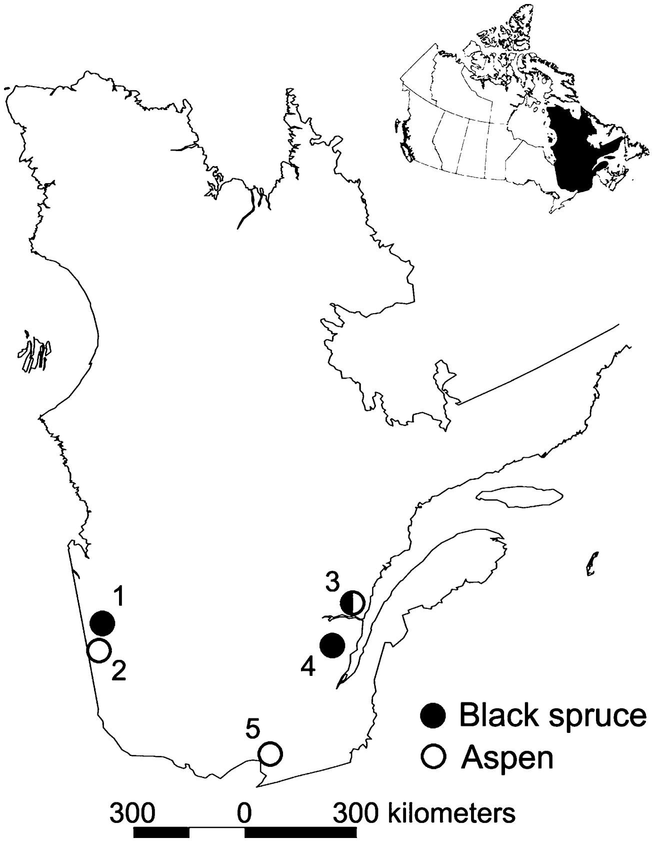


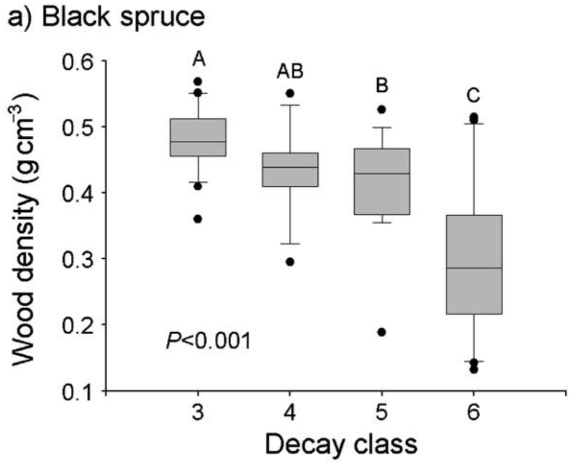
Fig. 1. Map of sites sampled within the province of Quebec, Canada for both tree species. (1) Selbaie 1–3; (2) Lake Duparquet research and teaching forest and Magusi 1–2; (3) Chauvin; (4) Grands-Jardins; (5) Oka.

with a Tukey's honestly significant difference (HSD) post-hoc test. An analysis of covariance was also conducted to compare the slopes of aspen and black spruce with regards to the relationship between wood density and snag age. Wood density was used in following analyses to represent the decay gradient as an independent variable. The wood density of all snags in which a given insect species was found was used to characterize preferences of that species over the decay gradient. Differences in preference among insect species in terms of degree of decay were tested both in aspen and in black spruce with one-way analyses of variance and Tukey's HSD. Results from these ANOVA and observations from the literature were used to discriminate between stressed-host and dead-host species. Probability plots from logistic regressions were used to illustrate host-use patterns of Cerambycidae along the decay gradient, with wood density as the independent variable and presence-absence of larvae as the dependant variable. For the two tree species, this was done with all species combined, and then with behavioural guilds separated. Analyses of variance and covariance were performed on SPSS 10.0.5 for Windows (SPSS, Chicago, IL, USA), while logistic regressions were performed on SYSTAT 11.00 (Systat Software, Point Richmond, CA, USA).

## Results

### Assessment of wood decay

There were significant differences in wood density between early and late visually-assessed decay classes for both tree species, but not between all four classes. For spruce, wood density of class 3 snags was significantly higher than that of class 5 and 6 snags, but class 4 snags were not different from either class 3 or 5 ($F_{3,75} = 21.13$; $p < 0.001$; Fig. 2a). For aspen, class 3 and 4 snags were significantly different from class 5 and 6 snags ($F_{3,75} = 20.22$; $p < 0.001$; Fig. 2b). As for the effect of time since tree death, wood density decreased significantly with increasing snag age ($F = 25.50$; $p < 0.001$; $R^2_{spruce} = 0.198$; $R^2_{aspen} = 0.556$). This decrease was significantly faster in aspen when compared to spruce (significant interaction, $F = 15.37$; $p < 0.001$) (Fig. 3), indicating different wood decomposition patterns for these two tree species. However, spruce of late-decay stages could not be included in the analysis, and for the trees that were included there are some clear indications that aging was less accurate for spruce than for aspen. Cherubini et al. (2002) showed that it is commonplace in coniferous species that the tree stops producing discernable growth rings well before it actually dies. In our study, stressed-host insect species were found in snags which were aged as having been dead for >10 yr; the presence of such species suggests that these age estimates were inaccurate. No such problem was suspected for aspen.


a) Black spruce

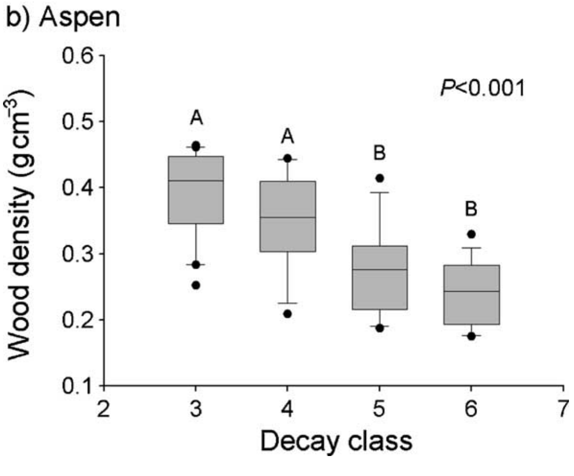

b) Aspen

Fig. 2. Boxplots showing wood density according to decay class based on visual appearance for (a) black spruce and (b) aspen. Wood density is considered here as being a more direct measurement of wood decay. Letters indicate significant differences following ANOVA and Tukey's HSD.

