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Ecological Consequences of Forest Thinning for Bark Beetles (Coleoptera: Scolytidae): Direct and Indirect Effects

by

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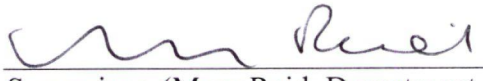
The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled " Ecological Consequences of Forest Thinning for Bark Beetles (Coleoptera: Scolytidae): Direct and Indirect Effects " submitted by Colleen Melanie Simpson in partial fulfilment of the requirements of the degree of Master of Science.



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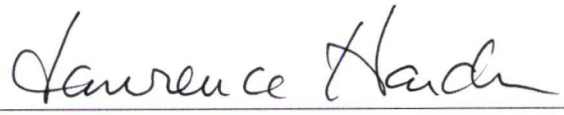

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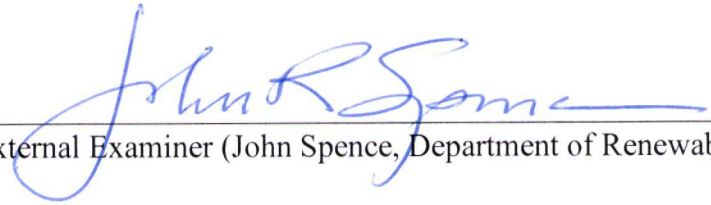

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Abstract

The implications of forest management for plant-insect interactions remain largely unknown, despite the significance of these relationships. Here I focus on effects of forest thinning on an herbivorous insect, the bark beetle *Ips pini* (Scolytidae). *Ips pini* was affected by forest thinning through both direct and indirect bottom-up and top-down mechanisms. After thinning, stand structure changed, host availability increased, and predation pressure declined, increasing the abundance of *I. pini* in thinned stands. *Ips pini* tended to colonize trees from thinned stands earlier and at higher densities even though they were poorer quality hosts and ultimately resulted in reduced performance. As predicted, thinned stands were warmer, though there was no general effect of thinning on beetle development. *Ips pini* remained more abundant in thinned stands seven years after harvest, suggesting that the decline in host quality is offset by improvements in stand structure and host availability and reduced predation pressure.

Acknowledgements

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CHAPTER 1: GENERAL INTRODUCTION: ENVIRONMENTAL CHANGE AND PLANT-INSECT INTERACTIONS

Environments are changing, whether due to the impact of anthropogenic effects or natural processes. These changes are likely to influence plant-insect interactions, a major ecological process, because both plants and insects are sensitive to changes in biotic and abiotic environments (Amwack and Leather 2002, Bale *et al.* 2002). The effects of changing environments could impact herbivorous insects both directly and indirectly (Figure 1.1). Insects may be affected directly by the environmental disturbance that changes host species abundance or microclimatic conditions (Amwack and Leather 2002, Bale *et al.* 2002). Two possible indirect pathways may also affect herbivores. First, changes in abiotic conditions and plant species abundance may alter the quality and quantity of potential host plants. Second, predators may also respond to changes in microclimate and host plant quantity or quality, thereby altering the predation pressure experienced by herbivores (Amwack and Leather 2002). Given the ecological importance and economic impact of herbivorous insects, it is important to understand how and why specific changes to the environment impact plant-insect interactions. Although recent attention has focused on the effects of plant quality (Amwack and Leather 2002) or rising temperatures (Bale *et al.* 2002) on insect herbivores, no comprehensive review exists on the simultaneous changes in biotic and abiotic conditions that result from environmental disturbance.

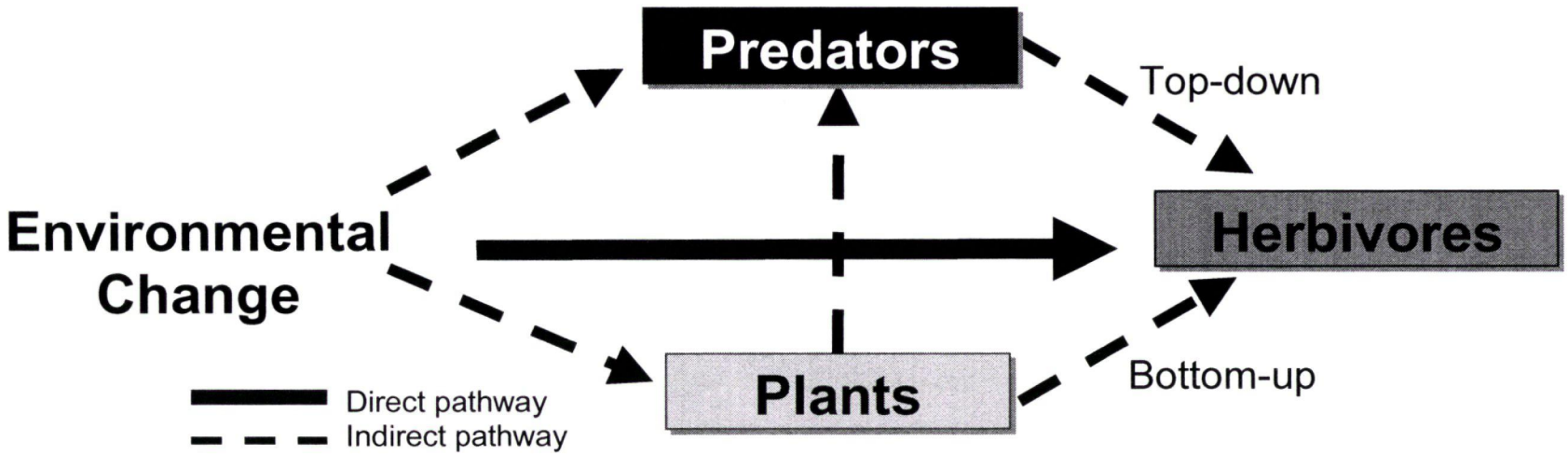

Figure 1.1. The possible impacts of environmental change on herbivorous insects.

Forest Management

Forest management includes a suite of silvicultural practices to increase timber yield from forests. One such management strategy, stand thinning, is applied increasingly in Canada's forests (Sougavinski and Doyon 2002). Silvicultural thinning involves harvesting some trees in a stand, leaving some trees remaining to continue growth.

Stand thinning changes the biotic and abiotic characteristics of forests at two spatial scales. The immediate effects of thinning occur at the stand level: stand structure, composition and microclimate may be altered. After harvest, thinned stands are less dense and therefore may be windier (Bartos and Amman 1989, Hindmarch and Reid 2001). Increased wind velocities and more widely spaced trees can increase windfall (Laiho 1987, Lohmander and Helles 1987, Quine *et al.* 1995). Tree removal also opens the canopy, facilitating sunlight penetration; so thinned stands tend to be warmer (Wickman and Torgersen 1987, Bartos and Amman 1989, Schmid *et al.* 1991, 1992a, Hindmarch and Reid 2001). However, an open canopy reduces insulation, causing thinned stands to cool down to lower minimum temperatures (Bartos and Amman 1989, Schmid *et al.* 1992a, Anderson and Brower 1996). Finally, species composition within stands may become more uniform after harvest, if thinning removes sub-dominant tree species.

At the scale of an individual tree, tree quality may be affected due to reduced competition and increased nutrient and light availability (Goodell 1952, Donner and Running 1986). Changes in growth and defence capabilities, occur slowly, possibly over several years. Trees growing in thinned stands may assimilate more nutrients in growing

tissues, and may also have greater levels of constitutive defences (Entry *et al.* 1991, Matson *et al.* 1987, Kimball *et al.* 1998, Hemming and Lindroth 1999). Alternatively, the increase in wind sway after thinning may reduce the vigour of individual trees due to damage of the conducting vessels (Silins *et al.* 2002).

Study Objectives

The central goal of this study was to discern the effects of the biotic and abiotic changes caused by stand thinning on the abundance, reproduction and development of *Ips pini* (Say), an insect herbivore. This beetle attacks trees that have already been severely weakened or killed by other agents, such as wind or disease (secondary attack). Most previous studies of the effects of thinning on secondary bark beetles have documented the changes that occur immediately after tree harvest (Mason 1969, Safranyik *et al.* 1999, Hindmarch and Reid 2001, Park 2002). My study is the first to look at the impacts of thinning after the transient high inputs of fresh conifer debris produced during harvest have likely dissipated. In addition, trees in thinned stands should have responded to the new conditions, initiating an indirect process by which thinning may affect insect herbivores. Here, I focus on changes at both the stand and tree level that result up to seven years after forest thinning.

Study Design

This study was conducted during 2001 and 2002 in a forest management area in the boreal forest near Whitecourt, Alberta (54°N, 115°W). The region receives an average of 564 mm of precipitation per year, with average monthly temperatures ranging from 15 °C in July to -11 °C in December and January. Major forest types in the area

include those dominated by coniferous species (lodgepole pine *Pinus contorta* var. *latifolia* Engelm. black and white spruce (*Picea mariana* (Mill.) B.S.P. and *Picea glauca* (Moench) Voss), and mixed wood stands (with some combination of conifers and deciduous trees such as aspen (*Populus tremuloides* (Michx.)). Forestry is one of the major industries in the area, harvesting wood for lumber, pulp and paper.

I conducted my research in six pairs of thinned and unthinned lodgepole pine stands. Stand pairs were chosen based on similar age, location and species composition. Several of the stand pairs in the study had been used for a previous investigation of the immediate effects of thinning (Hindmarch 1999). Stands were approximately 50 ha in area. Pairs of stands were located in three different regions within the larger forest management area. One pair of stands was located in the Chickadee region (54°12' N, 115°54' W), three pairs of stands were located in the Tom Hill region (54°03' N, 116°15' W) and two pairs of stands were located in the West Windfall region (54°04' N, 116°30' W; see Table 1.1). These regions were separated by about 15 km. Within a region, stands in a pair were separated by less than 2 km. Average age of trees in these stands was approximately 100 yrs.

Stands were thinned between two and six years prior to the start of the study. The harvest prescription in these stands was salvage thinning. Salvage thinning is employed when stands are over-mature, yet foresters will not be able to harvest them for several more years. Selective harvest is initiated to remove any weakened or subdominant trees that are likely to die before the rest of the stand is available for harvest (Côté 2003). Salvage thinning therefore removes subdominant tree species and smaller members of the dominant tree species in a stand. The result is an evenly spaced stand with a more

Table 1.1. UTM coordinates of study stands near Whitecourt, Alberta. Coordinates apply to zone 11 U.

Stand	Region	Treatment	Easting	Northing
CT	Chickadee	Thinned	057 224	600 633
CA	Chickadee	Unthinned	057 099	600 685
TH 621	Tom Hill	Thinned	054 909	598 916
TH 625	Tom Hill	Thinned	054 920	599 001
TH 626	Tom Hill	Thinned	054 948	598 948
TH 347	Tom Hill	Unthinned	054 924	598 853
TH 348	Tom Hill	Unthinned	054 872	598 925
TH 349	Tom Hill	Unthinned	054 828	598 893
WC 1	West Windfall	Thinned	053 438	599 260
WW 607	West Windfall	Thinned	053 156	599 003
WW 306-1	West Windfall	Unthinned	053 142	599 112
WW 306-2	West Windfall	Unthinned	053 122	599 094

uniform species composition and a larger mean tree diameter. During harvest approximately two-thirds of trees were removed. See Chapter 2 for a summary of stand characteristics.

Study Species

The focal herbivore in this system is *Ips pini* (Say) (Coleoptera: Scolytidae), a phloem-feeding herbivore. The only naturally occurring host tree of *I. pini* in my study area is lodgepole pine, although they colonize any *Pinus* species (Bright 1976). *Ips pini* has a transcontinental range in Canada and they have been collected as far north as Alaska. The southern end of the range of *I. pini* extends into the southern United States and northern Mexico (Bright 1976). Though *I. pini* primarily attack trees that have been killed or severely weakened by other agents, when population densities become high enough they are able to mass-attack living trees (Anderson 1948, Schenk and Benjamin 1969, Bright 1976, Wood 1982a).

At northern latitudes *I. pini* is univoltine. Overwintered adults emerge during late spring in search of new breeding habitats. Males attack trees first. They locate hosts using semio-chemical cues from trees and other beetles (Miller and Borden 1990). Once males arrive at a suitable host, they burrow under the bark and excavate a nuptial chamber in the phloem. They then begin releasing pheromones that attract females and other males to the tree (Wood 1982b). Females enter the nuptial chamber of a male, mate and then excavate egg galleries in the phloem, which radiate away from the central nuptial chamber. *Ips pini* are polygynous, and males attract an average of three females (range 1-5) forming the 'Y' shaped gallery systems in the phloem layer that are characteristic of this species (Schenk and Benjamin 1969). Males tend to remain with

their harem throughout egg laying, providing a form of paternal care by clearing frass away from the gallery (Reid and Roitberg 1994). Females lay eggs in individual egg niches along the sides of their galleries. Development occurs entirely within the phloem of the natal tree. Larvae hatch, begin feeding on phloem, thereby forming individual larval galleries perpendicular to their mother's egg gallery. After several larval instars, larvae pupate in pupation chambers located at the ends of larval galleries. New adults emerge from natal trees during late summer, while parental beetles re-emerge shortly before their offspring. Adults overwinter in the duff (Schenk and Benjamin 1969, Bright 1976).

Trypodendron lineatum (Oliver) (Coleoptera: Scolytidae) is another species of secondary bark beetle common in the boreal forest. *Trypodendron lineatum* feed on a fungus, which they transport and inoculate into host trees (Bright 1976). Much of their breeding biology is similar to *I. pini.* However, unlike *I. pini*, the mycophagous mode of feeding allows *T. lineatum* to exploit the hard wood of trees. Thus, egg galleries of this species are found within the xylem perpendicular to the wood grain (Bright 1976). In addition, *T. lineatum* is a conifer generalist, colonizing any conifer species within its range (Chapman 1963, Bright 1976, Pullainen 1983).

Abiotic Effects on Bark Beetles

Like all ectotherms, bark beetle larvae that experience higher temperatures develop faster and emerge earlier than those experiencing lower temperatures (Haack *et al.* 1985, 1987b, Bentz *et al.* 1991, Hui 1994). However, the accelerated development rate at warmer temperatures typically results in smaller final body size for most insects (Atkinson 1994).

Abiotic conditions, such as temperature, wind and stand structure influence habitat search behaviour of bark beetles. Bark beetles, like other insects, require a minimum temperature threshold to fly. This threshold may be exceeded more often under warmer temperature regimes, increasing the opportunity for habitat search (Hindmarch 1999). Bark beetles rely on volatile semio-chemical cues to locate hosts and mates, and these are influenced by airflow patterns. Increased wind speed may disperse volatile chemical cues over a wider area (Bartos and Amman 1989), yet beetles have difficulty flying in windy conditions (Seybert and Gara 1970, Salom and Mclean 1991a, b, Hindmarch 1999) or locating habitat in less concentrated volatile plumes. Finally, habitat structure may influence the search ability of bark beetles. Beetles may expend less energy searching for hosts in areas with a more simplified habitat structure (Hindmarch 1999).

Host Plant Effects on Bark Beetles

For bark beetles and other insects, host quality is a function of nutritional content, balanced by the presence and amount of defensive chemicals (Amwack and Leather 2002). Bark beetles that attack live trees should perform better when hosts are stressed and induced defence mechanisms are compromised (Larson *et al.* 1983, Hard 1985, Waring and Pitman, 1985, Shroeder 1987). However, *I. pini* typically breed in host material that is already dead and unable to mount an induced defensive response, so they benefit when breeding in hosts that were growing more vigorously before they died (Reid and Robb 1999, Reid and Glubish 2001). In general, bark beetles achieve higher reproductive success when breeding in trees with phloem that has a higher nutritional content (Popp *et al.* 1989) or in trees with thicker phloem (Haack *et al.* 1985, 1987a, b,

Amman and Pasek 1986). Resource abundance also influences offspring size at emergence. Offspring that developed in trees with thicker phloem are larger at emergence than those from trees with thinner phloem (Haack *et al.* 1985, 1987b).

Predator Effects on Bark Beetles

The primary predators of bark beetles include members of the family Cleridae (Coleoptera). Clerids are generalist predators on bark beetles and their associated fauna. These beetles cue into bark beetle pheromones (Miller and Borden 1990) and host tree volatiles (Zhou *et al.* 2001) to locate trees undergoing colonization. Adult clerids attack adult scolytids on the host tree (Amman 1972), and also deposit eggs at entrance to bark beetle galleries. Clerid larvae then prey on developing bark beetles within the gallery system (Cowan and Nagel 1965). Predation by clerids results in significant brood and adult mortality (Aukema and Raffa 2002). However, the role of top-down forces on bark beetle dynamics remains difficult to predict because attack rates decline at high prey densities, suggesting that clerids exhibit a type II functional response (Reeve 1997).

Thesis Organization

In this thesis, I explore direct and indirect effects of forest thinning on *Ips pini* at two spatial scales. In Chapter 2, I examine the effects of stand level changes in abiotic conditions, host abundance and predation pressure on bark beetle abundance and colonization. In Chapter 3, I focus on the effects of thinning on reproductive success of *I. pini* that may arise indirectly through host quality. Chapter 4 examines the interaction between abiotic conditions (stand scale) and host quality (tree scale) on development and

emergence of offspring in *I. pini*. Finally, I draw some general conclusions about the effect of environmental change on herbivorous insects in Chapter 5.

CHAPTER 2: BARK BEETLE RESPONSE TO THE STAND LEVEL EFFECTS OF FOREST THINNING

INTRODUCTION

Populations of insects are regulated by interacting biotic and abiotic factors that are in turn influenced by the biological and physical structure of habitat. Biotic factors include those operating from the bottom-up (food or host resources) or top-down (predation). For insect herbivores, bottom-up influences consist of the effects of host quality and availability. Although the importance of host quality is self-evident, the role of host availability is less clear. Root's (1973) resource concentration hypothesis predicts greater herbivore abundance where host plants are concentrated or more abundant. This effect is likely due to more efficient search for hosts. Top-down forces may also respond to habitat diversity, as proposed by Root's (1973) natural enemies hypothesis. The natural enemies hypothesis postulates that in areas of high plant diversity there will also be a wider diversity of herbivores, causing generalist predator abundance to be high, which in turn limits herbivore populations. Both of Root's hypotheses have received empirical support (resource concentration: Risch 1981, Bach 1984, Turchin 1987a, but see Grez and Gonzalez 1995, natural enemies: reviewed in Russell 1989, Andow 1990, Schellhorn and Sork 1997).

In addition to biological influences, populations of herbivorous insects are regulated by abiotic factors including climate, weather (Andrewartha and Birch 1954, Cloudsley-Thompson 1962, Strong 1983, Kingsolver 1989) and habitat structure (Coll and Botrell 1994). The ultimate geographic distribution of insects is determined in part

by their tolerance of the environmental extremes they encounter (Loxdale and Lushai 1999), but on a smaller scale, microclimatic conditions are also important determinants of insect distribution and abundance. Microclimate includes a suite of local environmental variables, such as temperature, relative humidity, light and wind. For example, changing microclimatic conditions can affect insect physiology, development, social behaviour and movement, as well as the overall suitability of a given habitat (Cloudsley-Thompson 1962).

The relative contributions of abiotic, top-down, and bottom-up processes to determine insect distributions may depend on environmental heterogeneity, though no consistent trends have been found (Kingsolver 1989, Andow 1990, Hunter and Price 1992). The question becomes of particular interest when humans manipulate ecosystems. Often these manipulations reduce plant diversity and change the physical structure of habitats, influencing microclimate.

I studied the effects of a large-scale forest manipulation, stand thinning, on two bark beetle species (Scolytidae) and their insect predator, a clerid beetle (Cleridae) *Thanasimus undatulus* (Say). Stand thinning is an increasingly common technique for managing forest productivity (Sougavinski and Doyon 2002). Because of the scale of the habitat manipulations relative to the size of insects, the microclimate and host availability alterations that result from stand thinning provide an opportunity for understanding these dual effects on insect herbivore abundance.

Few previous studies have considered the impacts of forest thinning on herbivore abundance. When the consequences of thinning are documented, most authors have only speculated as to the causes of changing herbivore abundances that result from thinning

(e.g. Amman *et al.* 1988, Ross 1995, Liebhold *et al.* 1998). However, elucidating the key mechanisms responsible for changing herbivore distributions can benefit forest managers and aid in our understanding of patterns of organism distribution and abundance. Much of the current research has focused on the effects of thinning on herbivores immediately after harvest (Heliovaara and Vaisanen 1984, Brown *et al.* 1987, Mendel *et al.* 1992, Ross 1995, Hindmarch and Reid 2001, Park 2002). Logging slash and fresh stumps left in the stand immediately after thinning provide a one-time pulse of breeding material for bark beetles (Mendel *et al.* 1992, Gara *et al.* 1999, Hindmarch and Reid 2001, Park 2002). Whether or not the trends documented during the early years after thinning persist during the long term is not known.

