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Colleen Simpson and Mary Reid

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Consequences of stand thinning for bark beetles: direct and indirect effects

Colleen Simpson and Mary Reid
Dept. of Biological Sciences and Environmental Science Program
University of Calgary
Calgary, AB
T2N 1N4

colsim@telus.net
mreid@ucalgary.ca

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1. RESEARCH OBJECTIVES

Stand thinning can affect forest herbivores, such as bark beetles (Scolytidae), both directly and indirectly. Thinning directly changes microclimate and stand density that can in turn affect insect activity and host location. Indirectly, thinning also may change the quality or abundance of host plants, such as trees, which in turn affect the performance of herbivores. Both of these mechanisms have been proposed to explain the effectiveness of stand thinning in reducing successful tree attack by mountain pine beetles, *Dendroctonus ponderosae* Hopkins (Waring and Pitman 1985, Bartos and Amman 1989). This management approach, known as 'beetle-proofing' (e.g. Whitehead *et al.* 2001**)**, is commonly employed, yet it remains unclear whether it works through the direct or indirect mechanisms, or both (Waring and Pitman 1985, Amman *et al.* 1988, Bartos and Amman 1989, Schmid *et al.* 1991, 1992). Moreover, for less aggressive species of bark beetles that breed primarily in trees lacking defences, such as windfalls, thinning has been found to increase rather than decrease bark beetle abundance (Hindmarch and Reid 2001, Park 2001). However, these latter studies were conducted in the years immediately following thinning, when the effects of logging slash would still be present and before tree vigour would likely have changed. The current study was designed to examine the effects of thinning on the abundance and reproductive success of secondary (non-aggressive) bark beetles up to 7 years after thinning, and to relate these responses to both stand and tree characteristics.

This study (Simpson 2004) focused on pine engravers, *Ips pini* Say, in thinned and unthinned stands of lodgepole pine, *Pinus contorta* var *latifolia* Engelmann, with secondary attention to striped ambrosia beetles, *Trypodendron lineatum* Oliver. Specifically, we asked:

1) Are these bark beetles more likely to be found in thinned stands or unthinned stands? Is their abundance related to stand features of microclimate and tree density (direct effects) or predator abundance (indirect effects)?

2) Does pine engraver reproductive success differ between trees grown in thinned stands or unthinned stands (indirect effects)?

2. METHODS

This study was conducted in 6 pairs of thinned and unthinned stands near Whitecourt, Alberta (54ºN, 115ºW) in 2001 and 2002. Trees were ca. 100 years old, and salvage thinning was conducted whereby subdominant trees and non-lodgepole pine trees tended to be removed, leaving approximately one-third of the live trees (Table 1a). Four stands were thinned in winter preceding the summer of 1996, one was thinned in 1997, and one was thinned in 1999. An unthinned stand was matched with each thinned stand on the basis of proximity and stand composition and age. Several stand characteristics pertinent to bark beetles were measured in each stand (listed in Table 1a).

To measure beetle abundance in the stands, beetles were captured in baited traps and in experimentally felled trees. Twelve-funnel Lindgren traps were used, and in each stand there were two traps baited with commercial pine engraver pheromone baits (ipsdienol and lanierone) and one trap baited with the tree volatile alpha-pinene (all traps and baits from Phero Tech Inc.). The number of pine engravers, striped ambrosia beetles, and their beetle predator *Thanasimus undatulus* (Say) captured in each trap type in each stand was tallied for each year. The density of pine engravers settling in logs of freshly felled lodgepole pine that were placed in each stand was also determined. Beetle abundance was related to stand type and the characteristics of each stand type.

To determine the effects of tree quality on pine engraver reproductive success, logs were taken from freshly felled lodgepole pine trees in the thinned and unthinned stands of each pair of stands. These logs were placed in sets of 3 logs (all 3 from the same tree) at separate sites within the thinned stands of the pair of stands. Size, growth rate and phloem characteristics were measured for each tree (listed in Table 2a). The timing and density of pine engraver settlement on the logs was recorded, and a subset of pine engraver egg galleries were excavated to determine mating success and egg-laying behaviour (variables listed in Table 2b). Logs were then placed in rearing cages in both thinned and unthinned stands to collect offspring. Reproductive traits were examined as a function of log origin (thinned or unthinned) and of individual tree characteristics.

3. KEY FINDINGS

3.1 Effects of thinning on stands and trees

Changes in stand conditions and tree quality that are pertinent to bark beetles were measured and are summarized briefly below.

Stand Characteristics (Table 1a): Compared to unthinned stands, thinned stands had higher maximum temperatures, lower minimum temperatures, and were windier, as expected from the lower tree density. They also had a higher percentage of lodgepole pine in the canopy, as a result of the harvesting method, and more fresh pine coarse woody debris attributed to both higher wind speeds and a higher proportion of standing pine.