## Host-use patterns

A total of 1433 wood-feeding Coleoptera were collected (709 in spruce, 724 in aspen), including 22 taxa identified to species level (16 in spruce, 6 in aspen), four identified to genus (two in spruce, three in aspen) and 13 individuals identified only to family (details in Table 2 and 3). Assemblages were dominated by Cerambycidae in aspen, while Scolytinae were more frequently dissected from spruce snags.

In spruce, assemblages of wood-feeders were most diverse and numerous in the early stages of decay (Fig. 4a). In Cerambycidae, stressed-host species dominated the assemblages. *Acmaeops proteus* was the most commonly collected, occurring at every site. Other early species were locally common but absent at some sites (i.e. *Acanthocinus pusillus*, *Meriellum proteus*, *Phymatodes dimidiatus*, *Tetropium cinnamopterum*). Only two of the 10 species of Cerambycidae collected, *Cosmosalia chrysocoma* and *Stictoleptura canadensis* can be considered as dead-host species. *Cosmosalia chrysocoma* was infrequently collected, and *S. canadensis* was rather common in some Abitibi sites but absent from the more eastern sites (Table 2). Differences between cerambycid species in host condition, when compared with an ANOVA, were detected between *S. canadensis* and all other common early cerambycid species (*A. proteus, M. proteus, P. dimidiatus*), ($F_{6,63} = 4.02$; $p = 0.002$; Fig. 4a). For Scolytinae, again all species were found at the beginning of the decay gradient, where both ambrosia beetles (*Trypodendron lineatum*) and phloeophagous species (all others) were found. No differences were detected within Scolytinae in terms of preference for specific part of the gradient (Fig. 4a). Some species were

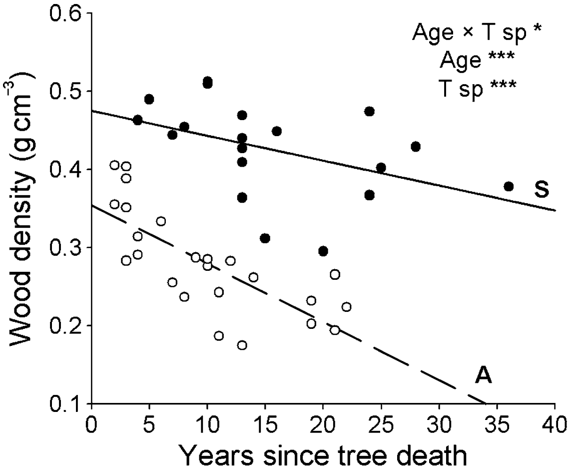


Fig. 3. Relationship between snag age and wood density for black spruce (S) and aspen (A). Significance levels are showed for the effects of snag age (age), tree species (T sp) and their interaction on wood density, following ANCOVA.

Table 2. Number of individuals found for each species (number of snags in parenthesis) at all sites sampled in black spruce snags, according to behavioural guild.