Upon thinning, stand characteristics change immediately and enduringly. Tree removal results in a less dense, homogeneously spaced stand. Stand composition may also change as a result of harvest. Depending upon the thinning regime employed, subdominant tree species may be removed, resulting in an arboreal monoculture. For the trees that remain, removal of neighbouring trees reduces competition, potentially allowing them to grow more vigorously (Brown *et al.* 1987; but see Silins *et al.* 2002). Microclimate will also change. A more open canopy facilitates light penetration, and thinned stands may be warmer than unthinned stands (Wickman and Torgersen 1987, Bartos and Amman 1989, Schmid *et al.* 1991, 1992a, Hindmarch and Reid 2001), increasing phloem temperatures (Bartos and Booth 1994). However, as a result of poor insulative capacity of the canopy, thinned stands may also be cooler than unthinned stands (Bartos and Amman 1989, Schmid *et al.* 1992a, Anderson and Brower 1996). More open, less cluttered, thinned stands also tend to be windier (Bartos and Amman

1989, Hindmarch and Reid 2001). Increased wind velocities and more widely spaced trees can increase the incidence of windfall (Laiho 1987, Lohmander and Helles 1987, Quine *et al.* 1995).

Changes to the abiotic environment in thinned stands can in turn influence insect search behaviour (Wickman and Torgeresen 1987, Bartos and Booth 1994). Studies have documented a preference for unshaded habitats in some Coleoptera species (e.g. Bach 1984). Thus, beetles may prefer thinned stands because of increased light penetration, although several species of bark beetles may avoid very high light intensities when choosing habitat (Furniss 1962, Bowers *et al.* 1996, Villa-Castillo and Wagner 1996). If thinned stands are warmer, then temperatures may exceed the threshold for beetle flight more often, allowing beetles greater search capacity in thinned stands (Hindmarch 1999). Furthermore, beetles may expend less energy searching for breeding habitats in more open, less cluttered, thinned stands (Hindmarch 1999). However, warmer temperatures resulting from thinning may deter *Dendroctonus ponderosae* attacks (Bartos and Amman 1989, Schmid *et al.* 1991). Increased wind speeds in thinned stands may disperse pheromone plumes more widely (Bartos and Amman 1989), but beetles may have more difficulty flying in windier situations (Seybert and Gara 1970, Salom and Mclean 1991a, b, Hindmarch 1999) or detecting conspecifics in less concentrated pheromone plumes. In addition, radiant heat may disrupt air currents, and confuse pheromone communication (Schmid *et al.* 1991).

The biotic changes that follow forest thinning can also impact bark beetles. More vigorous trees may be better able to resist beetle attack (Brown *et al.* 1987), but bark beetles that breed in dead trees may benefit from enhanced vigour prior to tree death

(Reid and Robb 1999). Finally, greater incidence of windfall in thinned stands translates into greater input of bark beetle breeding habitat. The resource concentration hypothesis (Root, 1973) predicts that bark beetles will be most abundant in areas of high host density. Thus, beetles may concentrate in thinned stands because of greater availability of suitable habitat (Peltonen *et al.* 1998, Park 2002).

Numerical response of bark beetles to forest thinning has not been consistent across all species in all locations. In the northern boreal forest, *Ips pini* and *Trypodendron lineatum* were more abundant in thinned stands during the first three years after harvest (Hindmarch and Reid 2001, Park 2002). Conversely, stand thinning is often employed to inhibit population expansion of *Dendroctonus ponderosae* (Amman *et al.* 1988, Bartos and Amman 1989, Schmid *et al.* 1991).

The response of predators to stand thinning is more difficult to predict. The natural enemies hypothesis predicts greater predation rates in areas of high plant diversity (Root 1973), thus I expect populations in thinned stands to be relieved of predation pressure if thinning decreases habitat diversity. However, the natural enemies hypothesis has typically been applied to generalist predators, whereas the clerid species in this system is a specialist on Scolytidae. Furthermore, many of the factors that influence bark beetle ecology may also impact the abundance of their insect predators. For example, because clerids use bark beetles pheromones to locate prey, thinning may disrupt or enhance their ability to find bark beetles, whereas thinning could hinder their flight. Previous work found contrasting impacts of thinning on predation rates. Wickman and Torgersen (1987) found greater predation and parasitism on Douglas-fir tussock moths (*Orgyia psuedotsugata* (McDunnough)) in thinned stands. In contrast, Leibhold *et al.*

(1998) found no difference in parasitoids of gypsy moth (*Lymantria dispar* (L.)) and Grushecky *et al.* (1998) determined that while thinning increased the abundance of small mammalian predators of gypsy moth, it did not change predation rates on gypsy moth larvae or pupae.

Here I examine the simultaneous effects of thinning on abiotic conditions, habitat availability and predator abundance, and determine their impacts on two bark beetle species. My study is the first to look at the impacts of thinning after the transient high inputs of fresh conifer debris produced during harvest have likely dissipated.

METHODS

Study System

The study was conducted in the northern boreal forest, near Whitecourt, Alberta, Canada (54°N, 115°W), within six pairs of thinned and unthinned lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) stands. All data were collected during 2001 and 2002. Refer to Chapter 1 for a complete description of the study area.

Adult *I. pini* emerge from the forest floor during late spring (May-June) to search for suitable breeding substrate. These beetles typically occupy *Pinus* spp. (Bright 1976); lodgepole pine is the host in this region. *Ips pini* are secondary bark beetles, meaning that they feed and reproduce on hosts that have already been killed or severely stressed by other agents, such as wind or disease (Anderson 1948, Wood 1982a). Males are the first to colonize hosts, using host-tree volatiles and pheromones of conspecifics to locate suitable breeding material (Miller and Borden 1990). They bore into the bark, enter the phloem layer and begin releasing pheromones that attract females and other males (Wood 1982b). This species is polygynous and males each attract an average of three females

(Schenk and Benjamin 1969). Once females arrive, they mate with the male and begin constructing galleries within phloem where eggs are laid. Larvae hatch and undergo development within the phloem. Teneral adults typically emerge during late summer or early fall (August to September: Schenk and Benjamin 1969, Bright 1976).

Trypodendron lineatum (Oliver) (Coleoptera: Scolytidae) is another species of secondary bark beetle common in the northern boreal forest. These beetles are 'ambrosia beetles' because they feed primarily upon an ambrosia fungus, which they transport and inoculate into host material (Bright 1976). Adults emerge during April and May seeking breeding material. *Trypodendron lineatum* attack any species of conifer within its range (Chapman 1963, Bright 1976, Pullainen 1983). In B.C., adults may re-emerge to begin another brood (Bright 1976); but there is no evidence of this in the northern boreal forest (C.M. Simpson, pers. obs.). Offspring emerge during early fall to seek overwintering sites in the duff and bark crevices of standing trees (Bright 1976)

The main predator of bark beetles in this system is *Thanasimus undatulus* (Say) (Coleoptera: Cleridae). *Thanasimus undatulus* is a specialist predator of Scolytidae, known to be associated with *I. pini* (Reid 1957b, Miller and Borden 1990), *Dendroctonus rufipennis* (Kirby) (*engelmanni* Hopk.; Knight 1961), *Dendroctonus pseudotsugae* Hopk.(Kline and Rudinsky 1964, Cowan and Nagel 1965) and *Scolytus unispinosus* LeConte (Cowan and Nagel 1965). Clerid adults use scolytid pheromones (Miller and Borden 1990) and host tree kairomones (Zhou *et al.* 2001) to locate sites of bark beetle attack. Adult *T. undatulus* prey on adult bark beetles (Amman 1972), whereas larvae feed on eggs and immature scolytids within the gallery (Cowan and Nagel 1965).

Stand Characteristics

When measuring stand density and species composition, if data from previous years did not exist (mainly from T.D. Hindmarch), I measured standing tree densities using three randomly located, 5.64m radius ($100m^2$) circular plots. For all trees I recorded the species and diameter at breast height (DBH; 1.3m above ground level). Results from the sample plots were combined to estimate the total stems/ha for each stand. Estimates of pre-thinning stand densities were obtained from Millar Western Industries (Whitecourt, Alberta) if T. D. Hindmarch did not collect data in previous years.

I quantified input of fresh, coarse, woody debris (CWD) in all 12 stands during 2002. I set up large (ca. 1 ha), randomly located plots within which I walked parallel transects, separated by approx. 4 m, and quantified the diameter, length and species of all freshly (< 1 yr old) fallen trees as determined by the presence of green needles. Input of bark beetle habitat was expressed as the volume of freshly fallen lodgepole pine/ha.

I measured tree growth rates for four years before (1992-1995) and four years after thinning (1997-2000) from disks cut from four trees in each stand. Trees felled from one stand (WW 607) were omitted from the analysis on growth rates after thinning because this stand was thinned only two years prior to the start of the study. Disks were cut from the remaining bole after experimental logs were cut approximately 6 m above ground level in 2001 and 4 m above ground level in 2002 (differences due to the different number of logs cut in each study year). I quantified growth rates by measuring the growth rings under a dissecting microscope fitted with an ocular micrometer at 20x

magnification. Rings were measured at four locations per disk and averaged to obtain an estimate of growth rate.

To quantify stand temperatures, I measured temperature half-hourly (2001) or hourly (2002) with HOBO data loggers (Onset Computer Corporation) (2001: 17 June to 16 September; 2002: 20 May – 15 September) in a subset of stands. During 2001 data loggers were located in three thinned (TH 621, TH 625 and TH 666) and four unthinned stands (CA, TH 347, TH 348 and TH 349), whereas during 2002 data loggers were in a slightly different set of seven stands (thinned: TH 666, WC 1 and WW 607; unthinned: CA, TH 347, TH 349, WW 306-1). Data loggers were mounted on the north side of trees near beetle emergence cages. Data loggers were sealed within two Ziploc brand freezer bags to prevent moisture accumulation. Half-hourly and hourly Hobo data logger readings were summarised into daily minimum and maximum values for each study year. These data were analysed for each year separately, since Hobos were placed in different stands in each study year. To obtain temperature data for all stands during 2002, I monitored ambient minimum and maximum air temperatures with digital thermometers every two weeks in all 12 stands from 8 May to 22 August. I mounted thermometers at breast height (1.3 m above ground level) on the north side of a tree, to maintain consistent sun exposure.

I monitored wind speeds using a digital anemometer (Sper Scientific) in all stands in 2002 every three days (20 May - 15 July) or every week (23 July - 26 August). On each sampling day, average, maximum and minimum wind speed during one minute (m/s) were measured at breast height at a fixed location within a given stand. Before each measurement, I used the anemometer to determine the direction of maximum

airflow and the instrument was held in that position for the duration of the measurement. To facilitate comparisons between stands in either treatment type, wind speed in each stand pair was measured as closely together as possible in time (i.e. within 15 min. of the other stand in the pair).

Beetle Abundance

During both study years I monitored all experimental stands for bark beetle and clerid abundance using baited Lindgren 12-funnel traps. Three traps were used per stand: two traps were baited with *I. pini* pheromones (ipsdienol, released at 110 *u*g/day and lanierone, 10 *u*g/day) and a third trap was baited with a tree kairomone (α-pinene; 150 mg/day; all baits and traps from Phero Tech Inc., Delta, BC). Traps were hung approximately 50 m apart from each other, and 75 m away from forest edge. A $1cm^2$ piece of Vapona™ (19.2% Dichlorvos) insecticide was placed within each trap collection cup. Trap contents were collected every two weeks. Samples were stored in plastic bags and frozen. Bark beetles and clerid beetles were identified to species according to Bright (1976), Rasmussen (1976) and Wood (1982) in the laboratory.

Most (> 99.9%) *I. pini* were captured in pheromone-baited traps, so all catches from kairomone traps were eliminated from analyses. *Trypodendron lineatum* captures were distributed evenly between the pheromone and kairomone traps (51% and 49% respectively). There was no significant difference in the number of *T. lineatum* caught in the two trap types within a stand (paired t-test; t_{23}=-1.88, $p<0.075$), therefore pheromone and kairomone trap catches were combined. During my study, only one species of clerid beetle was collected, *Thanasimus undatulus.* Like *I. pini, T. undatulus* were caught more often in pheromone-baited traps (ca. 95%), therefore analyses considered only

pheromone-baited trap catches. I further divided catches of *I. pini* into two biologically distinct flight periods, based on known phenology of the species in my study area and visual inspection of trap-catch data. The emergence period of overwintering adults was defined as the peak period of beetle flight during spring and early summer. This period included all trap catches before 15 June 2001 and before 30 June 2002. The period of offspring emergence was defined as the peak beetle flight during late summer and included all trap catches after 1 August in 2001 and after 29 July 2002.

Because pheromone plumes are volatile and influenced by wind conditions and stand density (Fares *et al.* 1980), a beetle's ability to detect pheromones could differ between thinned versus unthinned stands which could cause differences in trap catches independent of differences in beetle abundance. To address this, during 2002 I set up two whorls of three unbaited funnel traps surrounding a pheromone-baited trap in three thinned and three unthinned stands. The first whorl of traps was located 2 m from the central baited trap and the second whorl was 4 m away and staggered in circular arrangement from the first whorl. I collected contents of unbaited traps using the same sampling regime as the pheromone-baited traps.

To test for differences in beetle settlement density between thinned and unthinned stands, I felled two trees in each of the 12 stands during 2001 (also used to determined tree growth rates, above). This gave me a total of 12 trees felled in thinned stands and 12 trees felled in unthinned stands. Trees were chosen to reflect the average DBH of the stand. Each tree was then partitioned into six 75cm logs. For each pair of stands (one thinned and one unthinned stand), half of the logs from each tree were switched to the opposite stand type. Thus half of the logs in each stand originated from the two trees

felled in that stand, and the other half of the logs originated from trees felled in the opposing stand treatment type. Within a stand, logs from each tree were placed at separate sites for a total of four sites per stand. Each of the sites consisted of three logs placed end-to-end surrounded by branches from the same tree, to best simulate a freshly fallen tree.

Beetles were allowed to settle naturally at each log site. Sites were monitored every three days for evidence of new beetle attacks. When colonizing logs, male bark beetles leave distinctive frass piles above the opening to their nuptial chambers. These frass piles were used to indicate new male settlement, and each new male's gallery was marked with a numbered pushpin. Thus, I could keep track of the total number of males per log. Male density was determined by averaging the number of males on three 10x10 cm (100 cm^2) areas chosen randomly from the colonized surface of a given log.

Analyses

Statistical analysis involved the JMP IN version 4.0 computer package (SAS Institute, 2001). If necessary, data were transformed to meet the assumptions of normality and homogeneous variance, based on examination of the residuals after fitting a model. To avoid multicolinearity, all terms with variance inflation factors >10 were excluded from final models. A Type I error rate of $\alpha = 0.05$ was used for all tests. When tests included random factors, a restricted maximum likelihood method was employed for estimating mean squares (unless otherwise noted). All means are presented $\pm$ one standard error unless otherwise indicated. Interaction terms that tested biologically relevant predictions were included in initial models, and removed if $p>0.05$ or variance inflation factors were greater than 10. Though some stands were thinned in different

years, I did not include time since thinning in my analyses because there was not enough variation over the course of my study (Table 2.1). Where backwards elimination was applied effects were removed from the model if variance inflation factors were >10, or p >0.05.

RESULTS

Stand Characteristics

Before thinning, stand density did not differ significantly between treatments (R^2=0.22, t_{10}=1.70, p>0.1, thinned 2314 ± 397 stems/ha, unthinned 3400 ± 500 stems/ha; Table 2.1).

Thinning removed approximately two-thirds of the trees (R^2= 0.68, t_{10}=4.58, p<0.002, thinned 1028 ± 135 stems/ha, unthinned 3400 ± 500 stems/ha; Table 2.1). Thinned and unthinned stands also varied in stand composition. The percentage of lodgepole pine trees was significantly higher in thinned than in unthinned stands (R^2=0.83, t_{10}=-6.88, p<0.001, thinned 82.1 ± 4.2 % lodgepole pine, unthinned 41.3 ± 4.2 % lodgepole pine; Table 2.1).

Lodgepole pines growing in thinned stands had significantly larger diameters than trees growing in unthinned stands (R^2=0.48, t_{10}=-3.03, p<0.02, thinned 23.2 ± 1.3 cm DBH, unthinned 17.8 ± 1.3 cm DBH; Table 2.1). I used an ANCOVA to determine if mean growth rate (square root transformed) varied among treatments, controlling for the variables listed below. I included study year as a random variable to control for any effects of year of felling or differences due to the way trees were selected for experiments. The iterations of the restricted maximum likelihood method did not

Table 2.1. Attributes of experimental stands used in this study. Diameter at breast height includes values only for lodgepole pine trees.

Stand	Treatment	Year of Thinning[a]	Pre-Thinning Stand Density (Stems/ha)	Post Thinning Stand Density (Stems/Ha)	% Lodgepole Pine	Mean DBH (cm)	SE DBH	n DBH
CA	Unthinned	n/a	3400	n/a	33.6	17.0	0.86	36
TH 347	Unthinned	n/a	2833	n/a	41.2	15.0	0.45	35
TH 348	Unthinned	n/a	5333**	n/a	41.1**	17.2**	0.65**	46
TH 349	Unthinned	n/a	1633**	n/a	45.7**	25.5**	1.64**	21
WW 306-1	Unthinned	n/a	3267	n/a	44.9	18.8	0.92	44
WW 306-2	Unthinned	n/a	3933	n/a	41.5	17.3	0.66	49
CT	Thinned	1996	1867**	733**	59.1**	23.2**	1.69**	13
TH 621	Thinned	1997	1867*	1233**	74.3**	25.4**	1.08**	26
TH 625	Thinned	1996	4233**	1033**	90.0**	22.2**	0.95**	27
TH 626	Thinned	1996	1700*	900	81.5	25.5	0.99	22
WC 1	Thinned	1996	2400**	700**	90.0**	22.7**	1.23**	18
WW 607	Thinned	1999	1814*	1567	97.8	20.5	0.64	46

[a]stands were thinned during the winter preceeding the indicated year
*indicates data were collected by Millar Western Industries
**indicates data were collected by Trevor D. Hindmarch

converge, therefore the traditional estimated mean squares method was employed. Growth rates did not differ between treatments ($F_{1,30}$=0.34, p>0.56, back transformed LSMs (95% CI): thinned 1.53 (1.25, 1.83) mm/4yrs, unthinned 1.41 (1.17, 1.69) mm/4yrs), nor were there differences in the sum of four years' growth after thinning between stands within treatments ($F_{9,30}$=1.56, p>0.17) or years ($F_{1,30}$=0.02, p>0.87). The growth rate of trees four years after thinning was positively correlated with their growth rate four years before thinning (R^2=0.80, $F_{1,30}$=34.3, p<0.0001), but not related to DBH ($F_{1,30}$=1.47, p>0.23). These conclusions were also obtained in analyses that examined each year since thinning individually.

The volume of fresh, lodgepole pine, coarse woody debris (CWD) was greater in thinned stands than in unthinned stands (t-test, R^2 = 0.46, $t_{1,10}$=-2.90, p<0.016, thinned 0.28 ± 0.06 m^3/ha, unthinned 0.02 ± 0.06 m^3/ha). Overall, there tended to be a higher percentage of lodgepole pine in the CWD sampled in thinned stands (t-test, R^2 = 0.31, $t_{1,10}$=-2.1, p<0.059, thinned 65.7 ± 16.2% lodgepole pine, unthinned 16.7 ± 16.3% lodgepole pine). Input of CWD that was not lodgepole pine did not differ significantly between treatments (t-test, R^2 = 0.10, $t_{1,10}$=-1.07, p>0.3, thinned 0.16 ± 0.08 m^3/ha, unthinned 0.05 ± 0.08 m^3/ha).

During 2001 maximum temperatures varied significantly among treatments (thinned or unthinned; $F_{1, 629}$=16.62, p<0.0001), stands (within treatment; $F_{5, 629}$=2.87, p<0.02) and Julian date ($F_{1, 629}$=5.48, p<0.02; whole model R^2 = 0.05). Minimum daily temperatures during 2001 also differed between treatments ($F_{1, 629}$=4.03, p<0.05), and among days ($F_{1, 629}$=33.5, p<0.0001), though not between stands ($F_{5, 629}$=0.50, p>0.77; whole model R^2 = 0.06). I obtained similar results when the same analysis was carried

out on the 2002 data, daily maximum: treatment ($F_{1, 819}$=39.2, p<0.0001), stand ($F_{5, 819}$ =2.26, p<0.05) and Julian date ($F_{1, 819}$=22.0, p<0.0001); whole model R^2 = 0.08, daily minimum: treatment ($F_{1, 819}$=3.55, p<0.06), stand ($F_{5,819}$ =1.76, p>0.11) and date ($F_{1, 819}$=1.06, p>0.3); whole model R^2 = 0.02). During both years, thinned stands had significantly higher daily maximum temperatures than unthinned stands. Daily minimum temperatures were lower in thinned stands than in unthinned stands, though the effect was barely significant (2001) or not significant at p=0.05 (2002, Figure 2.1). In both study years, there was a significant positive correlation between minimum and maximum daily temperatures, controlling for treatment, stands within treatments and date (2001: $F_{1, 628}$ = 591, p<0.0001, whole model R^2 = 0.53; 2002: $F_{1, 818}$ = 2070, p<0.0001, whole model R^2 = 0.74).