Tree Characteristics (Table 2a): Trees in thinned stands were larger on average than those in unthinned stands, but this was related to removal of smaller trees at harvest. Growth rate in the 4 years after thinning occurred did not differ between trees in thinned and unthinned stands. Trees in unthinned stands had thicker phloem and more phloem nitrogen than those in thinned stands.

3.2 Beetle abundance in thinned and unthinned stands

Pine engravers were more abundant in thinned stands than unthinned stands, as measured in both trap catches and settlement densities (Table 1b). In contrast, striped ambrosia beetles were more abundant in unthinned stands than thinned stands, though less common overall than pine engravers (Table 1b). The number of the clerid predators did not differ between stand types (Table 1b). The differing responses to thinning of pine engravers and their clerid predators meant that the ratio of prey to predators was higher, and therefore predation risk likely lower, in thinned stands than in thinned stands (Table 1b). For all species, their relative abundance in thinned and unthinned stands did not differ detectably according to the time since thinning occurred, although a previous study in these stands found that striped ambrosia beetles were more common in thinned stands than in unthinned stands in the years immediately following thinning (Hindmarch and Reid 2001).

Despite the many differences in stand characteristics between thinned and unthinned stands (Table 1a), the relative abundance of each beetle species captured in traps over the season was not explained statistically by microclimate, as measured by mean maximum stand temperature or mean wind speed, or by habitat abundance, measured as the % lodgepole pine in the canopy and the abundance of fresh pine coarse woody debris in which the beetles breed. More pine engravers tended to be captured with stand densities were lower ($p < 0.06$), but stand type remained significant suggesting that there was something other than tree density that explained their greater abundance in thinned stands. More clerid predators were captured in stands where more pine engravers were captured. The relative capture rates in thinned and unthinned stands could not be attributed to differences in the detection distance of pheromone traps, as the proportion of pine engravers caught in unbaited traps placed 2 and 4 m from a subsample of pheromone traps did not differ between thinned and unthinned stands (both $p > 0.5$).

3.3. Pine engraver reproduction in logs from thinned and unthinned stands

Pine engravers tended to settle disproportionately on logs from thinned stands, but this was mainly detected when other log traits (those in Table 2a) were considered simultaneously. In both 2001 and 2002, male pine engravers settled earlier on logs from thinned stands (Table 2b), after controlling for log traits (no difference otherwise). In 2002, when settlement was sparse, 83% of 12 trees from thinned stands were settled compared to 50% of 12 trees from unthinned stand ($p < 0.08$) and final densities of male pine engravers were higher on trees from thinned stands whether or not individual tree traits were considered (Table 2b). In 2001, there was no difference in final settlement densities for the two types of trees (Table 2b).

There was little effect of log origin on male or female reproductive traits when origin was considered alone. However, when settlement traits and log traits were considered simultaneously, several measures of reproduction were lower in logs from thinned stands than in logs from unthinned stands (Table 2b). This negative effect of thinning was offset by the positive effects of early settlement, which tended to be earlier for logs originating from thinned stands, thereby giving no net benefit to breeding on either log type.

The tree characteristics that differed between logs that originated in thinned and unthinned stands (Table 2a) had little effect for most reproductive traits, while treatment level effects remain pronounced when they were considered. Therefore it remains unclear what caused the reduced reproduction for beetles breeding on logs from thinned stands.

The effect of tree origin was more important than the stand in which offspring developed. When logs from the same tree were placed in thinned and unthinned stands for development (after colonization had occurred in thinned stands), there was little effect of the stand on offspring development rate or offspring size or number.

4. CONCLUSIONS

The largest effect of stand thinning was the 7-fold increase in the abundance of pine engravers relative to unthinned stands. We speculate, but did not show, that this increase in pine engraver abundance in thinned stands is due to the increased availability of habitat, decreased stand complexity and potential decline in predation pressure. Traits associated with host quality did not improve after thinning as we had expected and as other studies in the boreal forest have shown (Valinger 1992, 1993, Yang 1998). Pine engravers tended to settle on logs from thinned stands earlier and at higher densities than on logs from unthinned stands, yet ultimately experienced similar reproductive success in both log types. Thus, the costs of declining phloem quality after thinning appear to be offset by the direct effects of earlier settlement and of a more simplified stand structure, and the indirect effects of increased host availability or decreased predation pressure.

These results contrast with previous work that indicates thinning is a good management strategy for preventing outbreaks of mountain pine beetle (see above). Thinning is thought to deter attack by mountain pine beetle because of enhanced stand temperature, interrupted pheromone signals and/or improved host defensive response (Waring and Pitman 1985, Amman *et al.* 1988, Bartos and Amman 1989, Schmid *et al.* 1991, 1992). We did not detect deleterious impact of increased temperature on pine engraver abundance. Furthermore, we found no difference in pheromone detection ability between thinned and unthinned stands. However, an improvement in host defensive capability may account for the pine engraver’s poor performance in trees from thinned stands, though we were unable to address this specifically.