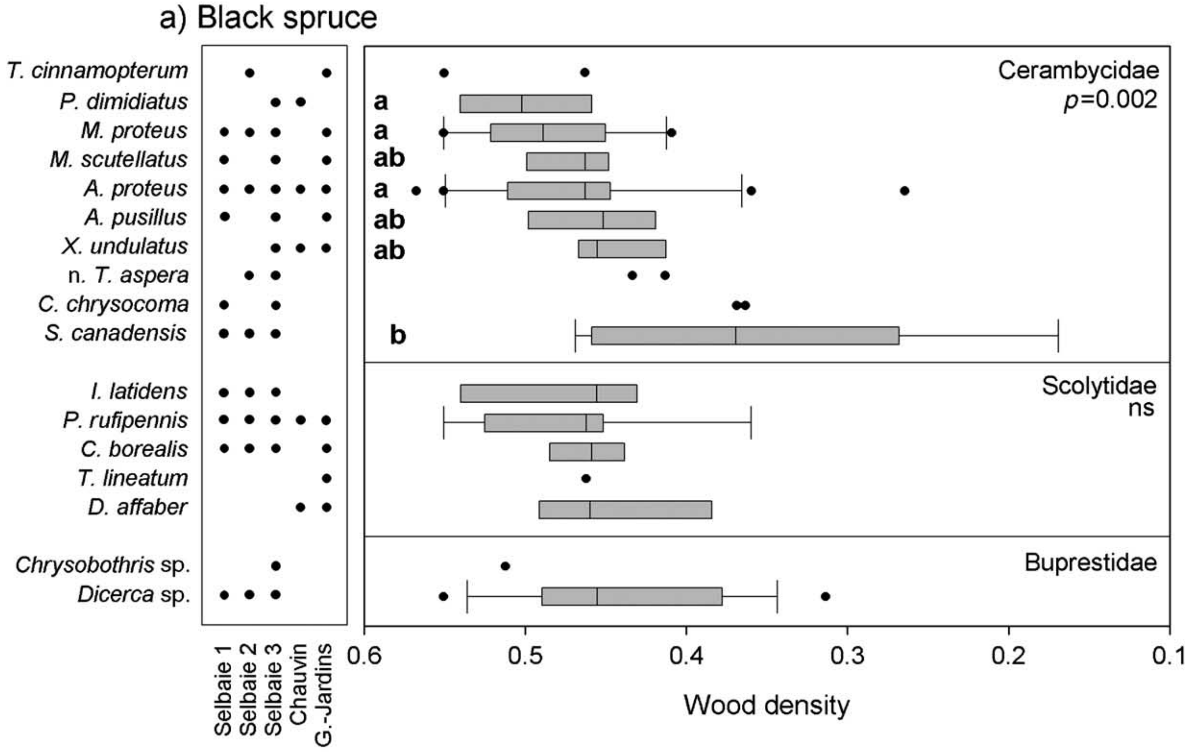
| | Selbaie 1 n = 24 | Selbaie 2 n = 12 | Selbaie 3 n = 12 | Chauvin n = 16 | G-J n = 16 | Total |
|---|---|---|---|---|---|---|
| Cerambycidae | | | | | | |
| Stressed-host species | | | | | | |
| *Acanthocinus pusillus* Kirby | 1 (1) | 0 | 22 (2) | 0 | 5 (1) | 28 |
| *Acmaeops proteus* (Kirby) | 28 (9) | 30 (5) | 13 (3) | 16 (4) | 20 (6) | 107 |
| *Meriellum proteus* (Kirby) | 7 (3) | 3 (2) | 6 (3) | 0 | 2 (2) | 18 |
| *Monochamus scutellatus* (Say) | 2 (1) | 0 | 1 (1) | 0 | 2 (1) | 5 |
| *Phymatodes dimidiatus* (Kirby) | 0 | 0 | 3 (1) | 21 (3) | 0 | 24 |
| *Tetropium cinnamopterum* Kirby | 0 | 1 (1) | 0 | 0 | 13 (1) | 14 |
| n. *Trachysida aspera* (LeConte) | 0 | 2 (1) | 2 (1) | 0 | 0 | 4 |
| *Xylotrechus undulatus* (Say) | 0 | 0 | 5 (3) | 3 (1) | 9 (3) | 17 |
| Dead-host species | | | | | | |
| *Cosmosalia chrysocoma* (Kirby) | 1 (1) | 0 | 3 (1) | 0 | 0 | 4 |
| *Stictoleptura canadensis* (Olivier) | 1 (1) | 11 (4) | 12 (4) | 0 | 0 | 22 |
| Not identified | 2 (2) | 1 (1) | 0 | 0 | 1 (1) | 4 |
| Buprestidae | | | | | | |
| *Chrysobothris* sp. | 0 | 0 | 1 (1) | 0 | 0 | 1 |
| *Dicerca* sp. | 13 (6) | 18 (6) | 14 (3) | 0 | 0 | 45 |
| Scolytinae | | | | | | |
| *Crypturgus borealis* Swaine | 4 (2) | 2 (1) | 118 (1) | 0 | 11 (2) | 135 |
| *Dendroctonus rufipennis* (Kirby) | 0 | 0 | 0 | 1 (1) | 0 | 1 |
| *Dryocoetes affaber* (Mannerheim) | 0 | 0 | 0 | 16 (2) | 6 (2) | 22 |
| *Ips latidens* (LeConte) | 17 (4) | 12 (3) | 47 (1) | 0 | 0 | 76 |
| *Polygraphus rufipennis* (Kirby) | 25 (1) | 12 (2) | 48 (1) | 3 (1) | 68 (4) | 156 |
| *Trypodendron lineatum* (Olivier) | 0 | 0 | 0 | 0 | 26 (1) | 26 |

only found in eastern sites (*Dryocoetes affaber* and *T. lineatum*), while *Ips latidens* was only found in Abitibi. The species-rich buprestid genus *Dicerca*, which likely included several species in our samples, was found throughout early and middle stages of decay (Fig. 4a).

When analysed with logistic regression, probability of presence of cerambycid larvae (all sites and species pooled) was significantly higher in early stages of decay of black spruce ($\chi^2_1 = 8.651$; $p = 0.003$) (Fig. 5a). Although the species composition of assemblages at the five sites was somewhat different, the relationship between wood density and probability of occurrence was similar for all 5 sites when analysed separately (Fig. 5b). This pattern is largely driven by the occurrence of the stressed-host guild ($\chi^2_1 = 21.611$; $p < 0.001$; Fig. 5c), which numerically dominated the dead-host guild, absent from most sites. However, probability of presence of *S. canadensis* and *C. chrysocoma* do increase

Table 3. Number of individuals found for each species at all sites sampled in aspen snags, according to behavioural guild.

| | LDRTF n = 24 | Magusi 1 n = 12 | Magusi 2 n = 12 | Chauvin n = 16 | Oka n = 16 | Total |
|---|---|---|---|---|---|---|
| Cerambycidae | | | | | | |
| Dead-host species | | | | | | |
| *Anthophylax attenuatus* (Haldeman) | 162 (15) | 6 (1) | 280 (8) | 46 (6) | 8 (3) | 502 |
| *Bellamira scalaris* (Say) | 8 (4) | 2 (1) | 1 (1) | 11 (5) | 10 (5) | 32 |
| *Clytus ruricola* (Olivier) | 0 | 0 | 0 | 0 | 1 (1) | 1 |
| n. *Trachysida mutabilis* (Newman) | 0 | 0 | 0 | 4 (2) | 0 | 4 |
| n. *Trigonarthris* sp. | 1 (1) | 0 | 0 | 0 | 0 | 1 |
| Not identified | 2 (2) | 1 (1) | 0 | 2 (2) | 2 (2) | 7 |
| Buprestidae | | | | | | |
| *Agrilus* sp. | 0 | 0 | 0 | 20 (2) | 0 | 20 |
| *Dicerca* sp. | 9 (5) | 5 (3) | 3 (2) | 26 (4) | 11 (3) | 54 |
| Scolytinae | | | | | | |
| *Trypodendron retusum* (LeConte) | 5 (1) | 0 | 0 | 46 (2) | 0 | 51 |
| *Xyloterinus politus* Say | 10 (2) | 0 | 0 | 36 (1) | 0 | 46 |
| Larvae | 0 | 0 | 6 (1) | 0 | 0 | 6 |