Wind speeds (averaged over one minute and ln transformed) were analysed by ANCOVA. Mean wind speed was greater in thinned stands ($F_{1,266}$=80.8, p<0.0001) and differed between stands ($F_{10,266}$=1.53 p<0.001; Figure 2.2). There was no effect of Julian date ($F_{1,266}$=0.56, p>0.45) on average wind speed (whole model R^2 = 0.30).

Beetle Abundance and Settlement Patterns

To assess treatment level differences in trap catches of *Ips pini, Trypodendron lineatum* and *Thanasimus undatulus,* I used an ANOVA model on ln transformed data including year (as a random variable) and treatment. I caught significantly more *I. pini* in thinned stands than in unthinned stands (LSM number (95% CI): thinned: 1998 beetles (916, 4359); unthinned 330 (150, 720); $F_{1,21}$=63.1, p<0.0001, Figure 2.3a). *Ips pini* were

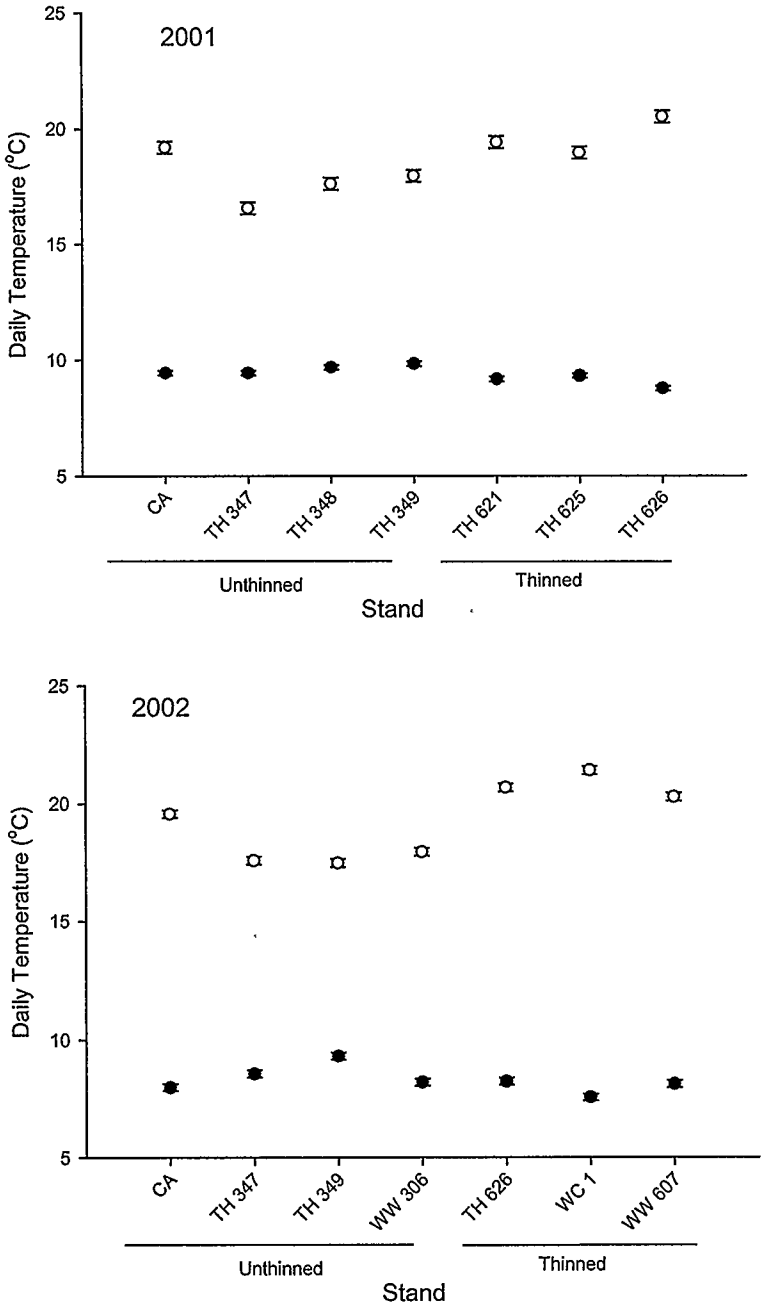

Figure 2.1. Maximum (○) and minimum (●) least squared mean temperatures for thinned and unthinned stands in 2001 and 2002. Each data point represents the least squared mean temperature for each stand ± 1 SE. See Results for statistical model.

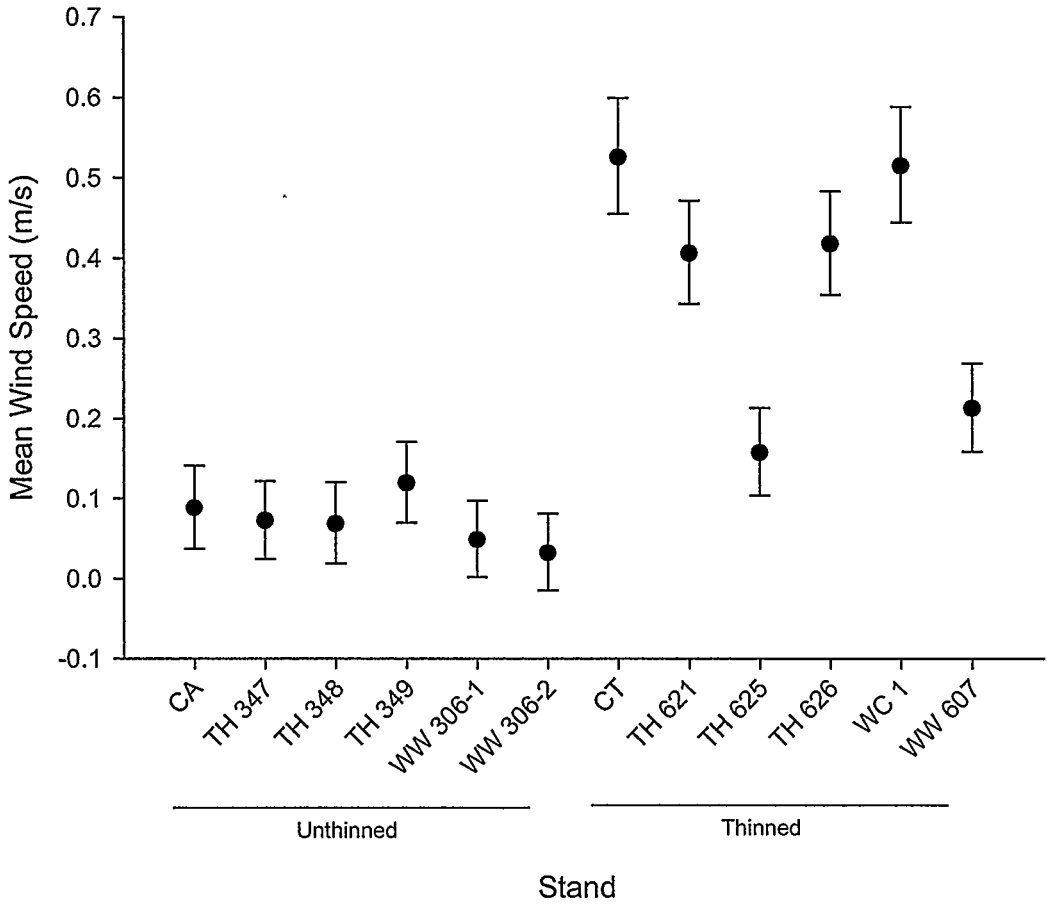

Figure 2.2. Average wind speed (m/s) for thinned and unthinned stands. Shown are least squared means ± one standard error back transformed from natural log transformed data used in analyses. See results for statistical model.

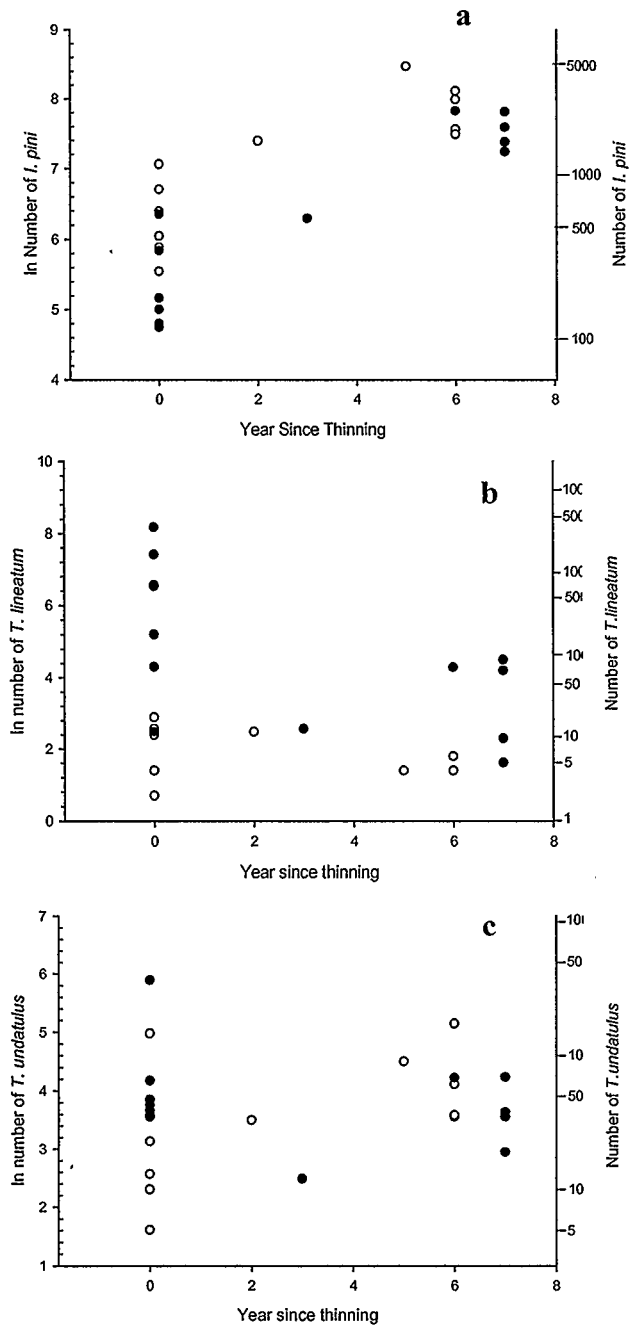

Figure 2.3. Number of a) *Ips pini*, b) *Trypodendron lineatum* and c) *Thanasimus undatulus* caught as a function of year since thinning. Each data point represents the total number of beetles caught per stand, per year. Open circles (⊠) represent data collected during 2001, closed circles (★) are data from 2002.

more abundant in 2001 (LSM number (95% CI):2001: 1119 beetles (808, 1549); 2002: 587 (424, 812) $F_{1,21}$=9.0, p<0.007; whole model R^2 = 0.77). By visual inspection, the effect of thinning did not dissipate in the years following thinning (Figure 2.3a). However, I was unable to test this formally since there was not enough continuity in year since thinning to consider it as a continuous variable. The effect of thinning held when I considered only the flight period of overwintered adults (ANOVA whole model R^2 = 0.88, treatment $F_{1,21}$=151.2, p<0.0001; mean number of *I. pini* (95% CI); thinned 290 (114, 735), unthinned 10 (4.0, 25.3), year $F_{1,21}$=8.63, p<0.008). Similarly, more *I. pini* offspring were captured in thinned stands (ANOVA whole model R^2 = 0.72, treatment $F_{1,21}$=40.1, p<0.0001; mean number of *I. pini* (95% CI); thinned 1261 (420, 3752), unthinned 257 (86, 765), year (random) $F_{1,21}$=15.5, p<0.0009).

In contrast to *I. pini, Trypodendron lineatum* were more abundant in unthinned stands than in thinned stands ($F_{1,21}$=7.0, p<0.02 (mean number of *T. lineatum* (95% CI); thinned 12 (1.1, 134), unthinned 68 (6, 765; Figure 2.3b). As with *I. pini*, the effect of thinning did not appear to change as time since thinning increased (Figure 2.3b). *Trypodendron lineatum* were more common during 2002 than during 2001 ($F_{1,21}$=10.6, p<0.004, whole model R^2 = 0.44).

The iterative REML procedure did not converge for analysis of *Thanasimus undatulus* abundance so I used a standard LMS procedure even though my model includes year as a random factor. Clerid trap catches did not differ significantly among treatments ($F_{1,21}$=0.28, p>0.61; (mean number of *T. undatulus* (95% CI); thinned 44 (25.0, 81.5), unthinned 36 (20.5, 64.1); Figure 2.3c) or year ($F_{1,21}$=0.48, p>0.47; whole model R^2 = 0.04). However, because *I. pini* was much more abundant in thinned stands,

the ratio of prey to predators (*I. pini* to *T. undatulus*) was significantly higher in thinned stands compared to unthinned stands (ANOVA, whole model $R^2 = 0.32$, $F_{1,21}=8.29$, $p<0.01$; (LSM ± SE); thinned 48.5 ± 9.2 *I. pini* to *T. undatulus,* unthinned 22.2 ± 9.2 *I. pini* to *T. undatulus*). The ratio of *I. pini* to clerids did not differ between years ($F_{1,21}=2.01$, $p>0.17$).

Because I detected treatment level differences in the abundance of bark beetles and their predators, I examined which stand-level factors affected the abundance of each species most strongly. To do so, I applied backwards stepwise elimination on a multiple regression model starting with treatment, volume of fresh lodgepole pine CWD/ha, stand density, percent lodgepole pine, mean maximum temperature and mean wind speed as effects. In analyses of *I. pini* abundance I also included abundance of their predators *T. undatulus*. Since most stand level effects were only measured in 2002, analyses were restricted to 2002 trap catches. All response variables were ln transformed for analyses.

Overall fewer *I. pini* were captured in stands with high tree densities ($F_{1,8}=4.73$, $p<0.062$; Figure 2.4a). Interestingly, I found more *I. pini* in stands with more predators ($F_{1,8}=7.34$, $p<0.03$; Figure 2.4b). Treatment significantly effected *I. pini* abundance, suggesting that there were some features of thinning in addition to those measured that influenced beetle abundance. *Ips pini* were more abundant in thinned stands ($F_{1,8}=11.8$, $p<0.01$; back transformed LSMs (95% CI): thinned 1230 (679, 2227), unthinned 260 (144, 472); whole model $R^2 = 0.91$).

Results were generally similar when catches of *I. pini* were divided into early and late season captures. Early emerging *I. pini* were more abundant in thinned stands

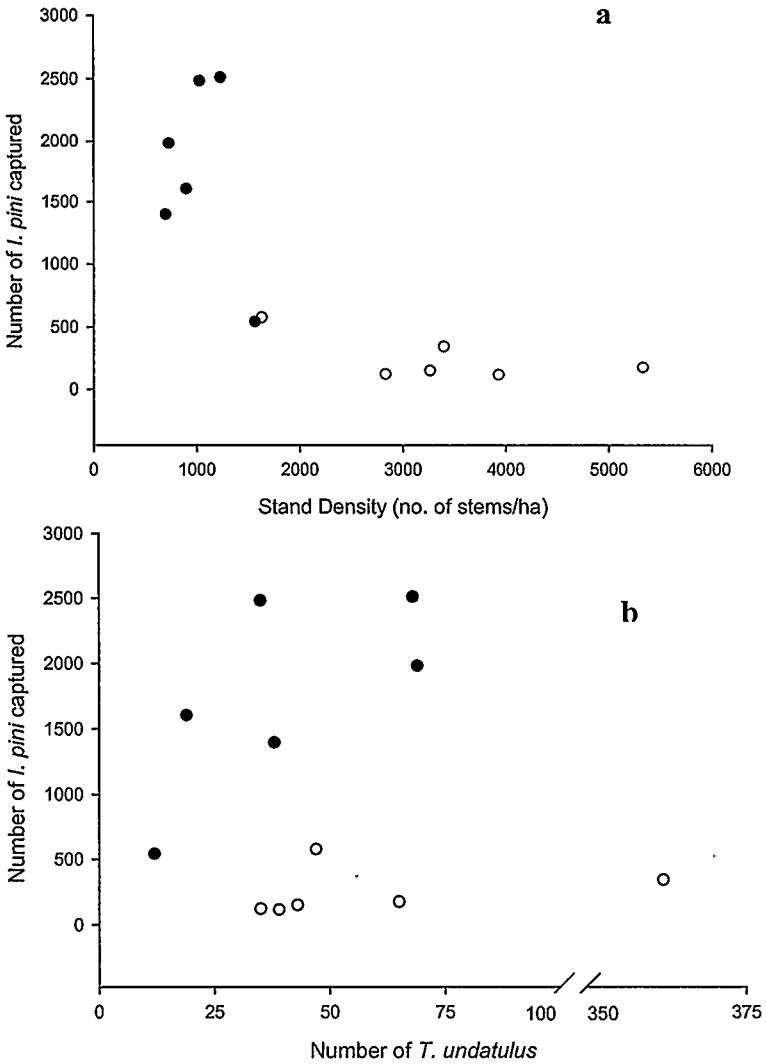

Figure 2.4. The number of *Ips pini* caught as a function of a) stand density and b) number of predators, *T. undatulus*. Shown are raw data, analyses were conducted on natural log transformed data. Open circles (⊠) represent data collected in unthinned stands and closed circles (★) are data from thinned stands.

($F_{1,7}$=94.4, p<0.0001; back transformed LSMs (95% CI): thinned 348 (190, 639), unthinned 4 (2, 7)). More *I. pini* were caught early in the season in stands with lower stand densities ($F_{1,7}$=9.69, p<0.018) and lower average maximum temperatures ($F_{1,7}$=26.2, p<0.002). More *I. pini* were caught in stands with more *T. undatulus* ($F_{1,7}$=5.71, p<0.05; whole model R^2 = 0.98). When only late season catches of *I. pini* were included in analyses, all stand characteristics were excluded from the model except treatment and number of *T. undatulus*. As in previous analyses, late season numbers of *I. pini* were greater in thinned stands ($F_{1,9}$=43.7, p<0.0001; back transformed LSMs (95% CI): thinned 1023 (614,1703), unthinned 114 (68, 189)). More *I. pini* were captured late in the season in stands with higher abundances of predators ($F_{1,9}$=7.85, p<0.021; whole model R^2 = 0.83).

Trypodendron lineatum abundance did not vary significantly with any of the continuous variables measured. It only varied with treatment (t_{10}=2.44, p<0.04, whole model R^2 = 0.37). As above, *T. lineatum* were less abundant in unthinned stands (back transformed LSMs (95% CI); thinned 25.8 (5.31, 124), unthinned 293 (61.0, 1408)).

I included abundance of *I. pini* when analysing trap catches of *Thanasimus undatulus*. Abundance of the predator *T. undatulus* did not vary significantly with any of the stand characteristics I measured. Abundance of *T. undatulus* increased with increasing *I. pini* abundance ($F_{1,9}$=5.05, p<0.06, Figure 2.4b). *T. undatulus* were more abundant in unthinned stands ($F_{1,9}$=7.63, p<0.03; back transformed LSMs (95% CI): thinned 15 (5, 42), unthinned 141 (51, 387); whole model R^2 = 0.46).

Bark beetle trap catches may be explained by their ability to detect pheromones. The results of my pheromone detection experiment indicated that a beetle's ability to

detect pheromones did not differ between thinned or unthinned stands (Figure 2.5). There was no significant difference between thinned and unthinned stands in the percentage of all *I. pini* caught in the baited traps and the corresponding inner whorl (2 m away from central baited trap; t_4=-0.560; p>0.6), or outer whorl (4 m; t_4=-0.601; p>0.5). Furthermore, there was no significant difference in the number of *I. pini* caught in the baited trap surrounded by unbaited traps, and a single baited trap (paired t-test, t_{11}=1.40, p>0.18), suggesting that the presence of the unbaited traps did not significantly impact trap catches.