The response of pine engravers seven years after thinning further contrasts with another species of secondary bark beetle, the striped ambrosia beetle, which was more abundant in unthinned stands. Previous work (Hindmarch and Reid 2001, Park 2002) found the striped ambrosia beetle to be more abundant in thinned stands up to two and three years after harvest. Logging slash and stumps may be better habitat than windfalls for striped ambrosia beetles, unlike pine engravers.

5. MANAGEMENT IMPLICATIONS

a. Salvage thinning alters the physical and biological components of the forest environment. This changes the abundance of two characteristic species of bark beetles and their predator-prey relationships, albeit in different ways. Following thinning, forest managers should be vigilant of forest pest species that may increase in abundance. The changes in biotic and abiotic factors that we document may help predict how different pest species may respond to thinning.

b. Pine engravers may become economically important if their populations become large enough to damage live trees, if their associated staining fungi degrades lumber value in tree decks, or if they facilitate other pests (such as mountain pine beetle). To reduce these risks in thinned stands, windfalls should be minimized and removed from the stands, and log decks should be removed by early spring before pine engravers disperse.

c. Conversely, though outside the scope of this study, the higher numbers of pine engravers in thinned stands may contribute to increases in the abundance and diversity insect-eating birds and insects.

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Table 1. Summary of differences in stand characteristics and beetle abundance in thinned and unthinned stands. Values reported are least square means ± SE (or 95% CI) controlling for other variables (see Simpson (2004) for details).

Response	**Thinned**	**Unthinned**	**P**
a) Stand Characteristics			
Tree density (stems/ha)	1028 ± 397 SE	3400 ± 500	< 0.002
% Lodgepole pine	82.1 ± 4.2	41.3 ± 4.2	< 0.001
DBH (cm)	23.2 ± 1.3	17.8 ± 1.3	< 0.02
Growth rate (mm/yr)	1.53 (1.25- 1.83)	1.41 (1.17- 1.69)	> 0.5
Fresh CWD (m^3/ha)	0.28 ± 0.06	0.02 ± 0.06	< 0.02
Daily maximum temperature ^oC	2001: 19.6 ± 0.3, 2002: 20.8 ± 0.3	2001: 17.8 ± 0.3 2002: 18.1 ± 0.3	both < 0.0001
Daily minimum temperature ^oC	2001: 9.1 ± 0.2 2002: 7.9 ± 0.2	2001: 9.6 ± 0.2 2002: 8.5 ± 0.2	< 0.05 < 0.06
Wind (m/s)	0.35 ± 0.06	0.08 ± 0.04	< 0.0001
b) Beetle Abundance			
Pine engraver (# in traps per season)	1998 (916-4359 CI)	330 (150-720 CI)	< 0.0001
Pine engraver (males/100 cm^2 on logs)	1.8 (1.4-2.2)	0.1 (-0.1-0.2)	< 0.0001
Striped ambrosia beetle (# in traps per season)	12 (4-39 CI)	68 (21-219 CI)	< 0.02
Clerid beetle (# in traps per season)	44 (25-82)	36 (21-64)	> 0.6
Pine engravers/clerid	48.5 ± 9.2	22.2 ± 9.2	< 0.01

Table 2. Summary of differences in tree characteristics and pine engraver reproductive traits between logs originating in thinned and unthinned stands. All reproductive traits are derived from logs placed in thinned stands. Values reported are least square means (with SE or 95% CI) controlling for other variables (see Simpson (2004) for details); for reproductive traits, there were no differences in reproductive traits (except for male clutch size in 2002) when tree variables were not considered.

Response	**Year**	**Thinned Origin**	**Unthinned Origin**	**P**
a) Tree traits				
Phloem nitrogen (% Total Kjeldahl nitrogen)	2001	0.26 ± 0.04	0.44 ± 0.04	< 0.04
Phloem thickness (mm)	2001, 2002	0.64 ± 0.03	0.76 ± 0.03	< 0.02
Sum of four years' growth after thinning (mm)	2001, 2002	1.51 ± 0.003	1.40 ± 0.003	> 0.5
Phloem moisture content (g moisture/g phloem)	2002	1.33 ± 0.15	1.38 ± 0.15	> 0.8
b) Beetle breeding traits (only significant differences shown)				
Mean settlement date (Julian day)	2001 2002	154 166	163 171	<0.0001 < 0.02
Final density (males/100cm2)	2002	2.2	1.2	< 0.04
Male clutch size	2002	32 ± 4	52 ± 7	<0.0002
Longest gallery (mm)	2002	65 ± 5	101 ± 7	<0.0001
Eggs per first female	2002	17 ± 2	30 ± 4	< 0.0001
Emerged offspring per female	2002	0.4 (0.2-1.6)	1.0 (0.6-1.4)	< 0.005