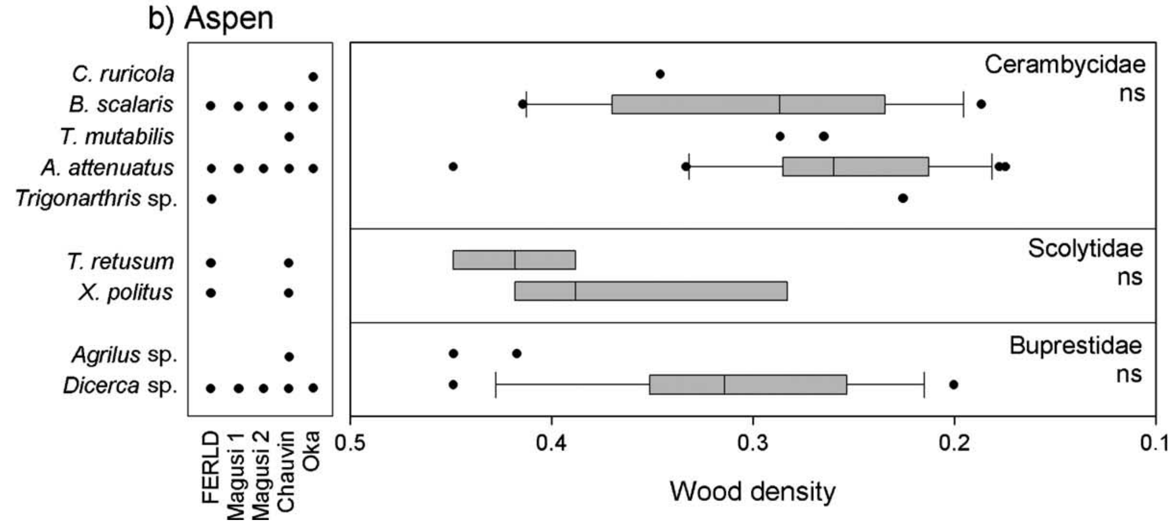


Fig. 4. Boxplots showing wood density of snags in which all species were found for (a) black spruce and (b) aspen. Sites in which species were found are indicated in box at left. Letters indicate significant differences between mean wood density of hosts of different species, following ANOVA and Tukey's HSD.

from near 0 in early stages of decay to over 80% in later stages in Selbaie 2 and Selbaie 3 sites ($\chi^2_1 = 7.263$; p = 0.007; Fig. 5d), in which these species are more numerically important. In the data we collected the two dead-host species found in spruce co-occurred in the same stages of decay, so there is no evidence of succession among this guild in this tree species.

Patterns observed in aspen were different (Fig. 4b). Scolytinae were marginal in numbers (Table 3) and mostly restricted to early decay stages (Fig. 4b).