Finally, to assess stand level differences in settlement densities of *I. pini* on experimental logs I used ANOVA. Male settlement density was ln transformed to meet assumptions of normality. Settlement densities of *I. pini* were greater in thinned stands than in unthinned stands ($F_{1,35}$=75.7, p<0.0001; mean males/100cm^2 (95% CI); unthinned 0.061 (-0.094, 0.242), thinned 1.76 (1.35, 2.23); Figure 2.6). In fact, only 3 out of the 24 sites in unthinned stands were colonized by *I. pini*, compared to 22 out of 24 in thinned stands. Neither stand nor the treatment origin of the log significantly affected male settlement density (both p>0.5, whole model R^2 = 0.71).

DISCUSSION

Stand Characteristics

Thinning resulted in changed both the biotic and abiotic environments even seven years post-harvest. Not surprisingly, thinned stands had significantly fewer stems per hectare after harvest (Table 2.1). As in previous studies, I found that thinned stands had higher maximum temperatures (Wickman and Torgersen 1987, Bartos and Amman 1989, Schmid *et al.* 1991, 1992a, Hindmarch and Reid 2001) and lower minimum temperatures

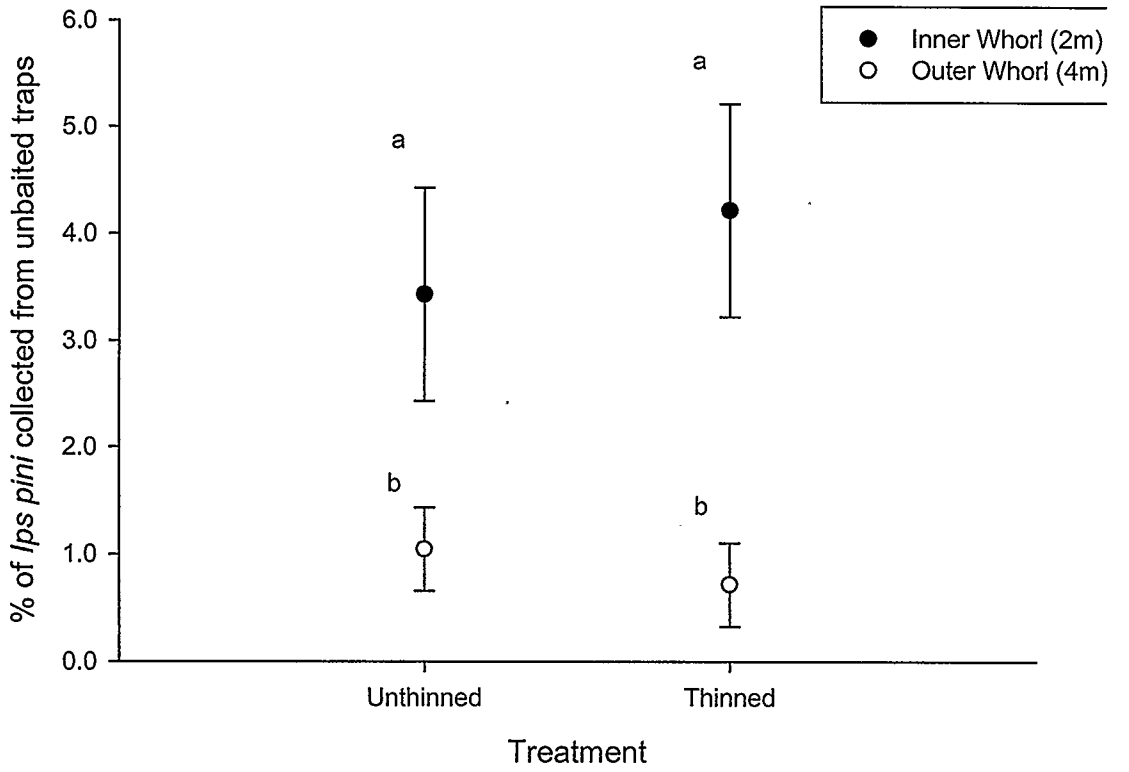

Figure 2.5. Percentage of *Ips pini* caught in unbaited Lindgren funnel traps at two distances from a centrally baited funnel trap. Means are presented ± one standard error. Similar letters indicated no significant difference between means.

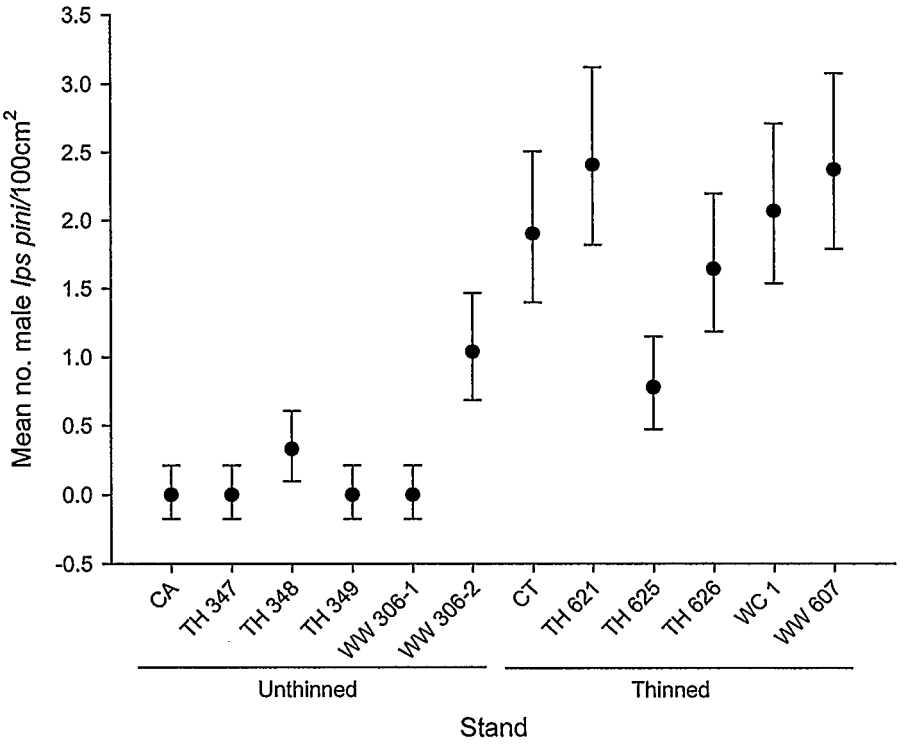

Figure 2.6. Mean (± SE) settlement density of male *Ips pini* on experimental logs for each stand. Means represent the average of four logs per stand. Data were natural log transformed for analysis. Shown are back transformed means ± one standard error.

(Bartos and Amman 1989, Schmid *et al.* 1992a, Anderson and Brower 1996) than their unthinned counterparts (Figure 2.1). Thinned stands were windier on average than unthinned stands (also see Bartos and Amman 1989, Hindmarch and Reid 2001; Figure 2.2).

Tree harvest altered stand species composition. After thinning, stands were largely dominated by lodgepole pine, with some stands having up to 98% lodgepole pine (Table 2.1). Unthinned stands included larger proportions of spruce (*Picea glauca* (Moench) Voss and *Picea mariana* (Mill.) B.S.P.), paper birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* (Michx.))

Thinned stands received more fresh coarse woody debris of lodgepole pine than in unthinned stands (Table 2.1), even seven years past initial harvest date, presumably because of the higher wind speeds. Previous work in these stands (Hindmarch and Reid 2001) found that CWD input returned to pre-harvest levels two and three years after an initial pulse resulting from logging slash left after harvest. Discrepancies may reflect sampling effort. I censussed large (ca. 1 ha) plots and usually encountered only a few (one or two) freshly fallen trees. Less effort could have easily resulted in missed debris. Composition of fresh coarse woody debris also differed between thinned and unthinned stands, with CWD in thinned stands being mainly lodgepole pine as expected given that most standing trees were lodgepole pine. Thus, in thinned stands, the combination of changes in an abiotic factor (wind speed) and the biotic landscape (species composition) caused further changes in the biotic environment, namely habitat abundance for pine-breeding beetles.

Beetle Abundance

Ips pini were more abundant in thinned stands (Figure 2.3a), as reported by a previous study in the same area (Hindmarch and Reid 2001). In fact, total trap catches of *Ips pini* during the season were an order of magnitude greater in thinned than unthinned stands even seven years after thinning. This result was evident for both early and late season trap catches (overwintered adults and current season's offspring, respectively). In addition, *I. pini* settled at higher densities on experimentally placed logs in thinned stands, with beetles failing to settle at all on most experimental habitat in unthinned stands (Figure 2.6).

As Hindmarch and Reid (2001) mentioned, differences in trap catches of *I. pini* may reflect actual differences in abundance, or differences in a beetle's ability to detect pheromones. More beetles may be caught in traps within thinned stands if beetles can detect pheromones better in thinned stands, thus increasing the effective catchment area of the trap. Results from my pheromone detection experiment suggest that there were no differences in a beetle's ability to detect pheromones in thinned stands versus unthinned stands (Figure 2.5). Thus trap catches likely reflect an actual difference in distribution, as opposed to ability to detect pheromones.

Alternatively stands may have had as many or more beetles as thinned stands, but trap catches were lower because unthinned stands contained more standing trees that absorbed these beetles. However, this alternative seems unlikely considering that *I. pini* preferentially attack horizontal stems (Seybert and Gara 1970). Furthermore, there was no evidence of widespread disease or recent catastrophic events (such as wind storms or fire) in my study sites that would typically predispose natural unmanaged stands to attack

from *I. pini* (Erbilgin *et al.* 2002). I also did not detect a difference in growth rate between the two stand types. Consequently, the number of beetles absorbed in the two stand types would correspond to the density of trees. If so, the three-fold greater density in thinned stands should have resulted in a three-fold difference in trap catches between thinned and unthinned stands. Instead, I found a six-fold difference in *I. pini* abundance in thinned stands. Moreover, throughout the course of my study I did not encounter a single successful or attempted *I. pini* attack on living trees.

Although thinning treatment had a large effect on the abundance of *I. pini* (alone it explained 67% of the variance in catches), it was not clear what mechanisms were responsible. In analyses that included individual stand characteristics (biotic and abiotic), few characteristics explained significant variation not accounted for by treatment differences, suggesting that some unmeasured component was influencing abundance. Alternatively, my measures of stand characteristics may have been too coarse to detect their effects.

Overall, my results do not clearly support the resource concentration hypothesis. Although both fresh lodgepole pine CWD and *I. pini* were more abundant in thinned stands, my analyses did not detect a significant influence of CWD on *I. pini* abundance, either during the entire season, or during both early season and late seasons. Since I measured CWD late in the season (August), I may have included habitat that was not available during beetle colonization. Nonetheless, it is likely that continued input of fresh lodgepole pine CWD in thinned stands was at least partly responsible for the persistent elevated abundance of herbivores in thinned stands. Previous research has found greater abundance of specialized insect herbivores in habitats with higher host

density (Root 1973, Risch 1981, Bach 1984, Turchin, 1987, Andow 1990, Coll and Botrell 1994, Schellhorn and Sork 1997). I predict that *I. pini* will remain more abundant in thinned stands until the trees growing in these stands become more windfirm as a result of differential growth allocation. This may take up to eight years and will depend on tree species and size (Mitchell 2000).

The effects of resource concentration may be noticeable as a response to the proportion of living lodgepole pine trees in a stand, which was greater in thinned stands than in unthinned stands. *Ips pini* may use chemical cues from living lodgepole pine trees to find areas when habitat input is most likely. In unthinned stands, chemical cues from lodgepole pine may be diluted by cues from non-host trees. Avoidance of non-host volatiles has been documented in bark beetles (Dickens *et al.* 1992, Borden *et al.* 1997, Poland *et al.* 1998, Zhang, *et al.* 1999a, b, 2001, Byers *et al.* 2000, Poland and Haack 2000, Hubner and Borden 2001) and other insects (Levinson and Hiaisch 1984, Puttick *et al.* 1988, Tingle *et al.* 1990, McNair *et al.* 2000, Bedard *et al.* 2002). However, the percentage of living lodgepole pine trees did not significantly influence variation in *I. pini* abundance. In general, the proportion of living lodgepole pine may not be a sufficiently good predictor of the availability of freshly downed trees; about 53% of the variation in density of CWD is explained by the percentage of living lodgepole pine trees alone (simple linear regression $F_{1, 10} = 11.6$, $p<0.007$). However, Park (2002) found that trap catches of *T. lineatum* correlated positively with the proportion of host trees (conifers) in the canopy.

Host quality seems unlikely to determine differences in *I. pini* abundance between thinned and unthinned stands, as I did not detect any differences in tree growth rates

between them. Thus, although I found no direct evidence for the influence of bottom-up forces on *I. pini* abundance, host availability is more likely to play a role than host quality.

The physical structure of the forest partly explained the abundance of *I. pini* (Figure 2.4a). The negative relationship between stand density and total and early season abundance of *I. pini* may result from beetles avoiding complex, cluttered habitats that are difficult to navigate during habitat search (Hindmarch and Reid 2001). *Ips pini* may avoid such habitats because they are more energetically expensive to search in (Hindmarch 1999). Avoidance of structurally complex habitats has been observed in bark beetles (Forsse and Solbreck 1985, Safranyik *et al.* 1992) and other herbivorous beetles (Risch 1981, Coll and Botrell 1994). Thus *I. pini* benefit from the abiotic changes in stands that result from thinning.

In addition to stand density, the only direct effect of abiotic conditions on *I. pini* abundance was the negative effect of high temperatures on the number of beetles caught early in the season. This effect is difficult to explain, because beetles should benefit from increased flight opportunities when searching in stands with warmer temperatures (Hindmarch and Reid 2001). Alternatively, *I. pini* may be similar to *D. ponderosae* that avoid high temperature thinned stands (Amman *et al.* 1988), trees (Schmid *et al.* 1991) or sun-exposed areas of trees (Bartos and Amman 1989, Bartos and Booth 1994).

Effects of stand characteristics may have gone undetected because beetle abundance reflects the conditions over many years. Although stand characteristics should correlate highly among years, there might be enough variation and/or a lack of statistical power to detect their effects. Typically, insects are more likely to colonize, and less

likely to leave, concentrated patches of host plants (Risch, 1981, Bach 1984, Andow 1990, Coll and Botrell 1994). If input of CWD is consistent across years in thinned stands, most *I. pini* will likely emerge in thinned stands to a renewed input of freshly fallen trees. Beetles may remain in such patches of concentrated habitat to search for breeding substrate. The low trap catches and settlement densities that I observed in unthinned stands in the absence of differences in pheromone detection may reflect the fact that beetles that emerge in thinned stands tend to concentrate their habitat search in those stands. Although flight mills and mark-and-recapture experiments demonstrate that bark beetles can fly long distances (kms) during habitat search (Forsse and Solbreck 1985, Safranyik *et al.* 1992), most beetles are recaptured close (<100m) to the release point (Safranyik *et al.* 1992, Zumr 1992, Duelli *et al.* 1997). It is possible that very few beetles leave thinned stands when searching for new breeding substrates.

Bark beetle attraction of conspecifics and mates may also be enhanced in thinned stands through greater dispersal and consistency of pheromone plumes (Fares *et al.* 1980, Elkinton *et al.* 1987). Turchin (1987b) showed that aggregative movement (such as that seen in bark beetles) can amplify the response of insects to resource concentration. However, I did not detect differences in pheromone detection ability between thinned and unthinned stands.

The influence of top-down mechanisms on *I. pini* abundance is not clear. I found that the ratio of prey to predators was much greater in thinned stands. However, there was no numerical response of predators (*T. undatulus*) to increased prey (*I. pini*) abundance in thinned stands (Figure 2.3c). Schroeder (1999) also did not detect a numerical response of clerid predators to increased bark beetle density after thinning.

Because the study only examines response of predators two years after thinning, Schroeder (1999) suggests that clerid abundance would not increase until the following year because of their longer development time. However, my data suggest that there is no numerical response of predators even seven years after harvest, despite continued high prey populations. One explanation may be that my measure of clerid abundance (numbers caught in pheromone baited traps) does not accurately reflect predator distributions. Clerid beetles are larger than *I. pini* and have greater dispersal ability (Cronin *et al.* 2000). Thus, clerids may respond to pheromone traps in unthinned stands, even if they may not naturally occur there at such high numbers. Similarly, Erbilgin *et al.* (2002) found that predators were more abundant in stands that often contained lower numbers of *I. pini* as opposed to stands where trees where more susceptible to attack. They speculated that this effect may be driven by the availability of alternate prey, which in turn may be determined by habitat diversity (Root 1973) or more favourable environmental conditions, both of which may also be applicable in my system.

Total, early and late season trap catches of *I. pini* in 2002 were all greater in stands with higher predator abundance (Figure 2.4b). Combined with the increased ratio of prey to predators in thinned stands this may indicate a decelerating functional response between *I. pini* and the predator *T. undatulus,* such that at high densities of *I. pini* (such as those seen in thinned stands), predators become satiated and the per capita mortality rate of *I. pini* is reduced. Similarly, Reeve (1997) suggests that attack rates of clerid predators decline when bark beetle densities are high. Nonetheless, predator abundance may not yield an accurate estimate of mortality due to predators (Russell 1989, Andow 1990). A more convincing test of the importance of natural enemies would include direct

measures of *I. pini* mortality from *T. undatulus* predation. Thus, whether or not, and to what extent, reduced predation pressure in thinned stands results in increased populations of *I. pini* is uncertain.

In contrast to *I. pini*, abundance of *Trypodendron lineatum* was significantly greater in unthinned stands than in thinned stands (Figure 2.3b). The only variable that explained significant variation in *T. lineatum* abundance was treatment. That input of fresh lodgepole pine CWD fell out of the model is not surprising, as *T. lineatum* usually prefer debris between six months and two years old (Dyer and Chapman 1965, Bright 1976). In addition, *T. lineatum* is a conifer generalist (Bright 1976). Thus, their abundance may not be tightly linked to input of fresh lodgepole pine debris. A similar inability to explain variation in *T. lineatum* abundance with habitat variables was observed by Peltonen *et al.* (1998), who concluded that the distribution of these beetles might be governed by other factor, because they depend on an ambrosia fungus to survive. Other factors not measured, which also might change after thinning may be more important for successful fungus cultivation, such as humidity.

Interestingly, both Park (2002) and Hindmarch and Reid (2001) found consistently higher numbers of *T. lineatum* in thinned stands for all years up to two and three years after thinning harvest, respectively. Abundance of *T. lineatum* correlated positively with availability of conifer stumps (Park 2002) or wind speed (Hindmarch and Reid 2001) in a harvested landscape. It seems likely that *T. lineatum* became concentrated in thinned stands for up to three years after thinning in response to the increased availability of conifer stumps and logging slash in thinned stands of suitable age for the growth of ambrosia fungus. However, as years passed slash and stumps left

behind after logging became unsuitable for *T. lineatum* colonization (Dyer and Chapman 1965, Bright 1976). The opposing conclusions regarding thinning effects between the current study and Park (2002) and Hindmarch and Reid (2001) highlight the importance of long-term studies of forest management practices.

The results for *I. pini,* but not *T. lineatum*, contrast with those obtained from *Dendroctonus ponderosae* in response to thinning. Stand thinning is used to protect stands against aggressive, tree-killing species such as *D. ponderosae* (Amman *et al.* 1988, Bartos and Amman 1989, Schmid *et al.* 1991). The success of this technique has been attributed to changes in microclimate (Amman *et al.* 1988, Bartos and Amman 1989, Schmid *et al.* 1991, Bartos and Booth 1994), such as observed in this study, or changes that may influence pheromone communication (e.g. Schmid *et al.* 1992b) (not detected in the current study). The opposing effects of thinning on *I. pini* versus *D. ponderosae* suggest that mechanisms inferred from differences in stand conditions between thinned and unthinned stands must be viewed with caution. Improvements in tree vigour after stand thinning, another explanation for the success of thinning in deterring *D. ponderosae*, could explain the contrasting results for *D. ponderosae* and *I. pini.* Whereas tree vigour can be detrimental to beetles that attack live trees (e.g. *D. ponderosae*; Larson *et al.* 1983, Mitchell *et al.* 1983, Waring and Pitman, 1985), improved vigour may promote reproductive success of *I. pini* that breed in those trees after felling (Reid and Robb 1999). However, I did not detect any treatment level effects on tree vigour after thinning.