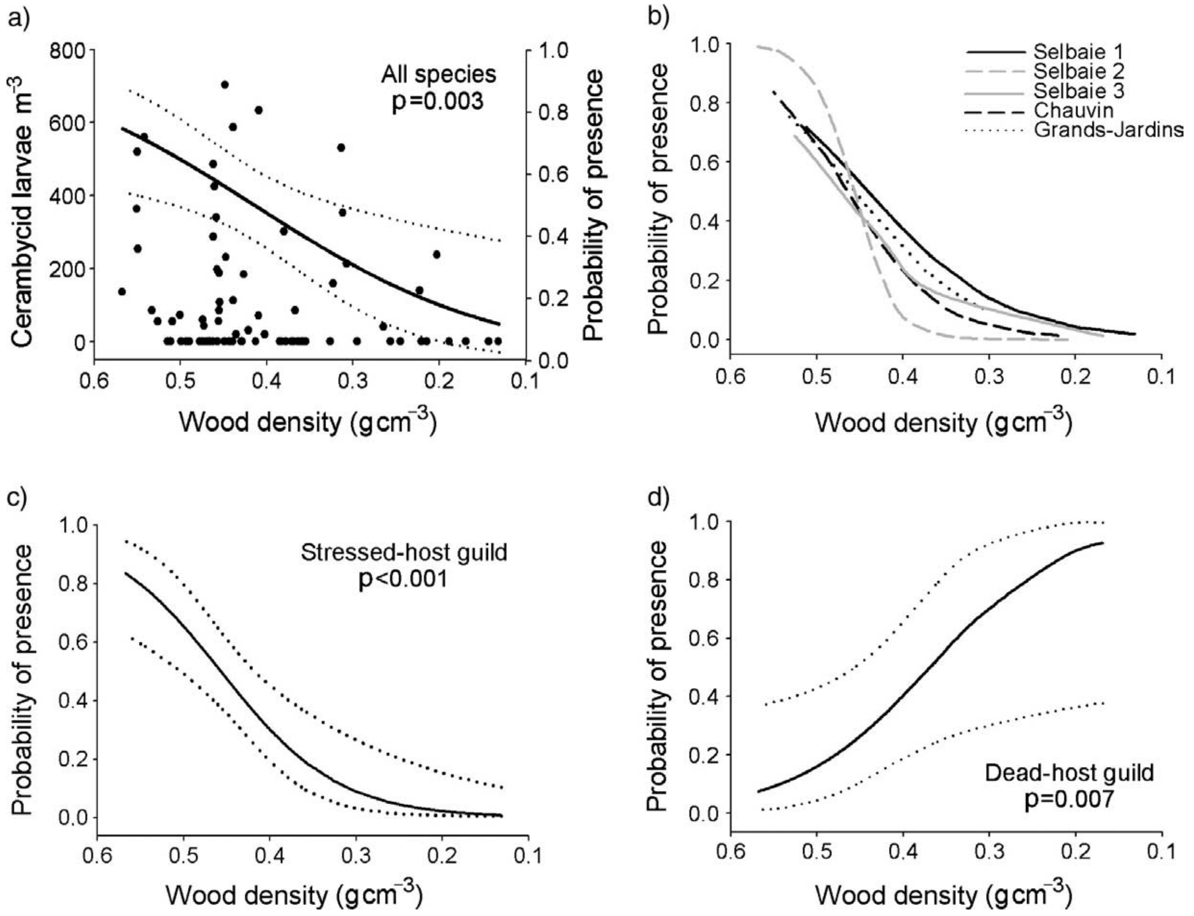


Fig. 5. Probability of presence of cerambycid larvae along the decay gradient (wood density) for black spruce, produced using logistic regressions with species occurrence (presence/absence) as the response variable with (a) all species and all sites combined, with abundance on y axis 1 and probability of presence on y axis 2; (b) probability of presence for each site with all species combined; (c) all sites, stressed-host species only; (d) dead-host species only for Selbaie 2 and 3 sites.

Cerambycids were less diverse but more numerous, with *Anthophylax attenuatus* being the dominant species (Table 3). All cerambycid species were concentrated in middle to late stages of decay; aspen cerambycid assemblages were thus exclusively composed of dead-host species. We saw no significant difference in preference ($p > 0.05$) between the two numerically important species (*A. attenuatus* and *Bellamira scalaris*) (Fig. 4b). These two species were found in all five sites sampled. Again the species-rich buprestid genus *Dicerca* was widespread and covered most stages of decay.

Probability of presence of cerambycid larvae (all sites and species pooled) was significantly higher in late stages of decay ($\chi^2_1 = 13.067$; $p = 0.001$; Fig. 6a). Again, the observed patterns were similar in all sites, but with two sites in which probability of presence appeared lower in middle stages (LDTRF, Magusi 1) (Fig. 6b). No similar analysis was made for stressed-host species, as they were totally absent from our samples in aspen.

## Discussion

The use of dissection as a sampling method enabled an unprecedented characterization of wood-feeding saproxylic Coleoptera assemblages, as most published studies focusing on coniferous hosts generally consider only the first few years following tree death (Gardiner 1957, Lindhe and Lindelöw 2004, Saint-Germain et al. 2004a) while such characterization of assemblages is even scarcer in the extant literature for deciduous host species. Our results showed communities dominated by stressed-host species in spruce, in which most species of Cerambycidae and Scolytinae were found only in the early stages of decay. Few species were found in later

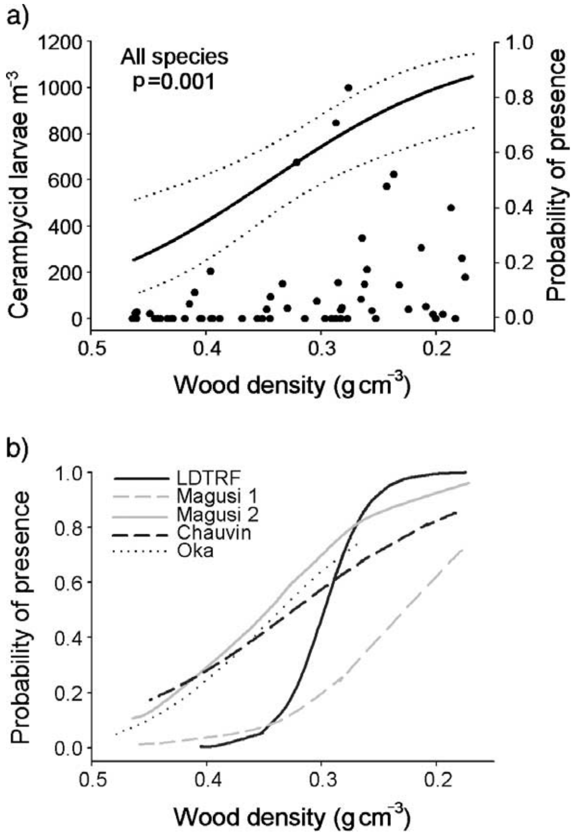


Fig. 6. Probability of presence of cerambycid larvae along the decay gradient (wood density) for aspen, produced using logistic regressions with species occurrence (presence/absence) as the response variable with (a) all species and all sites combined, with abundance on y axis 1 and probability of presence on y axis 2; (b) probability of presence for each site with all species combined (dead-host only).

stages of decay, and those species were totally absent from several of the sites we sampled. Patterns observed in aspen were opposite from those seen in black spruce. Communities were dominated by a few dead-host cerambycid species, and only a few scolytids and buprestids were found in early stages. This divergence in patterns between coniferous and deciduous host is of particular interest as it as rarely been demonstrated to this level in the literature before.

## Host-use patterns in black spruce

Fifteen of the seventeen taxa found in spruce in our study, representing over 95% of collected specimens, were restricted to early-decay classes. Such importance of the stressed-host guild has been reported in the literature in spruce and in other coniferous genera in different contexts. Early studies (Graham 1925, Savely 1939) and Vanderwel et al. (2006) which investigated changes in species composition of whole saproxylic communities along several decay classes in logs noted the general predominance of wood-feeding guilds in recently-dead trees and a shift in dominance towards fungivore and saprophage species in later stages of decay. Several other studies focusing on assemblages in snags recently killed by fire (Gardiner 1957, Saint-Germain et al. 2004a) or insect defoliators (Belyea 1952) reported abundant and species-rich assemblages. However, we found no reports of species occurrence of wood-feeding beetles in later stages of decay, probably because later decay stages were rarely investigated at all, not because of the paucity of the dead-host guild itself.

The abovementioned studies also observed similar species composition. *Monochamus scutellatus* has been found in early stages of decay in all four of the abovementioned studies, whether it be in spruce (Saint-Germain et al. 2004a), pine (*Pinus* spp., in Gardiner 1957) or balsam fir (*Abies balsamea*, in Belyea 1952). *Acmaeops proteus*, the most abundant species in our samples, has been reported in fire-killed spruce and pine one year after fire (Gardiner 1957, Saint-Germain et al. 2004a). Other species found in unburned forests in our study, such as *A. pusillus, T. cinnamopterum* and *Xylotrechus undulatus*, are also reported in one or more of these studies. The two species classified in the dead-host guild in our study, *C. chrysocoma* and *S. canadensis*, were occasionally found in recent disturbances in pine (Gardiner 1957), albeit in very small numbers. This may indicate that these species may not be deterred by very fresh snags.

Although probability of occurrence varied along the wood density gradient in similar ways among the five sites sampled, several species were locally common in one site and absent from others. This study was not designed to link these variations with the different landscape contexts within which those stands were located. Also, some of these species were found in only one or two trees (*T. cinnamopterum* in Grands-Jardins, *A. pusillus* in Selbaie 3). This may indicate an aggregated distribution; in such cases, the absence of some species in our samples may not indicate absence from a site altogether, but rather insufficient sampling effort to detect species with such distribution. This difference in distribution between common, widespread species and aggregated species could reflect differences in host-selection and mating behaviour.

## Host-use patterns in aspen

We found no previous studies reporting wood-feeder assemblages for aspen from eastern North America. Some studies produced in western Canada (Hammond 1997, Hammond et al. 2001, 2004) reported the presence of *Trypodendron retusum*, *Xyloterinus politus* and *Agrilus* sp. in early stages of decay of aspen, and of *B. scalaris* using flight-intercept traps.

It was notable that stressed-host species were absent from aspen snags. However, galleries from buprestid *Agrilus* sp. were seen on a high proportion of the snags sampled, but live larvae were found in only one tree which died a few weeks prior to sampling, as it still had foliage. Occurrence patterns of *Agrilus* and the biology of species like the poplar borer *Saperda calcarata*, known to be of widespread occurrence on live aspen, suggest that weakened-host species (i.e. species favoured by non-lethal stress, sensu Hanks 1999) might occupy to some extant in aspen the niche usually occupied by stressed-host species in coniferous trees.

Contrary to what was seen in black spruce, no major differences in species composition were seen between the different stands of aspen. *Anthophylax*, *Bellamira* and *Dicerca* were dissected from snags in every site, and other species were either marginal or found at extremities of the sampled decay gradient. However, there were important differences in terms of abundance, as very few individuals were collected at Oka and Magusi 1 sites. This was expected in Oka, in which aspen is marginal, but that was not the case at Magusi 1. Snags at Magusi 1 were smaller in diameter than other sites, but the landscape context alone as considered in our sampling design cannot explain differences in abundance of species or species composition.

## Differences between black spruce and aspen as hosts

Many factors could explain the opposite host-use patterns seen in black spruce and aspen. The different defence mechanisms and secondary compound profiles of aspen and spruce could provide an explanation on why stressed-host species are dominant in spruce, while this niche seems to be occupied by weakened-host species in aspen. Besides some species of Scolytinae which have evolved complex behavioural systems enabling them to overcome healthy trees' defences (Wood 1982), there are very few healthy-host or weakened-host wood-feeding species thriving on coniferous trees in North America, especially when compared to deciduous trees (Hanks 1999). This may be due in part to the production of oleoresin, composed mainly of monoterpenes and resin acids. The flow of resin will increase following physical damage or introduction of a pathogen and prevents the establishment of insect larvae in healthy trees. Reduction of the resin flow in heavily-stressed trees gives a window of opportunity to secondary insects to successfully colonize the tree (Klepzig et al. 2005, Lombardero et al. 2006). Oleoresin not being produced by deciduous trees might explain why healthy-host and weakened-host species are common in deciduous trees and rare in coniferous trees.

For specialization to evolve for a host in a very specific physiological state, cues allowing the location of appropriate hosts must exist. In coniferous trees, dying or recently dead individuals release both monoterpenes and ethanol, produced by fermentation occurring in dead plant cells (Chararas 1981). This mixture of compounds occurs in a definite proportion at this moment, as ethanol is not produced in significant quantities in healthy trees and the release of monoterpenes decreases and eventually ceases following the death of the tree, as they are oxidized or polymerized by bacteria (Chararas 1981). Ethanol and monoterpenes act synergistically to elicit a behavioural response in stressed-host species (Chenier and Philogène 1989, Byers 1992). Coniferophagous stressed-host species thus benefit from a clear chemical signal contributing significantly to their host selection. Semiochemicals released by deciduous trees of different physiological states have mostly been studied for their deterrent effect on coniferophagous insects (Huber et al. 2000). It is still unclear at this stage if host selection by aspen-feeding insects is based to some degree on such semiochemicals.