In the managed lodgepole pine forest ecosystem, changes to the abiotic and biotic environment that result from stand thinning affect members of the insect community

differently. *Ips pini*, a specialist herbivore on lodgepole pine, were more abundant in thinned stands up to seven years after harvest. This abundance seems likely to be a result of increased host availability in thinned stands (a bottom up effect driven by abiotic changes after thinning) and a decrease in predation pressure (a top-down influence). Previous studies have also found *I. pini* populations to be jointly affected by habitat quantity and predation (Erbilgin *et al.* 2002). Changes in the physical structure of the forest also benefited *I. pini*, possibly facilitating habitat search. The conifer generalist, *T. lineatum*, is initially more abundant in thinned stands, likely in response to increased habitat input. However, several years after thinning, *T. lineatum* abundance declined as logging debris became unsuitable for colonization, and they were eventually more abundant in unthinned stands. Abundance of the scolytid predator, *T. undatulus,* remained largely unchanged as a result of thinning. Predator-prey relationships were altered as a result. Unfortunately, generalizations about the effects of thinning on even ecologically-similar insects remain elusive, even when the species' natural histories are quite well known. This is an important cautionary conclusion, because the results from a single well-studied species may lead to over-confidence in the importance of proposed processes. My study links the long-term effects of forest management to increased abundance of a forest herbivore that is known to cause negative economic impacts when population sizes are high (Schenk and Benjamin 1969, Gara *et al.* 1999). Although forest management may be a successful tool for controlling some species of bark beetles (Amman *et al.* 1988, Bartos and Amman 1989, Schmid *et al.* 1991), even closely related species may respond quite differently to the same management regime. The

consequences of increased abundance of *I. pini* should be considered when thinning the forest.

CHAPTER 3: CONSEQUENCES OF FOREST THINNING ON TREES, BARK BEETLE COLONIZATION AND REPRODUCTION

INTRODUCTION

The implications of anthropogenic disturbance for plant-insect interactions remain largely unknown, despite the ecological and economic significance of these relationships. Herbivore performance is tightly linked to host-plant physiology (White 1984, Lorio 1993): insects consume plant tissue as a means of acquiring nutrients for growth and reproduction, while plants deter herbivores with an array of structural and chemical defences. Host plant quality depends upon the availability of resources and the allocation strategy of the plant. Plants may respond to environmental changes by altering the allocation of resources between growth and defence (Bryant *et al.* 1983, Herms and Mattson 1992). Insects may therefore be influenced indirectly by environmental change through changes in the quality of their host.

Two main hypotheses have been proposed to explain allocation strategies by plants to growth and defence in response to resource availability. The carbon-nutrient balance (CNB) hypothesis (Bryant *et al.* 1983) and the growth-differentiation balance (GDB) hypothesis (Herms and Mattson 1992) similarly predict that if nutrients are limited, but photosynthesis is not, then synthesis of carbon-based secondary compounds is favoured. However if nutrients are abundant and growth is favoured, less effort should be expended on carbon-based defensive metabolites. These two hypotheses have received empirical support (reviewed in Koricheva *et al.* 1998a). However, allocation of resources to specific defensive compounds may not be governed by such a simple trade-

off (Koricheva *et al.* 1998a). Because herbivores tend to be most affected by a single compound or group of closely related compounds, compound-specific responses make it difficult to predict the consequence of changing resource availability for phytophagous insects (Koricheva *et al.* 1998a, Hemming and Lindroth 1999). However, if increases in resource availability increase allocation to defence, herbivores should pay a cost when consuming these tissues.

Resource availability may affect plant nutrients as well as defences. The plant-stress hypothesis proposes that herbivores benefit from feeding on stressed or senescing plants or plant parts, because stress increases the availability of nitrogen, which is limiting to herbivores (White 1984). In contrast, the plant-vigour hypothesis predicts enhanced performance of certain herbivore species when feeding on the fastest growing or largest plants or modules in a population (Price 1991). Herbivores should benefit from feeding on vigorously growing tissue because it is more likely to regenerate and maintain resource availability and less likely to contain defences (Price 1991). Both of these hypotheses have received empirical support (Price 1991, Koricheva *et al.* 1998b), and therefore neither is sufficient to explain the performance of all herbivorous insects. Rather, feeding guild may best determine insect performance on host plants of varying condition (Koricheva *et al.* 1998b), for reasons that are still unclear.

Forest management is an anthropogenic disturbance that could impact forest herbivores through changes to tree physiology. In particular, forest thinning is an increasingly common means of managing forest productivity, yet the significance of this management strategy for plant-insect interactions remains largely unknown (Sougavinski and Doyon 2002). Predictions about these interactions can be derived from the plant

allocation hypotheses discussed above. Thinning increases light, water and nutrient availability to remaining plants (Goodell 1952, Donner and Running 1986). According to the CNB and GDB hypotheses, trees remaining in a stand after thinning would allocate more resources towards growth and less towards carbon-based defensive compounds than trees growing in unthinned stands. However, the increase in light availability may further increase the total carbon resources available for allocation. Overcrowding in forest stands reduces production of defensive compounds, suggesting that thinning could improve tree defence status (Waring 1983, Brown *et al.* 1987, Christiansen *et al.* 1987). Thus, due to an increase in the total resource budget, there may be a simultaneous increase in growth and defence after thinning (Hemming and Lindroth 1999).

Most previous studies document the thinning response of young coniferous stands (< 40 yrs old; e.g. Harrington and Weirman 1990, Entry *et al.* 1991, Barbour *et al.* 1992, Mitchell *et al.* 1996, Tasissa and Burkhart 1997, Kimball *et al.* 1998) or young plantations (e.g. Matson *et al.* 1987, Velaquez-Martinez *et al.* 1992, Sheriff 1996) in temperate zones. All of the studies that monitored both growth and defence, found that thinning typically increased both some index of growth and carbon-based secondary compounds (Entry *et al.* 1991, Matson *et al.* 1987, Kimball *et al.* 1998). In mature, naturally regenerated stands, several studies have found increased growth and vigour after thinning (Mitchell *et al.* 1983, Larson *et al.* 1983, Waring and Pitman 1985, Fiddler *et al.* 1989). Fewer studies have measured both growth and defences in mature trees, and those that have done so have found conflicting results. In mature ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.), decreases in stand basal area resulting from thinning were associated with enhanced resin response, thicker phloem, higher foliar

nitrogen content (Kolb *et al.* 1998) and enhanced growth and a reduction in mortality from disease (Fiddler and Fiddler 1989). However, one and two years after thinning foliar sugars increased and monoterpenes declined in mature balsam fir (*Abies balsamea* (L.)) (Bauce 1996).

Coniferous trees in boreal forests may respond more strongly to thinning than species in more temperate regions, because they are particularly nitrogen limited (Bryant *et al.* 1983, Yang 1998). Forty-five year old Scots pine (*Pinus sylvestris* L.) in northern Sweden grew more after thinning, with thinned trees allocating more growth towards the lower bole (Valinger 1992, 1993). Semi-mature lodgepole pine trees (*Pinus contorta* var. *latifolia* Engelm.) in northern Alberta also grew faster after thinning (Yang 1998). Although the previous studies did not measure allocation to defensive compounds, there is some evidence that thinning of mature stands can improve tree condition and enhance production of defence compounds (Lorio 1993).

The response of forest herbivores to thinning has received limited attention. As discussed above, hypotheses predict all combinations of changes in defence and nutrient content of plants in response to increased resources associated with thinning. Thinning did not alter biomass or density of western spruce budworm (*Choristoneura occidentalis* Freeman) feeding on mature grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.) during the succeeding four years (Mason *et al.* 1992). However, when feeding on balsam fir immediately after thinning, spruce budworm developed faster and consumed more foliage (Bauce 1996). Conversely, thinning has been used to deter mountain pine beetle (*Dendroctonus ponderosae* Hopkins) based on a presumed increase in tree defences; increases in induced resin responses have been observed (Larsson *et al.* 1983, Mitchell *et*

al. 1983, Waring and Pitman 1985). However, microclimate changes may be more important than tree vigour alterations in deterring beetle attack in thinned stands (Amman *et al.* 1988, Bartos and Amman 1989).

To understand better the complex chain of interactions that result from a reduction in stand density, I investigated the effects of the thinning of mature lodgepole pine forests on selected tree characteristics and their subsequent effects on reproductive traits in a secondary bark beetle species, *Ips pini* (Say). *Ips pini* typically breed in the phloem of freshly dead pine trees. Koricheva *et al.* (1998b) determined that boring insects, such as bark beetles, perform best when feeding on stressed hosts. Bark beetles that attack live trees benefit from reduced induced defences resulting from low host vigour (Larson *et al.* 1983, Hard 1985, Waring and Pitman, 1985, Shroeder 1987). However, *I. pini* typically colonize dead trees, so Reid and Robb (1999) and Reid and Glubish (2001) suggested they may benefit from breeding in trees that grew vigorously before they died. Nonetheless, the constitutive defences that remain in the tissue of dead trees may affect *I. pini* negatively. In general, bark beetles benefit reproductively from breeding in thicker phloem (Haack *et al.* 1985, 1987a, b, Amman and Pasek 1986) or more nutritious phloem (Popp *et al.* 1989). Several species of bark beetle attack the largest trees in a population preferentially, presumably because they have thicker phloem (Hard 1985, Annila and Heikkila 1991, Preisler and Mitchell 1993, Reid and Glubish 2001). Thus, breeding in trees from thinned stands could benefit *I. pini,* if the trees in these stands are growing faster, or if their tissues are more nutritious because of increased nutrient availability. In contrast, thinning will hinder *I. pini* performance if trees in thinned stands show a

concomitant increase in secondary defensive compounds (Larsson *et al.* 1983, Mitchell *et al.* 1983, Waring and Pitman 1985).

METHODS

Study System

This study was conducted during 2001 and 2002 in a forest management area in the boreal forest near Whitecourt, Alberta (54°N, 115°W). I chose six pairs of thinned and unthinned lodgepole pine stands. Average age of trees in these stands was approximately 100 yrs. *Ips pini* is the most common bark beetle in this system. Refer to Chapter 1 for a complete description of the study area and the breeding biology of *I. pini.*

To test for differences in beetle colonization and reproduction among trees from thinned and unthinned stands, I felled two trees in each of the 6 thinned stands and 6 unthinned stands during each year (a total of four trees per stand). Trees were felled before beetles emerged in spring (9 May 2001 and 16 May 2002). Trees were chosen to reflect the average diameter at breast height (DBH) of their source stand during 2001. As a consequence, all trees in thinned stands had larger diameters than those in unthinned stands. During 2002, trees were randomly selected from the same DBH range (16.0-21.0 cm) for both stand types. Logs from all trees felled within a pair of stands were moved to randomly selected sites in the thinned stand to measure colonization and reproduction as a function of tree origin (see below).

Tree Quality

I quantified the quality of my experimental trees using several different measures. For each experimental tree, I measured DBH. During 2001, I collected phloem samples

from all trees at breast height for nitrogen analyses. A 10 x 10 cm piece of phloem was sampled at the beginning of the beetle colonization period. Phloem samples were collected by cutting a $100cm^2$ area in the bole of an experimental tree with a pocketknife. The phloem and outer bark were peeled away from the hardwood, usually in one continuous piece. I removed the phloem from the outer bark by separating the two at the edge of the sample and peeling the phloem away from the bark along the length of the sample. This technique resulted in strips of phloem tissue completely separated from the outer bark. I immediately placed phloem samples from each individual in sealed plastic bags and stored on dry ice until they were returned to the lab and stored at -70°C. Total Kjeldahl nitrogen content was determined using micro-Kjeldahl digestion (Etherington and Morrey 1967).

I measured phloem thickness and growth rates of each tree from cross-sectional disks cut from the trees. During 2001, two disks were cut from each tree, one disk was cut near the base of the tree (approx. 1 m above ground level), immediately below the first experimental log and the second disk was cut approx. 6 m above ground level. Both disks were analyzed to determine whether the measurement differed significantly with height on the bole. During 2002, only one disk was cut, approximately 4 m above ground level. I quantified growth rates by measuring the growth rings for eight years; four years before thinning (1992-1995) and four years after thinning (1997-2000) under a dissecting microscope fitted with an ocular micrometer at 20x magnification. Trees felled from one stand (WW 607) were omitted from analysis of cumulative growth rates after thinning because this stand was thinned only two years prior to the start of the study. Rings were measured at four locations per disk and averaged to obtain an estimate of growth rate.

For analyses of beetle colonization and reproductive characteristics, I chose to use the last year's growth rate, because it will most closely reflect the conditions that the beetles experienced. Phloem thickness was measured in the same way as growth rate.

At the start of beetle settlement during 2002 I measured the phloem moisture content of each experimental tree. A $30cm^2$ piece of phloem was sampled from each tree on 19 June, and promptly placed in an individual sealed plastic bag. I collected phloem samples using the same technique as during 2001 when I collected phloem samples for nitrogen analysis. Phloem samples were stored at -4°C. To analyse phloem moisture content, samples were thawed to room temperature and weighed on a microbalance to the nearest $10^{-5}g$. Samples were then dried at 63 °C for 24 h and reweighed. The difference between the two masses was expressed over the mass of the dry phloem to get phloem moisture content per gram of dry phloem.

I was unable to measure constitutive defence content of phloem from my experimental trees. Analysis of secondary compounds was attempted on the phloem samples I collected for analysis of nitrogen, but technical problems prevented quantitative measurement.

Colonization and Reproduction

Each experimental tree was partitioned into three logs during 2001 and five logs during 2002 (four for beetle colonization and one to measure changes in phloem moisture), each 75 cm in length, starting 1 m from the base. For each pair of stands (one thinned and one unthinned stand), the logs from each tree were moved to randomly chosen sites within the thinned stand for beetle colonization, because *I. pini* rarely colonize logs in unthinned stands (Chapter 2). Sites were chosen randomly from a

predetermined collection of potential sites that were shaded from the midday sun and were more than 50 m from the stand edge. The logs from each tree were placed end-to-end at one of the sites surrounded by branches from the same tree. Each of the sites consisted of three logs during 2001 and four logs during 2002. All of the logs at each site were from the same tree. Thus two sites in each stand originated from the trees felled in the thinned stands, and the other two sites originated from trees felled in the unthinned stand.

Beetles were allowed to colonize each log site naturally. However, during 2002 colonization rates of experimental sites were low, so I baited sites that remained uncolonized after 30 days with *I. pini* pheromones (ipsdienol; released at 110 *u*g/day and lanierone; 10 *u*g/day) for 24 h. Sites were monitored every three days for evidence of new beetle attacks. When colonizing trees, male bark beetles leave distinctive frass piles above the opening to their nuptial chambers. These frass piles were used to indicate new male colonization, and each new male's burrow was marked with a numbered pushpin. I recorded the total number of males per log and when each individual male colonized.

Tree origin might affect the quality of colonizing beetles. To assess this, during 2002, two logs from each site were placed in emergence cages once colonization was complete. These cages allowed me to collect parents as they emerged from the log. Emergence cages were checked every three to seven days (depending on how many beetles were emerging) and beetles were collected and stored at –4°C. On 15 September 2002, logs were removed from field emergence cages and transferred back to the laboratory and stored at -15°C for 10 days to arrest beetle emergence. I excavated all remaining beetles from the phloem by removing the bark from each log. In the

laboratory, all beetles were then sexed and classified as either parent or offspring, based on emergence time and degree of sclerotization. As an index of quality, I measured the pronotal width across the widest part of the pronotum for 20 parental *I. pini* of each sex from each tree. For trees from which more that 20 male or female parents were collected, the earliest individuals to emerge were selected for measurement. For some trees with low colonization densities, I was unable to collect 20 members of each sex, therefore data were collected from all available parental beetles.

During both study years, I randomly selected one log from each site to measure reproductive traits. Male density was determined during 2001 by averaging the number of males on three 10x10 cm areas randomly chosen from the colonized surface of a given log. During 2002, I counted all males that number colonized a given log and divided that by the total surface area of the log that was available for colonization.

Once egg laying was complete (approx. 4 weeks after the peak colonization bout), beetle locations were mapped and the bark was removed from one experimental log per site. Reproductive characteristics were measured from a total of 15 complete gallery systems per log. If a log had fewer than 15 complete gallery systems, I excavated additional galleries on other logs from the same site. I measured the following reproductive and colonization characteristics of beetles on each tree: date of male colonization, male density/100 cm^2, harem size (number of females/male), total gallery length, pre-egg gallery length, number of egg niches and male clutch size (the sum of the egg niches from all females associated with a given male).

Because *Ips pini* is a polygynous species, female reproductive characteristics were analysed by considering the average responses of all females in the harem, and the

responses of the first and last female to join a male separately. However, because the first female to join a male should be most affected by the characteristics of the tree in which she is bred and least susceptible to the negative effects of crowding and reduced paternal care as more females join the harem, I present only data from these analyses. I determined the order in which females joined a male based on egg gallery length. The female with the longest gallery was assumed to have arrived first (reviewed in Kirkendall 1983).

Analyses

Data were analysed using the JMP IN version 4.0 computer package (SAS Institute, 2001). If necessary, data were transformed to meet the assumptions of normality and heteroscadacity following examination of residuals. A type I error rate of 0.05 was used for all tests. When tests included random factors, a restricted maximum likelihood method was employed for estimating mean squares (unless otherwise noted). All means are presented $\pm$ one standard error unless otherwise indicated. First-order interactions that tested biologically relevant predictions were included in initial models and eliminated with backwards stepwise regression if $p>0.05$ or if variance inflation factors >10.

RESULTS

Tree Quality

During 2001 I felled experimental trees to reflect the average DBH of a stand, and thinned stands had trees with larger average DBH than unthinned stands (ANOVA $p<0.0001$, Table 3.1). DBH also differed among stands within treatments ($F_{10, 12}=15.3$,

Table 3.1. Mean (± SE) tree characteristics measured.

Tree Characteristic	Year	Least Squared Means ± SE		Test Statistic
		Thinned	Unthinned	
DBH (cm)	2001	21.1 ± 0.16*	19.0 ± 0.16*	$F_{1, 12}$=85.4
	2002	18.4 ± 0.37	17.8 ± 0.37	$F_{1, 12}$=1.40
Phloem Nitrogen Content (% Total Kjeldahl Nitrogen)	2001	0.26 ± 0.04*	0.44 ± 0.04*	$F_{1, 9}$=6.3
Phloem Thickness (mm)	2001 and 2002	0.64 ± 0.03*	0.76 ± 0.03*	$F_{1,34}$=6.9
Sum of four years growth after thinning (mm)	2001 and 2002	1.51 ± 0.003	1.40 ± 0.003	$F_{1,30}$=0.34
Phloem Moisture Content (g moisture/g dry phloem)	2002	1.33 ± 0.15	1.38 ± 0.15	$F_{1, 11}$=0.05

* indicates means are significantly different $p<0.05$

$p<0.0001$; whole model $R^2=0.95$). To avoid this potentially confounding factor during 2002, trees were randomly chosen from the same range of diameters for all stands. Therefore during 2002, DBH did not differ between treatments or among stands within treatments ($p>0.25$ and $F_{10, 12}=0.58$, $p>0.79$, respectively; whole model $R^2=0.38$; Table 3.1).

To determine differences in nitrogen content between treatments and among trees in 2001, I used ANCOVA including the following variables. Trees from unthinned stands had significantly higher nitrogen content than those in unthinned stands ($p<0.034$; Table 3.1). Nitrogen content also varied significantly among stands within treatments ($F_{10, 9}=4.9$, $p<0.013$; whole model $R^2=0.89$). In addition, nitrogen content increased with DBH ($F_{1, 9}=5.5$, $p<0.044$) and decreased with phloem thickness ($F_{1, 9}=9.5$, $p<0.014$), but did not vary with growth rate during the preceding four years ($F_{1, 9}=4.4$, $p>0.064$).

Variation in phloem thickness was analysed by ANCOVA. I used the traditional method for estimating mean squares instead of the REML procedure because iterations did not converge. Trees from unthinned stands had significantly thicker phloem ($p<0.02$; Table 3.1). Phloem thickness did not differ between years ($F_{1,34}=0.99$, $p>0.32$). However there was a significant positive correlation between phloem thickness and DBH ($F_{1,34}=12.7$, $p<0.002$), and phloem thickness differed significantly between stands within treatments ($F_{1,34}=2.7$, $p<0.02$; whole model $R^2=0.53$).

To test for differences in moisture content from phloem sampled early during the season, I used ANCOVA. Moisture content of phloem sampled during peak beetle settlement did not differ between treatments (ANCOVA $F_{1, 11}=0.05$, $p>0.81$; Table 3.1) or

stands within treatments ($F_{10, 11}$=0.39, p>0.92) and did not covary significantly with DBH ($F_{1, 11}$=0.05, p>0.82; whole model R^2=0.27).