Typical stand dynamics of the two tree species could also provide an explanation for the observed differences in host-use patterns. In the northern boreal forest mostly dominated by coniferous species, stand dynamics are mostly driven by stand-replacing disturbances, mostly fire but also occasional insect epidemics (Bergeron et al. 2001, Bouchard et al. 2005). These disturbances produce, more or less periodically, large numbers of freshly-killed trees. Aspen is less prone to fire, and it rather exhibits gap-type dynamics (Hill et al. 2005). Because stressed-host species are receptive to a recently-dead tree only for a few weeks (Alya and Hain 1985), host availability is more restrictive to stressed-host species than to any other behavioural guild. There are important differences in the snag recruitment regimes between these two species, and the disturbance-driven dynamic might be more favourable to the evolution of stressed-host insect species. Most of the stressed-host species collected during our sampling are also believed to respond to stimuli produced during forest fires, especially smoke (Gardiner 1957, Saint-Germain et al. 2004b, c); this emphasizes the possibility of a link between the stand dynamics typical of such species and the evolution of communities of wood feeders dominated by stressed-host species.

In this study, snag dissection proved to be a very productive method to characterize wood-feeding assemblages, despite the logistic implications of the method and the time and labour required to complete the sampling. It provided unprecedented information that cannot be collected using traditional sampling methods.

Further efforts should be made to study wood-feeding insects in different tree species and landscape contexts, and the information provided by this method should be seen as an additional tool of great interest to study the impact of management on such insects.

*Acknowledgements* – We would like to thank E. Bolduc, A. Dechene, D. Lesieur, Z. Sylvain and T. Work for field or laboratory work, and Oka National Park and the Lake Duparquet research and teaching forest for facilitating our work within their boundaries. Comments from four anonymous reviewers helped improve the manuscript. This project was funded by Action Concertées-Fonds forestiers grant (P. Drapeau, C. Buddle and coll.) and a new researcher grant (C. Buddle) from the Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT), by a Discovery grant to C. Buddle from the Natural Science and Engineering Research Council of Canada (NSERC), and by the partners of the NSERC industrial chair in sustainable forest management of Univ. du Québec en Abitibi-Témiscamingue (UQAT) and Univ. du Québec à Montréal (UQAM).

## References

Allison, J. D. et al. 2004. A review of the chemical ecology of the Cerambycidae (Coleoptera). – Chemoecology 14: 123–150.

Alya, A. B. and Hain, F. P. 1985. Life histories of *Monochamus carolinensis* and *M. titillator* (Coleoptera: Cerambycidae) in the Piedmont of North Carolina. – J. Entomol. Sci. 20: 390–397.

Belyea, R. M. 1952. Death and deterioration of balsam fir weakened by spruce budworm defoliation in Ontario. – Can. Entomol. 84: 325–335.

Berg, Å. et al. 1994. Threatened plant, animal, and fungus species in Swedish forest: distribution and habitat associations. – Conserv. Biol. 8: 718–731.

Bergeron, Y. et al. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. – Can. J. For. Res. 31: 384–391.

Bergeron, Y. et al. 2002. Using dendrochronology to reconstruct disturbance and forest dynamics around Lake Duparquet, northwestern Quebec. – Dendrochronologia 20: 175–189.

Bouchard, M. et al. 2005. Mortality and stand renewal patterns following the last spruce budworm outbreak in mixed forests of western Quebec. – For. Ecol. Manage. 204: 297–313.

Brattli, J. G. et al. 1998. Primary attraction and host tree selection in deciduous and conifer-living Coleoptera: Scolytidae, Curculionidae, Cerambycidae and Lymexylidae. – J. Appl. Entomol. 122: 345–352.

Bright, D. E. 1987. The insects and arachnids of Canada. Part 15: the metallic wood-boring beetles of Canada and Alaska (Coleoptera: Buprestidae). – Agricult. Can. Res. Br. Publ. 1810: 1–335.

Byers, J. A. 1992. Attraction of bark beetles, *Tomicus piniperda*, *Hylurgops palliatus*, and *Trypodendron domesticum* and other insects to short-chain alcohols and monoterpenes. – J. Chem. Ecol. 18: 2385–2402.

Chararas, C. 1981. Étude du comportement nutritionnel et de la digestion chez certains Cerambycidae xylophages. – Mater. Org. 16: 207–261.

Chenier, J. V. R. and Philogène, B. J. R. 1989. Field responses of certain forest Coleoptera to conifer monoterpenes and ethanol. – J. Chem. Ecol. 15: 1729–1745.

Cherubini, P. et al. 2002. Tree-life history prior to death: two fungal root pathogens affect tree-ring growth differently. – J. Ecol. 90: 839–850.

Craighead, F. C. 1923. A classification and the biology of North American cerambycid larvae. – Tech. Bull. no. 27, Canadian Dept of Agriculture.

Edmonds, R. L. and Eglitis, A. 1989. The role of the Douglas-fir beetle and wood borers in the decomposition of and nutrient release from Douglas-fir logs. – Can. J. For. Res. 19: 853–859.

Gardiner, L. M. 1953. Larval description of *Acmaeops proteus* (Kby.) (Coleopt., Ceramb.). – Can. Entomol. 86: 190–191.

Gardiner, L. M. 1957. Deterioration of fire-killed pine in Ontario and the causal wood-boring beetles. – Can. Entomol. 89: 241–263.

Graham, S. A. 1925. The felled tree trunk as an ecological unit. – Ecology 6: 397–411.

Grissino-Mayer, H. D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. – Tree-Ring Res. 57: 205–221.

Grove, S. J. 2001. Saproxylic insect ecology and the sustainable management of forests. – Annu. Rev. Ecol. Syst. 33: 1–23.

Hammond, H. E. J. 1997. Arthropod biodiversity from *Populus* coarse woody material in north-central Alberta: a review of taxa and collection methods. – Can. Entomol. 129: 1009–1033.