I used an ANCOVA to determine whether mean cumulative growth rate for four years after thinning varied among treatments. Again, the iterations of the restricted maximum likelihood method did not converge, therefore the traditional estimated mean squares method was employed. Growth rates did not differ significantly between treatments (p>0.56, Table 3.1), between stands within treatments ($F_{9,30}$=1.56, p>0.17), or between years ($F_{1,30}$=0.02, p>0.87). The growth rate of trees during the four years after thinning was positively correlated with their growth rate during the four years before thinning (R^2=0.80, $F_{1,30}$=34.3, p<0.0001), but not related to DBH ($F_{1,30}$=1.47, p>0.23). These conclusions were also obtained in analyses that examined each year since thinning individually, indicating that there was neither a transient nor a lagged response to thinning.

Growth rate for four years before thinning did not differ between treatments (ANCOVA $F_{1,34}$=1.9, p>0.17), stands ($F_{10,34}$=1.2, p>0.32) or years ($F_{1,34}$=0.4, p>0.54). However, larger diameter trees tended to have higher growth rates before thinning ($F_{1,34}$=8.8, p<0.01; whole model R^2=0.49).

Quality of Parental Beetles

To determine the effects of tree origin on quality of colonizing parents during 2002, I analysed the size of 20 individuals of each sex with ANOVA. Because of low colonization success of some sites, I was not able to include stand as a variable in the statistical model because the experiment was not fully crossed. Size of male parents did not differ between treatments ($F_{1,12}$ = 2.65, p>0.12) or trees ($F_{12, 236}$ =0.82, p>0.63, whole

model R^2=0.06). Similarly there was no difference in the size of female parents between trees originating from different treatments ($F_{1,12}$=2.70, p>0.12), nor did female size differ between trees ($F_{12, 263}$=0.07, p>0.99, whole model R^2=0.01).

To determine whether individual tree and colonization characteristics influence parental quality I used ANCOVA including treatment origin, tree diameter, phloem moisture content, phloem thickness, last year's growth rate, male colonization density, average date of male colonization, average harem size per male and the date of collection, again excluding stand from analysis. I chose to use the last year's growth rate for analysis of colonization and reproductive traits because it will reflect most closely the current conditions that the beetles experienced. Males that settled earlier tended to be larger ($F_{1, 240}$=6.42, p<0.02; whole model R^2=0.06). Tree and colonization characteristics did not affect the size of either male or female parents significantly (all p>0.05). The influences of tree and stand characteristics on offspring size are presented in Chapter 4.

Beetle Colonization

To determine whether a tree's treatment origin affected colonization densities of male *I. pini*, I examined the data from 2001 and 2002 separately because of sparse colonization during 2002 (see below). During 2001, male density did not vary significantly with treatment origin ($F_{1,12}$=0.009, p>0.92; Figure 3.1a), the stand a tree was located, ($F_{5,12}$=0.99, p>0.46), or their interaction ($F_{5,12}$=1.86, p>0.17; whole model R^2=0.54). Based on backwards-stepwise regression, treatment origin, stand, nitrogen content, DBH, last year's growth rate, and average date of colonization did not affect colonization density significantly (whole model R^2=0.18).

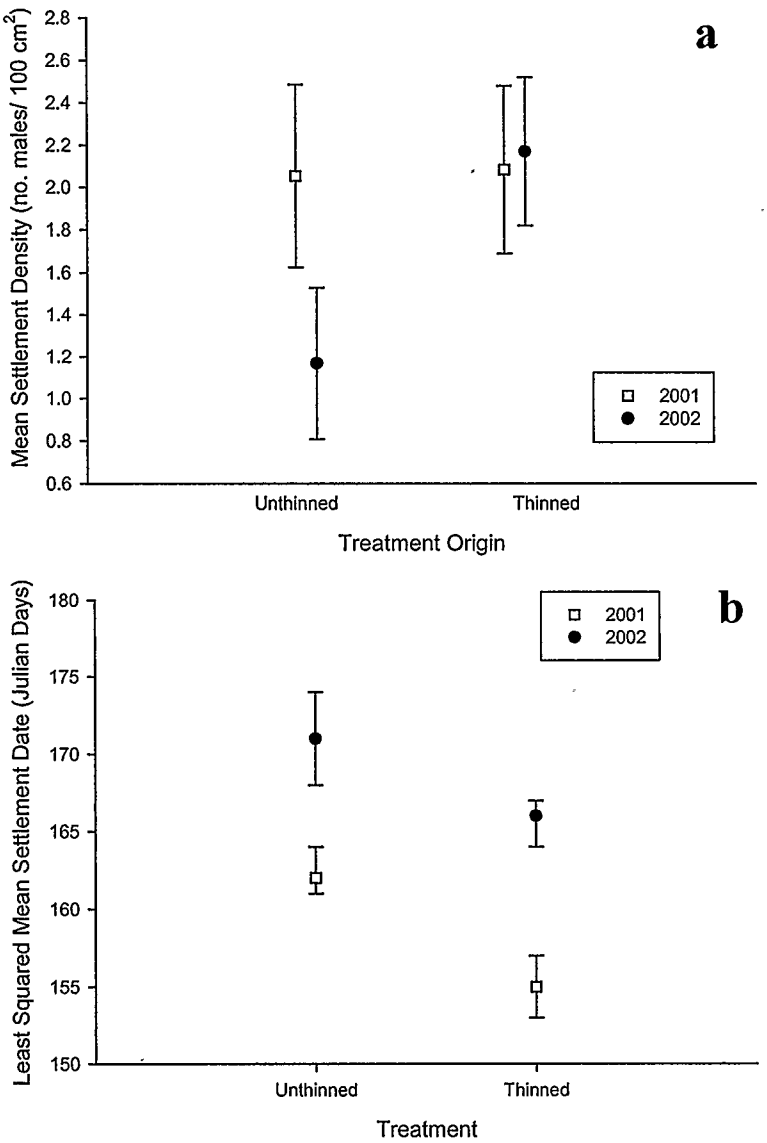

Figure 3.1. Male *I. pini* colonization characteristics. a) Average male *I. pini* colonization density for both study years. Means are presented ± one standard error. b) Least squared mean colonization date (w/ 95% CI) in both study years. See Results for statistical model.

The 2002 colonization period was characterized by low colonization by *I. pini* on experimental trees: only two-thirds (16/24) of my sites were colonized by *I. pini*. Another secondary species of bark beetle, *Polygraphus rufipennis*, colonized the remaining sites, and shared one site with *I. pini*. I used chi-square to test for differences in whether trees originating from thinned or unthinned stands were settled by *I. pini* or not. Although the differences were not significant, more trees originating from thinned stands (83% of 12 trees) were settled by pine engravers than in trees from unthinned stands (50% of 12 trees) (χ^2_{22}=3.10, p<0.078). This trend is supported by an ANOVA on all experimental trees in 2002 examining male *I. pini* colonization density as a function of stand, treatment origin and their interaction as variables. Males settled at significantly higher densities in trees originating from thinned stands ($F_{1,12}$=5.4, p<0.04; whole model R^2=0.60, Figure 3.1a).It was not possible to run the ANOVA analyses including stand, treatment and their interaction on male colonization densities when trees that were not colonized are excluded from analyses because of the incomplete data.

The low colonization of experimental trees during 2002 reduced statistical power. Therefore to test for causes of variation in colonization density among trees, I used a backwards elimination process on an original ANCOVA model including stand, treatment origin, DBH, phloem moisture content, last year's growth rate and phloem thickness. When analysing all trees including those not colonized by pine engravers (n=24), trees originating from thinned stands were colonized at higher densities than those originating from unthinned stands ($F_{1,15}$=8.1, p<0.013). Colonization density did not differ between stands ($F_{5,15}$=1.7, p>0.20). Males settled at higher densities on trees with higher recent growth rates ($F_{1,15}$=4.8, p<0.05) and thicker phloem ($F_{1,15}$=5.3,

$p<0.036$, whole model $R^2=0.55$, Figure 3.2). When I focused my analysis of male colonization density on only those 16 trees colonized by *I. pini*, no continuous variable was significant and all were removed from the model. Treatment origin and stand remained non-significant in the final analysis (stand $F_{5,9}=0.32$, $p>0.88$, treatment origin $F_{1,9}=0.63$, $p>0.44$, whole model $R^2=0.23$).

The effects of treatment origin of trees on colonization characteristics of individual male *I. pini* were analysed using two statistical models. The first model examined the effect of treatment origin on beetle colonization or reproduction controlling for stand and site (nested within treatment origin and stand as a random variable). Second, to examine the effect of specific tree characteristics on reproductive characteristics, I used a statistical model that removed the site variable and included tree characteristics (DBH, phloem nitrogen content, phloem thickness, last year's growth rate) and male colonization density, in addition to treatment origin and stand. I could not include the interaction between stand and treatment origin in this model because it caused variance inflation factor values to exceed 10. Other colonization characteristics were added to specific models as appropriate.

Low colonization rates in 2002 restricted analyses of individual male and female colonization and reproductive characteristics. Because *I. pini* colonized only 16 of 24 trees, the first model that was used to analyse treatment origin effects in 2001 (with site as a random variable) could not be used. Therefore only ANCOVA models similar to the second model used on 2001 data, which blocked for stand and treatment origin effects and included several appropriate continuous variables were employed.

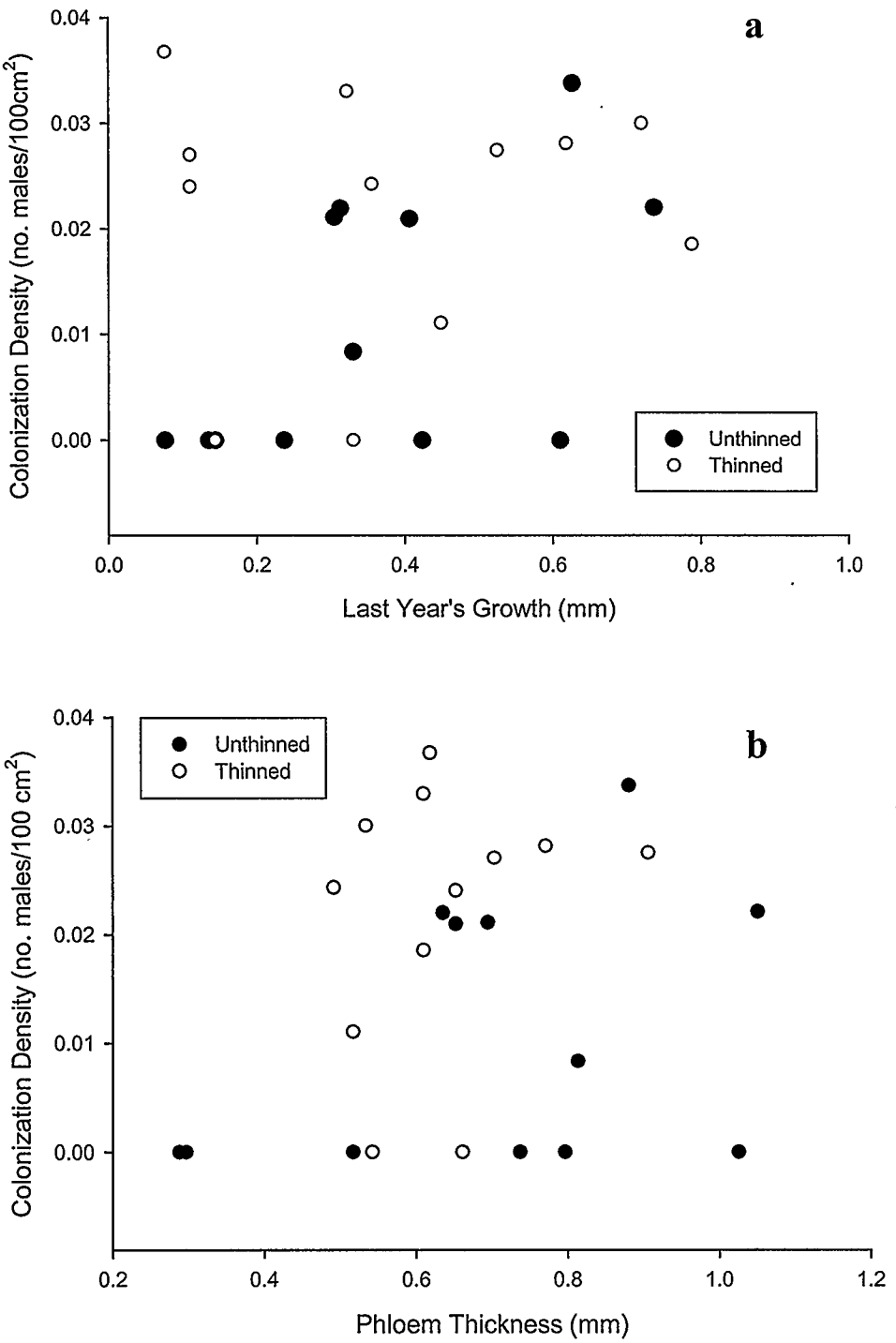

Figure 3.2. The relationship between male colonization density and a) last year's growth rate or b) phloem thickness on experimental logs in 2002. Raw data are shown.

The treatment origin of a tree significantly influenced date of male colonization in both study years and male clutch size during 2002, but only when individual tree characteristics were also considered (Tables 3.2 and 3.3). Trees originating from thinned stands were settled earlier than those originating from unthinned stands (Figure 3.1b). During 2002, males had smaller clutches when breeding in trees from thinned stands (Table 3.3).

Several tree characteristics were important determinants of time of male colonization, independently of treatment origin (Table 3.3). During 2001, the trees settled first were smaller, had less phloem nitrogen, slower recent growth rates but had thicker phloem. During 2002, trees settled first had larger diameters (the opposite effect to 2001) and moister phloem. Settlement characteristics also played a significant role in male colonization. During both years, trees that were settled earlier achieved higher final colonization densities (Table 3.3).

Beetle Reproductive Success

Measurements of male reproductive success were analyzed using the same models as used to analyse date of male colonization. Treatment alone did not affect male reproductive characteristics during 2001 (Table 3.2). During 2002, males breeding in trees from thinned stands had smaller clutches than those breeding in trees from unthinned stands (Figure 3.3; Table 3.3).

Tree characteristics also influenced male reproductive success (Table 3.3). During 2001 the only tree characteristic correlated significantly (but marginally so) with harem size was phloem nitrogen content; males in trees with lower phloem nitrogen content attracted fewer mates. During 2002, males in trees with thicker phloem or

Table 3.2. Stand and treatment origin level analyses on male reproductive characteristics of *I. pini* in 2001.

Male Characteristic	Source	Whole Model R^2	DF	F Ratio	Prob > F
Date of Male Colonization	Treatment Origin	**0.81**	1, 15	1.18	0.294
	Stand		5, 15	2.14	0.117
	Site[Stand,Treatment Origin]*		15, 272	30.93	<.0001
	Stand*Treatment Origin		5, 15	0.62	0.685
Harem Size/Male	Treatment Origin	**0.20**	1, 15	1.14	0.302
	Stand		5, 15	1.37	0.290
	Site[Stand,Treatment Origin]*		15, 302	2.39	0.003
	Stand*Treatment Origin		5, 15	0.18	0.967
Male Clutch Size	Treatment Origin	**0.34**	1, 15	1.68	0.215
	Stand		5, 15	3.81	0.020
	Site[Stand,Treatment Origin]*		15, 211	1.43	0.133
	Stand*Treatment Origin		5, 15	0.33	0.889

Table 3.3. Results of statistical analyses investigating the effects of tree characteristics on male reproductive traits of *I. pini*. PRC refers to the partial regression coefficient.

	2001					2002				
Source	Whole Model R^2	DF	PRC	F Ratio	Prob > F	Whole Model R^2	DF	PRC	F Ratio	Prob > F
Treatment Origin	**0.65**	1, 287		23.93	<.0001	**0.52**	1, 208		5.83	0.017
Stand		5, 287		61.98	<.0001		5, 208		35.34	<.0001
Last Year Growth Rate (mm)		1, 287	11.01	24.57	<.0001		1, 208	7.04	1.65	0.200
Phloem Thickness (mm)		1, 287	-21.59	19.90	<.0001		1, 208	7.75	1.09	0.298
DBH (cm)		1, 287	1.91	12.69	0.0004		1, 208	-5.10	31.26	<.0001
Nitrogen (% Total Kjeldahl Nitrogen)		1, 287	34.25	19.51	<.0001					
Phloem Moisture Content (g moisture/g dry phloem)							1, 208	-12.34	60.15	<.0001
Male Colonization Density (no. males/100cm^2)		1, 287	-5.18	116.65	<.0001		1, 208	-197.19	4.02	0.046
Treatment Origin	**0.15**	1, 286		0.18	0.669	**0.12**	1, 207		2.09	0.150
Stand		5, 286		3.35	0.006		5, 207		0.93	0.460
Last Year Growth Rate (mm)		1, 286	-0.07	0.08	0.773		1, 207	1.01	2.86	0.092
Phloem Thickness (mm)		1, 286	0.09	0.03	0.867		1, 207	1.59	3.90	0.050
DBH (cm)		1, 286	0.00	0.01	0.942		1, 207	-0.26	6.02	0.015
Nitrogen (% Total Kjeldahl Nitrogen)		1, 286	-1.73	4.11	0.044					
Phloem Moisture Content (g moisture/g dry phloem)							1, 207	0.04	0.04	0.842
Male Colonization Density (no. males/100cm^2)		1, 286	0.09	2.39	0.123		1, 207	-28.84	7.19	0.008
Mean Date of Male Colonization (Julian date)		1, 286	0.00	0.47	0.492		1, 207	-0.02	4.64	0.032
Treatment Origin	**0.62**	1, 203		0.06	0.800	**0.41**	1, 199		14.49	0.0002
Stand		5, 203		3.52	0.005		5, 199		2.54	0.029
Last Year Growth Rate (mm)		1, 203	0.36	0.83	0.364		1, 199	-0.52	0.28	0.599
Phloem Thickness (mm)		1, 203	0.21	0.07	0.799		1, 199	-4.61	11.71	0.001
DBH (cm)		1, 203	0.09	0.84	0.360		1, 199	0.25	1.96	0.163
Nitrogen (% Total Kjeldahl Nitrogen)		1, 203	-1.11	0.81	0.370					
Phloem Moisture Content (g moisture/g dry phloem)							1, 199	0.01	0.001	0.982
Male Colonization Density (no. males/100cm^2)		1, 203	-0.30	10.40	0.002		1, 199	53.69	8.36	0.004
Mean Harem Size/Male (no. females/male)		1, 203	1.13	147.28	<.0001		1, 199	1.21	104.73	<.0001
Mean Date of Male Colonization (Julian date)		1, 203	-0.04	14.69	0.0002		1, 199	0.02	2.21	0.139

smaller diameters had larger harems. None of the tree characteristics that I measured significantly affected male clutch size during 2001. Males had smaller clutches when breeding in thicker phloem during 2002 (Table 3.3).

Settlement characteristics played a significant role in male reproductive success. During both years, trees that were settled earlier supported higher final colonization densities (Table 3.3). During 2002, males that settled on trees with higher densities of other males or that settled later in the season attracted fewer females. As expected, males who settled at lower densities (2001) and who attracted more females (both years) had larger clutches. During 2001, males who settled earlier also had larger clutches (Table 3.3).

I analyzed the effects of treatment origin and stand on the first female's reproductive traits using the same statistical model as for the male reproductive characteristics (treatment origin, stand, their interaction, and site nested within origin and stand). To examine the effects of tree characteristics, including male colonization, on female reproductive traits I used ANCOVA including stand and treatment origin with diameter, phloem nitrogen content, phloem thickness, last year's growth rate, male density, date of male colonization and harem size as covariates. In general, there were fewer significant effects in the models for the mean of all females or the last female than the models for first female's reproductive traits, but the trends were similar.

Overall, females breeding in trees from thinned stands realized lower reproductive success. During 2001 first females constructed shorted pre-egg galleries in trees originating from thinned stands (Figure 3.3, Table 3.4). During 2002, once tree characteristics were taken into account, first females breeding in trees originating from

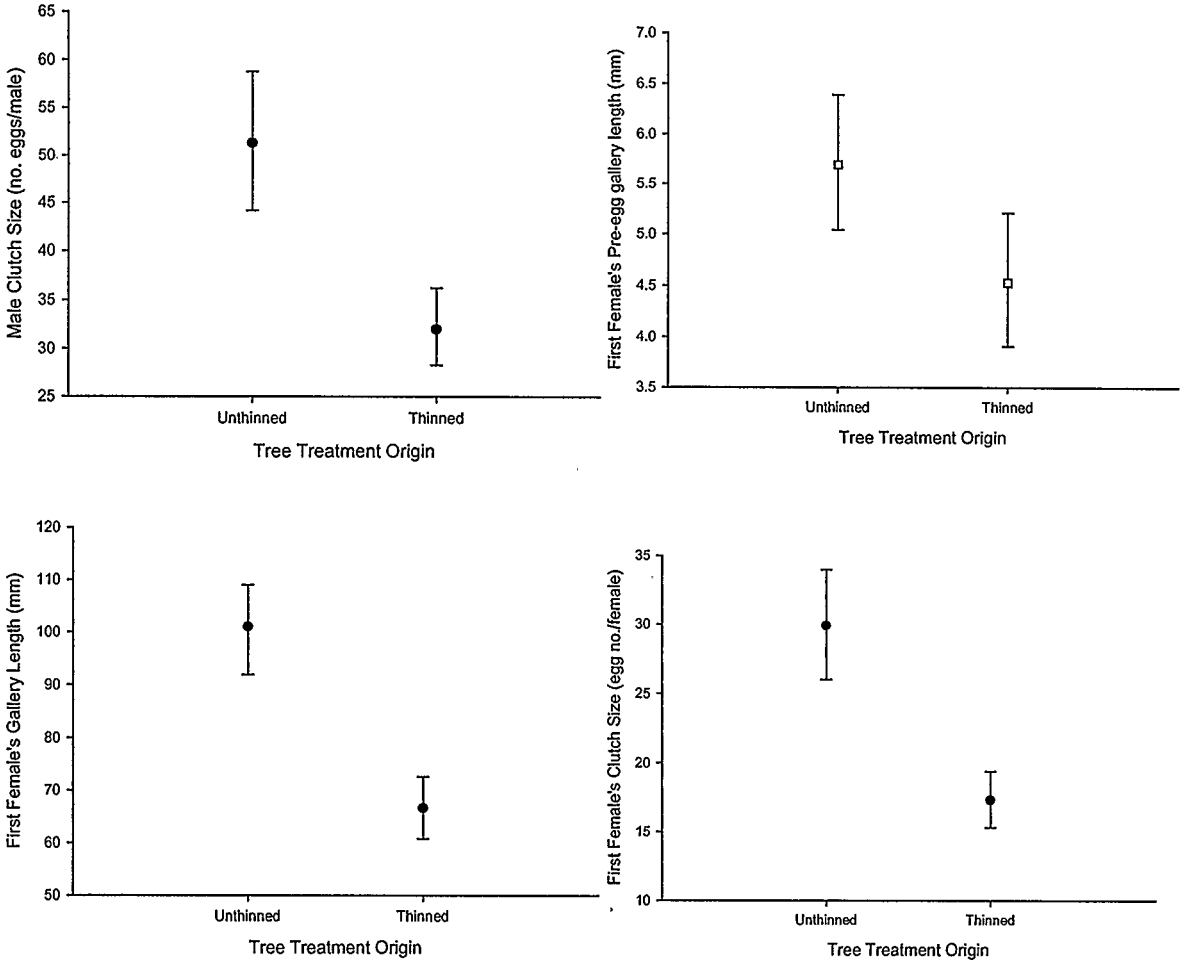

Figure 3.3. Reproductive traits of males and first females that differed significantly between trees originating from thinned and unthinned stands. Least squared means ± 95%CI for 2001 obtained from model reported in Table 3.4, whereas those for 2002 were obtained from models reported in Table 3.5. Open symbols (□) indicate data for 2001 and closed symbols (●) indicate data for 2002.

Table 3.4. Analyses of treatment origin and stand effects on the reproductive characteristics of the first female *I. pini* to join a male in 2001.

Female Characteristic	Source	Whole Model R^2	DF	F Ratio	Prob > F
Gallery Length	Treatment Origin	**0.17**	1, 15	1.40	0.255
	Stand		5, 15	0.40	0.844
	Site[Stand,Treatment Origin]*		15, 301	2.13	0.009
	Stand*Treatment Origin		5, 15	0.98	0.460
Pre Egg Gallery Length	Treatment Origin	**0.11**	1, 15	5.86	0.029
	Stand		5, 15	1.07	0.415
	Site[Stand,Treatment Origin]*		15, 279	0.48	0.949
	Stand*Treatment Origin		5, 15	1.16	0.374
Egg Niche Number	Treatment Origin	**0.24**	1, 15	2.18	0.161
	Stand		5, 15	2.76	0.059
	Site[Stand,Treatment Origin]*		15, 254	1.29	0.211
	Stand*Treatment Origin		5, 15	0.52	0.759

*indicates a random factor

thinned stands had shorter galleries. First females also laid fewer eggs in trees from thinned stands (Figure 3.3, Table 3.5).

Certain tree characteristics affected reproduction by first females, though never the same way in both study years (Table 3.5). During 2001, the only tree characteristics to affect the first female's reproductive behaviour were phloem nitrogen content and tree diameter. As phloem nitrogen increased so did gallery length of the first female to join a male. Increased tree diameter negatively effected pre-egg gallery length. During 2002, the first females to join a male had longer galleries in trees that grew slowly during the previous year. In trees that had thinner phloem, females had longer galleries and laid more eggs. Based on pre-egg gallery length, first females waited longer to lay their first egg when phloem moisture content was high (Table 3.5).

Settlement characteristics also influenced female reproduction. When colonizing trees with higher densities of males, first females tended to have shorter galleries and laid fewer eggs in total during 2001. Females that joined males who colonized later in the season had shorter galleries, waited longer to lay their first egg, and laid fewer eggs in total. First females whose mates had larger harems had longer galleries and waited longer to lay their first eggs (Table 3.5). During 2002, the first females to join a male had longer galleries and laid more eggs when breeding in trees with higher densities of males (contrary to 2001). As during 2001, first females who joined mates with larger harems during 2002 waited longer to lay their first eggs (Table 3.5).

Table 3.5. Analyses of the effects of tree and colonization characteristics on reproductive traits of the first female *I. pini* to join a male. PRC refers to the partial regression coefficient.

		2001					2002				
Female Characteristic	Source	Whole Model R^2	DF	PRC	F Ratio	Prob > F	Whole Model R^2	DF	PRC	F Ratio	Prob > F
Gallery Length	Treatment Origin	**0.16**	1, 285		1.53	0.217	**0.17**	1, 204		26.20	<.0001
	Stand		5, 285		1.70	0.135		5, 204		4.92	0.000
	Last Year Growth Rate (mm)		1, 285	-8.45	1.57	0.211		1, 204	-35.17	4.47	0.036
	Phloem Thickness (mm)		1, 285	27.53	3.58	0.060		1, 204	-84.61	14.02	0.0002
	DBH (cm)		1, 285	-0.48	0.09	0.765		1, 204	4.08	1.87	0.173
	Nitrogen (% Total Kjeldahl Nitrogen)		1, 285	53.98	5.29	0.022					
	Phloem Moisture Content (g moisture/g dry phloem)							1, 204	6.13	1.28	0.260
	Male Colonization Density (no. males/100cm^2)		1, 285	-8.09	23.77	<.0001		1, 204	888.32	8.02	0.005
	Mean Harem Size/Male (no. females/male)		1, 285	5.04	9.72	0.002		1, 204	3.64	3.24	0.074
	Mean Date of Male Colonization (Julian date)		1, 285	-0.46	7.16	0.008		1, 204	0.22	1.05	0.306
Pre Egg Gallery Length	Treatment Origin	**0.13**	1, 264		0.17	0.684	**0.13**	1, 203		0.63	0.429
	Stand		5, 264		0.35	0.882		5, 203		1.50	0.190
	Last Year Growth Rate (mm)		1, 264	-0.08	0.38	0.538		1, 203	0.72	2.67	0.104
	Phloem Thickness (mm)		1, 264	0.28	1.02	0.313		1, 203	0.17	0.08	0.777
	DBH (cm)		1, 264	-0.08	6.06	0.015		1, 203	-0.001	0.0002	0.990
	Nitrogen (% Total Kjeldahl Nitrogen)		1, 264	0.63	2.04	0.155					
	Phloem Moisture Content (g moisture/g dry phloem)							1, 203	0.29	4.11	0.044
	Male Colonization Density (no. males/100cm^2)		1, 264	0.03	0.75	0.386		1, 203	-9.38	1.28	0.260
	Mean Harem Size/Male (no. females/male)		1, 264	0.10	10.66	0.001		1, 203	0.10	3.74	0.055
	Mean Date of Male Colonization (Julian date)		1, 264	0.01	4.70	0.031		1, 203	0.004	0.46	0.498
Egg Niche Number	Treatment Origin	**0.26**	1, 243		0.00	0.981	**0.23**	1, 203		21.87	<.0001
	Stand		5, 243		2.83	0.017		5, 203		5.07	0.0002
	Last Year Growth Rate (mm)		1, 243	0.26	0.80	0.372		1, 203	-0.63	0.80	0.371
	Phloem Thickness (mm)		1, 243	0.21	0.12	0.731		1, 203	-3.71	14.92	0.0002
	DBH (cm)		1, 243	0.04	0.28	0.597		1, 203	0.14	1.18	0.279
	Nitrogen (% Total Kjeldahl Nitrogen)		1, 243	-1.04	1.11	0.293					
	Phloem Moisture Content (g moisture/g dry phloem)							1, 203	-0.16	0.48	0.491
	Male Colonization Density (no. males/100cm^2)		1, 243	-0.27	14.64	0.000		1, 203	35.76	7.29	0.008
	Mean Harem Size/Male (no. females/male)		1, 243	0.06	0.66	0.419		1, 203	0.06	0.54	0.465
	Mean Date of Male Colonization (Julian date)		1, 243	-0.03	14.78	0.000		1, 203	0.004	0.21	0.649

DISCUSSION

Tree Quality

Overall, thinning did not positively affect tree growth during the course of my study. Harvesting technique governed the association between treatment and DBH of experimental trees during 2001; the harvesting prescription called for weaker subdominant trees to be removed during thinning, leaving the larger trees behind. Thus, trees in thinned stands had greater diameters, but I did not detect any significant effect of thinning on recent radial growth rates, suggesting that the size difference between stands was due entirely to selective harvest (Table 3.1). Overall, radial growth may be a conservative estimate of current growth rates. Allocation of new growth to the bole may be a low priority (Waring and Pitman 1985). Other indices of recent growth rates, such as wood production/ unit leaf area, may give reflect tree allocation to new growth more accurately (see Waring 1983), but are difficult to measure. Furthermore, trees in my study area were considerably older (ca. 100 yrs old) than most trees documented to show a growth response after thinning (Matson *et al.* 1987, Fiddler and Fiddler 1989, Harrington and Weirman 1990, Entry *et al.* 1991, Barbour *et al.* 1992, Valinger 1992, 1993, Velaguez-Martinez *et al.* 1992, Mitchell *et al.* 1996, Tasissa and Burkhart 1997, Kimball *et al.* 1998, Yang 1998). Currently, no research documents a growth response to thinning in trees of similar age to those in my study.

Interestingly, trees felled from unthinned stands had thicker phloem than those from unthinned stands (Table 3.1). This may indicate that trees growing in unthinned stands allocated more resources towards growth than trees in thinned stands, because

phloem reflects accumulated growth over a number of years (Cabrera 1978). However, I did not detect any difference in growth rates of trees by measuring annual growth increments in xylem (Table 3.1). According to current hypotheses on resource allocation in plants (Bryant *et al.* 1983, Herms and Mattson 1992), increased allocation to growth would tend to occur when nutrients are available, but light is limited. Boreal forests tend to be nutrient limited (Bryant *et al.* 1983). The fact that percent phloem nitrogen content was also higher in unthinned stands than in thinned stands suggests that nutrients were available, but photosynthate production may have been limited by low light.

I was not able to measure the amount of secondary carbon-based compounds in my experimental trees. Given that trees growing in thinned stands may have allocated less to growth as indicated by thinner phloem, I would expect that the enhanced light conditions would lead to increased allocation to constitutive carbon-based defence compounds. Recent research in the boreal forest shows that nutrient availability was not affected by harvest intensity (Frey *et al.* 2003). Thus increased light availability may have a more profound effect on tree physiology than nutrient availability following thinning. More detailed analysis of phloem samples would be necessary to definitively address the potential increased allocation to defensive chemicals in thinned stands in my system. Alternatively, trees may allocate resources towards reproduction instead of growth or defence, though this is rarely considered within the context of forest management especially in fire-adapted species such as lodgepole pine (see Healy *et al.* 1999 for an example on red oak acorn production).

Beetle Colonization

I measured so many beetle reproductive and colonization traits during the course of my study, so that my analyses could have yielded significant results by chance alone. However, here I focus on results that are corroborated by several responses, most likely representing real biological trends.

Date of colonization and final male density may be indices of male habitat preference. If so, both of these responses indicate that males preferred logs from thinned stands. During 2002 (though not during 2001) beetles reached higher densities on trees originating from thinned stands, yet overall colonization density was higher in 2001. During both years, trees originating from thinned stands were settled earlier, controlling for male density (Figure 3.1). However, to determine whether these trends accurately reflect male preference, as opposed to simply the probability of detection I would have to ensure that males encountered both tree types during habitat search. Furthermore, because my experimental procedure did not control for the fact that thinned logs were in their stand of origin although unthinned logs were from a foreign stand. It is possible that beetles were responding to logs from thinned stands because they were more familiar somehow, not because they are of higher quality. One final consideration is that during 2002 I baited some of my experimental sites that were not colonized after four weeks of beetle flight. Thus, I may have artificially 'forced' beetles to colonize sites that would not have been found naturally. This may have impacted the colonization density and reproductive characteristics of the beetles that colonized baited logs.

During both study years, *I. pini* settled at higher densities on trees with higher recent growth rates (although during 2001, males settled earlier on trees that had grown

more slowly; Table 3.3, Figure3.2). A positive relationship between settlement density and growth rate concurs with the experimental work of Reid and Robb (1999) and Reid and Glubish (2001) who found greater beetle establishment on experimentally felled trees that had high growth rates. *Ips pini* may have settled preferentially on trees from thinned stands because these trees were growing more vigorously before they were killed, although my index of growth did not detect these differences.

In contrast, bark beetles that attack living trees tend to preferentially attack trees that have been growing slowly in recent years, or are less vigorous (Hard 1985, Waring and Pitman 1985, Schroeder 1987). Those species of bark beetles that attack live trees may benefit from choosing less vigorous hosts that may not be able to defend against successful attack. Several studies document vigour thresholds above which mountain pine beetle (*Dendroctonus ponderosae*) are not successful when initiating attack (Larsson *et al.* 1983, Mitchell *et al.* 1983, Waring and Pitman 1985, Preisler and Mitchell 1993).

Thicker phloem was associated with higher male densities during 2002 (Figure 3.2) and earlier settlement during 2001 (Table 3.3), although trees in thinned stands (preferred, as mentioned above) tended to have thinner phloem. A positive relationship between male attack density and phloem thickness has been observed in another *Ips* species (Haack *et al.* 1987a). Haack *et al.* (1987a) speculated that phloem thickness determines pheromone quality, leading to the production of higher quality pheromones in thick phloem, thereby attracting more conspecifics. Phloem thickness often correlates positively with tree diameter (this study, Reid and Glubish 2001). During 2002, male *I. pini* settled earlier on trees with larger diameters (Table 3.3), consistent with other studies (Hard 1985, Annila and Heikkila 1991, Preisler and Mitchell 1993, Reid and Glubish

2001). However, during 2001, smaller diameter trees were settled earlier, controlling for tree origin (Table 3.3). Haack *et al.* (1987a) did not detect any preference for diameter, and rather suggested that phloem thickness is a more important determinant of final male colonization density.

During 2002, trees with greater phloem moisture content were settled earlier (Table 3.3). Villa-Castillo and Wagner (1996) determined that phloem moisture content was not an important factor determining tree selection by *I. pini*, but beetles would ultimately benefit from choosing trees with higher moisture content. Curiously, during 2001, trees with low nitrogen content were settled earlier (Table 3.3). The earliest colonizers may have paid a cost of breeding in material with low nitrogen (Popp *et al.* 1989). However, we measured total Kjeldahl nitrogen content, which may not actually reflect the total amount of nitrogen that beetles receive from, phloem because it does not include nitrite or nitrate (Etherington and Morrey 1967).

In general, more females joined males on trees with more phloem. Males who settled on trees with higher nitrogen attracted more females during 2001, whereas during 2002 males settling on trees thicker phloem attracted more females (Table 3.3). In another closely related *Ips* species, harem size correlated positively with phloem thickness (Haack *et al.* 1987a). Enhanced mate attraction when resource quality is high may reflect better pheromone production or a willingness of males to admit more females to their harems when resource quality is high (Haack et al 1987a), in addition to female preference. In contrast to the general trends, during 2002, males in trees with smaller diameters attracted more mates (Table 3.3), for reasons that cannot be linked clearly to mate choice based on the quality of the resource held by.

I found no evidence that higher quality beetles colonized better quality habitats. The size of both male and female parents did not differ between trees originating from thinned or unthinned stands. However, I found that larger males typically arrive earliest at a tree, suggesting that larger males either emerge earlier than smaller males, or are better at locating habitat.

Beetle Reproductive Success

Haack *et al.* (1985) and Popp *et al.* (1989) proposed that female bark beetles may assess phloem quality when depositing eggs in phloem. They suggested that females are then able to allocate resources accordingly to maximize resource use and minimize competition between offspring. Thus I expected that beetles would have higher reproductive success when breeding in trees growing in thinned stands if those trees were more nutritious, or faster growing. Overall, females breeding in trees that originated from thinned stands may have ultimately paid a cost in terms of reproductive success, though results from 2001 and 2002 conflict. During 2001, first females breeding in trees from thinned stands laid their first eggs sooner than in trees from unthinned stands- a potential benefit (Figure 3.3). One possible explanation is that females in trees from thinned stands acquired more resources or nutrients from the phloem in thinned trees (Haack *et al.* 1984a) and could therefore begin egg laying after consuming less phloem than in trees from unthinned stands. In contrast to 2001, during 2002, females breeding in trees from thinned stands seemed to fare poorly relative to those in trees from unthinned stands. During 2002, first females had shorter galleries and laid fewer eggs in trees from thinned stands, resulting in smaller clutches for males (Figure 3.3). Again, even though analysis controlled for recent growth rates, tree diameter, phloem thickness

and moisture content, treatment significantly influenced female reproductive success. None of the factors that I measured accounted for the differences between treatments, suggesting that the difference in female reproduction between thinned and unthinned trees may have been due to some aspect of tree quality that I did not measure, potentially constitutive defence content.

Overall, females seemed to benefit by joining males in larger trees, as they laid their first eggs sooner (Table 3.5). Previous work found that *I. pini* benefit from breeding in trees that had grown more vigorously before they died (Reid and Robb 1999). Because trees were selected from even-aged stands, large trees must have been growing more vigorously to attain their greater diameters. Furthermore, thinning harvest left larger trees, on average, than those in unthinned stands, beetles may actually benefit when colonizing naturally downed habitat in thinned stands.

During 2002 higher recent growth rates of host trees were correlated with shorter gallery length of first females (Table 3.5). In contrast Reid and Robb (1999) found the exact opposite, that females in more vigorously growing trees tended to have longer galleries. However, Reid and Robb (1999) implanted beetles at low densities, whereas my data suggest that under natural condition tree vigour may influence female reproductive success only during the early stages of colonization. I did not detect any effect of tree growth rate on the gallery characteristics of last females (data not shown). Because tree vigour affected only the first females to join a male, crowding may be more important than tree characteristics for later arrivals (Kirkendall 1983).

Females breeding in trees with high phloem nitrogen content consumed more phloem tissue, but this did not translate into greater egg production. During 2001, longer

galleries for the first females to join a male were related to higher nitrogen content in phloem (Table 3.5). These results are contrary to my prediction (and previous research) that females benefit from increased nitrogen, consume less phloem and therefore lay eggs at higher densities in shorter galleries (Popp *et al.* 1989). Females may have increased gallery length if they could gain extra nitrogen from the particularly nutrient rich phloem. However, many foliage-feeding herbivores tend to consume less as nitrogen content increases (Ohmart *et al.* 1985, Fajer 1989, Kirsten and Topp 1991, Bauce *et al.* 1994, Wier and Boethel 1995, Williams *et al.* 1997, Henn and Schopf 2001).

Reproductive output of both males and females declined when they bred in trees with thick phloem. Shorter galleries and decreased egg number for females in 2002 was related to increased phloem thickness (Table 3.5). As a result, males breeding in trees with thick phloem during 2002 had smaller clutches (Table 3.3). These results are surprising for a phloem-feeding organism, and contrasts with earlier work. For *Ips calligraphus*, individuals in thicker phloem had longer egg bearing galleries, laid more eggs at greater density, and males had larger harems (Haack *et al.* 1987a). Amman and Pasek (1986) detected that brood production varied positively with phloem thickness in mountain pine beetle. Interestingly, Reid and Robb (1999) did not detect any effect of phloem thickness on female reproductive characteristics of *I. pini.* My contrary results are difficult to explain, but because several other tree variables and treatment origin were also considered simultaneously, it seems unlikely that the multiple negative relationships between reproductive traits and phloem thickness were due to spurious correlations, although it is possible. Trees from thinned stands had thin phloem, so perhaps the

apparent effect of phloem thickness resulted from an undetected benefit of breeding in trees from thinned stands.