Hammond, H. E. J. et al. 2001. Early colonization of *Populus* wood by saproxylic beetles (Coleoptera). – Can. J. For. Res. 31: 1175–1183.

Hammond, H. E. J. et al. 2004. Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. – Can. J. For. Res. 34: 1–19.

Hanks, L. M. 1999. Influence of the larval host plant on reproductive strategies of cerambycid beetles. – Annu. Rev. Entomol. 44: 483–505.

Harmon, M. E. et al. 1986. Ecology of coarse woody debris in temperate ecosystems. – Adv. Ecol. Res. 15: 133–302.

Hill, S. B. et al. 2005. Canopy gap disturbance and succession in trembling aspen dominated boreal forests in northeastern Ontario. – Can. J. For. Res. 35: 1942–1951.

Howden, H. F. and Vogt, G. B. 1951. Insect communities of standing dead pine (*Pinus virginiana* Mill.). – Ann. Entomol. Soc. Am. 44: 581–595.

Huber, D. P. W. et al. 2000. A survey of antennal responses by five species of coniferophagous back beetles (Coleoptera: Scolytidae) to bark volatiles of six species of angiosperm trees. – Chemoecology 10: 103–113.

Jonsson, B. G. et al. 2005. Ecology of species living on dead wood – lessons for dead wood management. – Silva Fenn. 39: 289–309.

Klepzig, K. D. et al. 2005. Effects of mass inoculation on induced oleoresin response in intensively managed loblolly pine. – Tree Physiol. 25: 681–688.

Krankina, O. N. et al. 1999. Nutrient stores and dynamics of woody detritus in a boreal forest: modeling potential implications at the stand level. – Can. J. For. Res. 29: 20–32.

Larsson, S. and Danell, K. 2001. Science and the management of boreal forest biodiversity. – Scan. J. For. Res. 3: 5–9.

Lecomte, N. et al. 2005. Effects of fire severity and initial tree composition on understorey vegetation dynamics in a boreal landscape inferred from chronosequence and paleoecological data. – J. Veg. Sci. 16: 665–674.

Lindhe, A. and Lindelöw, Å. 2004. Cut high stumps of spruce, birch, aspen and oak as breeding substrates for saproxylic beetles. – For. Ecol. Manage. 203: 1–20.

Lombardero, M. J. et al. 2006. Effects of fire and mechanical wounding on *Pinus resinosa* resin defenses, beetle attacks, and pathogens. – For. Ecol. Manage. 225: 349–358.

Martikainen, P. 2001. Conservation of threatened saproxylic beetles: significance of retained aspen *Populus tremula* on clearcut areas. – Ecol. Bull. 49: 205–218.

Maser, C. et al. 1979. Dead and down woody material. – In: Thomas, U. V. (ed.), Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. USDA Forest Service Agriculture Handbook no. 553.

Paine, T. D. et al. 1997. Interactions among scolytid bark beetles, their associated fungi, and live host conifers. – Annu. Rev. Entomol. 42: 179–206.

Rayner, A. D. M. and Boddy, L. 1988. Fungal decomposition of wood: its biology and ecology. – Wiley.

Saint-Germain, M. et al. 2004a. Xylophagous insect species composition and substratum use patterns on fire-killed black spruce in central Quebec. – Can. J. For. Res. 34: 677–685.

Saint-Germain, M. et al. 2004b. Comparison of Coleoptera assemblages from a recently burned and unburned black spruce forests of northeastern North America. – Biol. Conserv. 118: 583–592.

Saint-Germain, M. et al. 2004c. Landscape-scale habitat selection patterns of *Monochamus scutellatus* (Coleoptera: Cerambycidae) in a recently burned black spruce forest. – Environ. Entomol. 33: 1703–1710.

Saint-Germain, M. et al. 2006. Sampling saproxylic Coleoptera: scale issues and the importance of behaviour. – Environ. Entomol. 35: 478–487.

Savely, H. E. Jr 1939. Ecological relations of certain animals in dead pine and oak logs. – Ecol. Monogr. 9: 321–385.

Schroeder, L. M. and Eidmann, H. H. 1993. Attacks of bark-boring and wood-boring Coleoptera on snow-broken conifers over a 2-year period. – Scan. J. For. Res. 8: 257–265.

Schroeder, L. M. et al. 1999. Attacks by bark- and wood-boring Coleoptera on mechanically created high stumps of Norway spruce in the two years following cutting. – For. Ecol. Manage. 123: 21–30.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. – Ecol. Bull. 49: 11–41.

Švácha, P. and Danilevsky, M. L. 1986. Cerambycoid larvae of Europe and Soviet Union (Coleoptera, Cerambycoidea). Part I. – Acta Univ. Carol. Biol. 30: 1–176.

Švácha, P. and Danilevsky, M. L. 1987. Cerambycoid larvae of Europe and Soviet Union (Coleoptera, Cerambycoidea). Part II. – Acta Univ. Carol. Biol. 31: 121–284.

Švácha, P. and Danilevsky, M. L. 1988. Cerambycoid larvae of Europe and Soviet Union (Coleoptera, Cerambycoidea). Part III. – Acta Univ. Carol. Biol. 32: 1–205.

Sverdrup-Thygeson, A. and Ims, R. A. 2002. The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen. – Biol. Conserv. 106: 347–357.

Vanderwel, M. C. et al. 2006. Insect community composition and trophic guild structure in decaying logs from eastern Canadian pine-dominated forests. – For. Ecol. Manage. 225: 190–199.

Wood, D. L. 1982. The role of pheromones, kairomones, and allomones in the host selection and colonization of bark beetles. – Annu. Rev. Entomol. 27: 411–446.