In this study, females were less productive when breeding in trees with high phloem moisture content. During 2002, higher phloem moisture delayed production of the first female's first egg (Table 3.5). Previously, poor brood production has been associated with low phloem moisture content (Villa-Castillo and Wagner 1996). My results suggest that high phloem moisture content is largely deleterious for female reproduction. Trees with higher moisture content may be more susceptible to fungus colonization. Fungus can be an important competitor for resources in other endophytic insects (Strohm 2000).

In summary, thinning altered host quality for pine engravers. Surprisingly, although *I. pini* settled more densely on trees from thinned stands, these trees turned out to be detrimental to both male and female reproductive performance, even when tree quality and colonization characteristics were taken into account. I predicted that *I. pini* would benefit from breeding in trees originating from thinned stands if trees growing in these stands allocated more resources towards growth. However, if trees allocated resources towards carbon-based defensive compounds, *I. pini* reproductive success may be compromised. Thus, although I did not measure levels of carbon-based compounds, my results are consistent with the idea trees in thinned stands allocate more resources towards defence and *I. pini* pay a cost when breeding in these trees.

Furthermore, my results do not agree with the generalizations of Koricheva *et al.* (1998b) who proposed that feeding guild determines whether herbivorous insects perform better on stressed or vigorous plants. Their meta-analysis suggested that members of the

boring guild (including bark beetles) prefer to feed on less vigorous host plants. However, previous work (Amman and Pasek 1986, Haack *et al.* 1987a, Reid and Robb 1999) suggests that many variables associated with vigorous tree growth, such as large diameter, thick phloem and high recent growth rates can be beneficial to reproduction in *I. pini*. On the other hand, the effects of tree vigour will be quite different for insects that breed in dead material, compared to those who attack live trees. Furthermore, trees released from competition may shunt more resources toward defensive chemicals, which can hinder bark beetle performance.

I did not detect an increase in host quality after thinning. The trees I selected for my experiments had not responded to thinning as I had expected. Trees in thinned stands were larger, because of selective harvesting. Trees in thinned stands had thinner phloem and less phloem nitrogen than those growing in thinned stands. Moreover, beetles did not respond to tree quality as previous work suggests (Amman and Pasek 1986, Haack *et al.* 1987a, Reid and Robb 1999). I found that beetles suffered decreased reproductive success when breeding in trees with high recent growth rates, thick phloem, and phloem with greater moisture content, whereas the results for phloem nitrogen content were equivocal. In addition, it is possible that other characteristics, yet unknown, differed between thinned and unthinned stands, resulting in persistent treatment effects even when individual tree characteristics were considered. Overall, *I. pini* settled most often on trees originating from thinned stands, yet ultimately suffered reduced performance when doing so (see Mayhew 1997 for a recent review). Thus anthropogenic changes can result in a disconnection between herbivore host colonization and performance, resulting in reduced reproductive success.

CHAPTER 4: THE LIFE HISTORY CONSEQUENCES OF FOREST THINNING ON BARK BEETLES FACTORS.

INTRODUCTION

The factors that determine the size and number of offspring, and in turn an individual's fitness, are a central question of current life history theory (Stearns 1992). Biotic and abiotic factors can affect offspring size and number, both singly and through their interaction. For example, in herbivorous insects, food quality and temperature determine how many offspring are produced and their size and quality (Stearns 1992). Enhanced nutrition typically increases offspring production, juvenile development rate and adult size (Amwack and Leather 2002). However, in ectotherms, higher temperatures during development also increase growth rates of juveniles, yet result in smaller final body size (Atkinson 1994, Berrigan and Charnov 1994, Sevenster 1995, Kindlmann *et al.* 2001). Moreover, the effects of host quality and temperature can interact for insect herbivores, depending on the effects of the host's defensive compounds (Stamp and Yang 1996, Jansen and Stamp 1997). In particular, temperature may affect the efficacy of individual defensive chemical compounds, yet both warm and cool temperatures have resulted in enhanced toxicity (Stamp and Yang 1996). Thus the interactive effects of host quality and temperature may be difficult to predict.

Here I investigate the influence of changes in host nutrition and developmental environment caused by forest management on an herbivorous forest insect. Human influences, such as forest management, are likely to influence both plant quality and the general environment, both of which may have life history consequences for herbivores.

One forest management practice, stand thinning, is increasingly common (Sougavinski and Doyon 2002). Thinning causes changes at both the stand and tree level. After thinning, stands tend to be warmer (Wickman and Torgersen 1987, Bartos and Amman 1989, Schmid *et al.* 1991, 1992, Hindmarch and Reid 2001, Chapter 2) and trees growing in thinned stands may be more nutritious, yet have higher defensive capabilities (Lorio 1993, Kolb *et al.* 1998).

I focus on bark beetles (Coleoptera: Scolytidae), which may be particularly sensitive to these effects. Like other insects, bark beetle reproduction and development is influenced by environmental temperature. Bark beetles breeding at higher temperatures tend to lay their first eggs sooner (Sahota and Thomson 1979, Wagner *et al.* 1981, Haack *et al.* 1984a), lay more eggs in total (Wagner *et al.* 1981) in longer egg galleries (Reid 1962, Wagner et al 1981) with higher densities of eggs (Wagner *et al.* 1981, Haack *et al.* 1984a, 1985). Nevertheless, adult offspring emerge from breeding logs earlier at higher temperatures (Haack *et al.* 1987b). The number of emerging offspring per female increases (Haack *et al.* 1985, 1987b) and immature stages develop faster as temperature increases (Atkins 1967, Haack *et al.* 1985, 1987b, Wagner *et al.* 1987, Bentz *et al.* 1991, Hui 1994). When reared at higher temperatures, adult bark beetles tend to have a smaller body size than those reared at lower temperatures (Atkins 1967, Safranyik and Whitney 1985, Wagner *et al.* 1987).

Bark beetles are well suited for the examination of host quality effects on development, because immature bark beetles feed and complete their entire development within the phloem of a single host tree. In general, bark beetles gain reproductive benefits such as enhanced egg production and increased longevity from breeding in

thicker phloem (Haack *et al.* 1984a, b, Haack *et al.* 1985, 1987a, b, Amman and Pasek 1986, although see Ch. 3) or phloem that is more nutritious (Popp *et al.* 1989). Offspring that emerge from logs with thick phloem are larger (Haack *et al.* 1985, 1987b).

Because bark beetles are gregarious, their life history traits are influenced by breeding density, in addition to the effects of host quality and temperature. High breeding densities are largely deleterious to individuals. In crowded conditions, females tend to have shorter egg galleries (Robins and Reid 1997) and lay fewer eggs (Amman 1972). Breeding at high densities reduces the number of offspring produced per female (Anderbrant *et al.* 1985, Anderbrant and Schlyter 1989, Robins and Reid 1997), and offspring tend to emerge at a smaller size (Botterweg 1983, Anderbrant *et al.* 1985, Anderbrant and Schlyter 1989).

No previous studies have documented the effects of both biotic and abiotic interactions resulting from forest thinning on the life history traits of herbivorous insects. Previous work on bark beetles has focused on the influence on microclimate alterations on beetle development and reproduction. Hindmarch and Reid (2001) found that female *I. pini* breeding in logs in thinned stands had longer egg galleries containing more eggs laid at higher densities relative to those in unthinned stands. Researchers focusing on the effects of thinning on *Dendroctonus ponderosae* Hopk. speculated that beetles develop faster in thinned stands because of warmer temperatures (Bartos and Amman 1989, Bartos and Booth 1994), but this has yet to be tested empirically. Villa-Castillo and Wagner (1996) suggested that high temperatures and light intensity in thinned stands may degrade host quality by causing phloem to dry out too quickly, thereby reducing reproductive success of *Ips pini* (Say). Scattered accounts of the effect of thinning on

other forest herbivorous insects suggest that development rates increase in thinned stands (Wickman and Torgerson 1987, Ross 1995), likely because of increased temperatures after thinning. Regardless of the enhanced development rate, pupal size of *Coloradia pandora* remained the same between thinned and unthinned stands (Ross 1995).

In this study, I investigate the stand- and tree-level effects of thinning on *Ips pini* reproductive success and development. *Ips pini* is a secondary bark beetle, undergoing reproduction and development in the phloem of freshly dead pine trees, such as those felled by wind (Bright 1976). The breeding habitat allows me to separate the effects of thinning on the stand environment and on host quality by moving logs from trees felled in one stand type (e.g. thinned) to the opposing stand type (e.g. unthinned). In addition, all life stages are completed within the log where eggs are laid, permitting me to link offspring size, number and development rate to particular host characteristics. Males colonize suitable host trees during spring and attract an average harem of three females (Schenk and Benjamin 1969). Females mate with the male and lay eggs in galleries within phloem tissue. Eggs hatch and larvae develop and pupate within the phloem. New adults emerge from natal logs during late summer and early fall (Schenk and Benjamin 1969, Bright 1976).

I predicted that beetles breeding in trees located in thinned stands develop faster than those in unthinned stands because of higher stand temperatures in thinned stands, so that offspring emerge earlier and smaller. If phloem quality or quantity is also greater in thinned stands than in unthinned stands, because of reduced tree competition, beetles should emerge earlier than those in logs from unthinned stands, but also to be larger.

Therefore changes in host quality in response to stand thinning may offset the concurrent changes in stand temperatures.

METHODS

Study System

The study was conducted in the northern boreal forest, near Whitecourt, Alberta, Canada (54°N, 115°W) in 2002. I chose six pairs of thinned and unthinned lodgepole pine (*Pinus contorta* var. *latifolia* Englemann.) stands within which I reciprocally transferred logs from each stand type. Refer to Chapter 1 for a complete description of the study area.

Habitat and Tree Characteristics

To determine temperature effects on beetle development, I monitored ambient minimum and maximum air temperatures in each stand with digital thermometers (Radio Shack: Dual Display Big Digit LCD Thermometer) every two weeks from 8 May to 22 August 2002. I mounted thermometers at breast height (1.3 m above ground level) on the north side of a tree near the centre of the stand.

In insects and other ectotherms, the cumulative temperature above a minimum threshold temperature, referred to as degree-days, determines development rate (Taylor 1981). To quantify degree-days, I used Hobo data loggers (Onset Computer Corporation) for the entire field season (20 May – 15 September) to collect hourly microclimate data. Data loggers were mounted on the north facing side of a tree located near the location of beetle emergence cages. Loggers were sealed within two Ziploc freezer bags to prevent moisture accumulation. At the end of the season, I collected the data loggers and data

were downloaded to a PC computer using BoxCar Pro software (Onset Computer Corporation) for Windows. I calculated degree-days by averaging the hourly temperature reading for each day. Degree-days are based on the accumulation of temperature units above a lower threshold, below which insect development stops. Because I did not have data for the lower development threshold of *Ips pini,* I averaged the minimum temperature values necessary for the development of each life stage (egg, larva, pupa and pre-imaginal adult) determined by Wermilinger and Seifert (1998) for a related species, *Ips typographus* (L.). I then summed all accumulated degree-days from 20 May to 15 September 2002 with temperatures above the estimated lower minimum for development (9.25°C).

As correlates of tree quality for each experimental tree, I used diameter at breast height (DBH), recent growth rate, phloem thickness, and phloem moisture. To obtain tree growth rates, I cut cross-sectional disks from the midbole region of all of my experimental trees. I then quantified growth rates by measuring the most recent growth ring under a dissecting microscope (20x power) at four points around the disk. I measured phloem thickness similarly.

Because the effects of temperature may be mediated through its effect on phloem moisture, I used two logs (not used in beetle reproduction or emergence experiments) from each tree located in the stand of origin to monitor changes in phloem moisture content during the season along the length of the bole. I sampled a $30cm^2$ piece of phloem 20 cm from the end of one log at the peak of beetle colonization (19 June) to quantify baseline moisture content. At the end of the season (17 August), I collected samples at three locations (0, 20, 36 cm from the end of the log) from the other log to

avoid moisture loss due to previous sampling. Samples were sealed immediately in plastic bags and stored at –4°C until processing. To measure phloem moisture content, samples were thawed to room temperature and weighed on a microbalance to the nearest 10^{-5}g. Samples were then dried at 63 °C for 24 h and reweighed. The difference between the two masses was expressed over the mass of the dry phloem to get phloem moisture content per gram of phloem.

Beetle Reproduction and Development

To test for differences in beetle reproduction and development between thinned and unthinned stands and trees, I felled two trees in each stand, giving a total of 12 trees felled in thinned stands and 12 trees felled in unthinned stands. Trees were selected randomly from a range of 16.0-21.0 cm DBH and felled before the start of beetle emergence (on 16 May 2002). Each tree was then partitioned into logs 75 cm long. I placed logs originating from both thinned and unthinned stands in thinned stands for natural colonization by *I. pini,* because discovery by the beetles was unlikely in unthinned stands (Chapter 2). Thus half of the logs in each thinned stand originated from the two trees felled in that stand, and the other half of the logs originated from trees felled in the paired unthinned stand. Four logs from each tree were placed end-to-end, surrounded by branches from the same tree to simulate a freshly fallen tree; each set of logs is termed a site. Log sites were chosen randomly from a predetermined collection of potential sites with appropriate distances (>50m) from forest edge and from other sites and with suitable shading.

Beetles were allowed to colonize each log site naturally. However, colonization rates on experimental sites were low during 2002, so to facilitate beetle colonization, I

baited sites that remained uncolonized after 30 days with *I. pini* pheromones (ipsdienol; released at 110 *ug*/day and lanierone; 10 *ug*/day; Phero Tech Inc.) for 24 h. Once colonization was complete (14 June to 9 July 2002), two logs from each site were placed in individual emergence cages (Moeck 1988) to collect offspring as they emerged. To determine the effect of stand environment on development, one caged log was placed in the thinned stand where colonization occurred, and the other log was placed in the paired unthinned stand. Thus each stand contained four caged logs, placed side by side, consisting of two logs from trees in thinned stands and two logs from trees in unthinned stands.

Cages were checked every 3-7 days (depending on numbers emerging) to collect emerged beetles. On 15 September 2002, logs were removed from field emergence cages, transferred back to the laboratory and stored at -15°C for 10 days to arrest beetle emergence. I excavated all remaining beetles from the phloem by removing the bark from each log. All beetles were then sexed and classified as either parent or offspring, based on time of emergence and degree of sclerotization. I counted total offspring production, and number of offspring produced per female for each log. I determined the total number of females per log by removing the bark from the log and counting the total number of female egg galleries on each log used in the development experiment. I measured the size (pronotum width) of the last ten offspring to emerge of each sex under a dissecting microscope at 40x magnification. I also examined differences in time of emergence of offspring from each log. I calculated the percentage of total offspring collected that had emerged on the last day of field collection (14 September).

Analyses

Data were analysed statistically using the JMP IN version 4.0 computer package (SAS Institute, 2001). If necessary, data were transformed to meet the assumptions of normality and heteroscadacity following examination of residuals. A type I error rate of 0.05 was used for all tests. When tests included random factors, a restricted maximum likelihood method was employed for estimating mean squares (unless otherwise noted). All means are presented $\pm$ one standard error unless otherwise indicated, and are usually least-square means (LSMs) controlling for the other variables in statistical models. First-order interactions that tested biologically relevant predictions were included in models.

In general, I used two statistical models to investigate the effects of thinning on beetle development. The first model simply examined treatment effects: treatment origin (whether a tree originated from a thinned or unthinned stand) and development treatment (whether the beetles developed in a tree located in a thinned or unthinned stand). These models also included the interaction between these two effects and "tree" (nested within treatment) to control for individual tree effects.

To assess host effects specifically, I did another analysis replacing tree identity with characteristics thought to be related to host quality: growth rate (Reid and Robb 1999), phloem thickness (Haack *et al.* 1985, 1987b), diameter, and phloem moisture content (Villa-Castillo and Wagner 1996). Because intraspecific competition is so important for bark beetle reproductive success (Anderbrant *et al.* 1985), I also needed to consider as covariates male density and harem size. Finally, emergence time probably depends on time of colonization, whereas offspring size may be influenced by size of mothers and sex of offspring. Because multiple covariates can reduce statistical power

when samples are small, models were simplified by removing non-significant covariates in order of highest p values. To control for the effects of temperature, I used mean maximum temperature of each stand instead of degree-days in these analyses because I had maximum temperatures for all 12 stands, but measurements of degree-days for only eight of the 12 stands. For the eight stands for which I had both measurements, mean maximum temperature correlated significantly with degree-days (R^2=0.61 p<0.023,).

RESULTS

Habitat and Tree Characteristics

Thinned stands had higher maximum and lower minimum temperatures than unthinned stands (Chapter 2, Figure 2.1). Thinned stands accumulated significantly more degree-days above 9.25°C between 20 May and 15 September 2002 (t-test, R^2=0.27, t_6=-2.104, P<0.09; LSM ± 1SE: thinned stands 1502 ± 43.5 degree-days, unthinned stands 1373 ± 43.5 degree-days).

Trees from thinned and unthinned stands did not differ in recent growth rate (Chapter 3, Table 3.1). Interestingly, trees growing in unthinned stands had thicker phloem and more phloem nitrogen (Chapter 3, Table 3.1).

To test for differences in moisture content from phloem sampled early in the season I used ANCOVA including the following variables. Since logs were not moved between stands to measure moisture content changes, treatment refers to both the origin of the tree and the stand it was located in. Moisture content of phloem sampled early during the season did not differ between thinning treatments (ANCOVA $F_{1, 11}$=0.05, p>0.81) or stands within treatments ($F_{10, 11}$=0.39, p>0.92) and did not covary with DBH

($F_{1, 11}$=0.05, p>0.82; whole model R^2=0.27). To determine whether phloem moisture (20 cm from the end of the log) varied over the season for thinned and unthinned stands, I used an ANCOVA model. Logs had lower phloem moisture at the beginning of the season ($F_{1, 20}$=54.1, p<0.0001, LSMs ± 1SE: early season 1.35 ± 0.13 g moisture/g phloem, late season 2.42 ± 0.13 g moisture/g phloem) and this effect was consistent across treatments (interaction $F_{1, 20}$=1.91, p>0.18). Phloem moisture did not differ between treatments ($F_{1, 12}$=1.25, p>0.28), stands within treatments ($F_{10, 12}$=0.26, p>0.98), trees ($F_{12, 20}$=1.14, p>0.38) or diameters ($F_{1, 20}$=0.024, p>0.87; whole model R^2=0.71).

I further tested for differences in late season phloem moisture content between the three sampling locations on the log. One tree (TH 347-1) had to be removed from analysis because I was unable to collect a late season phloem sample. Overall, phloem moisture content sampled late during the season differed significantly between sampling locations on the log ($F_{2, 40}$=8.01, p<0.002): phloem sampled from the end of the log had less moisture than the two interior samples (Tukey's HSD, P <0.05; LSMs for each distance from the end of the log ± 1SE in g moisture/g phloem: 0 cm from end 1.90 ± 0.12 g, 20 cm from end 2.42 ± 0.12, 36 cm from end 2.37 ± 0.13). This effect was consistent among treatments (interaction: $F_{2, 40}$=0.55, p>0.58). Late season phloem moisture content did not differ between thinned and unthinned stands ($F_{1, 11}$=3.06, p>0.10) or among stands within treatments or trees (stand: $F_{10, 11}$=0.60, p>0.78; tree nested within stand and treatment & random: $F_{11, 40}$=1.40, p>0.21; DBH $F_{1, 40}$=0.13, p>0.71; whole model R^2=0.60).

Beetle Reproduction and Development

Number of Offspring

When only the treatment effects were considered, the total number of offspring produced per log (ln transformed + 1) did not differ between logs originating from thinned or unthinned stands ($F_{1, 9}$=0.09, p>0.76) or logs developing in thinned or unthinned stands ($F_{1, 14}$=0.44, p>0.51), nor was their interaction significant ($F_{1, 14}$=0.34, p>0.56; whole model R^2=0.61). There was also no difference in offspring production between the stands where logs were colonized ($F_{5, 14}$=0.66, p>0.65), but there tended to be differences among trees ($F_{9, 14}$=2.62, p<0.052). Similar results were obtained when analysing the number of male and female offspring separately (results not shown).

Using the same statistical model I investigated differences in the average offspring output per female on each log. The average number of offspring produced per female did not differ significantly between logs originating from thinned or unthinned stands ($F_{1, 9}$=0.01, p>0.91), logs that were located in thinned or unthinned stands ($F_{1, 14}$=0.29, p>0.60) nor between their interaction ($F_{1, 14}$=0.39, p>0.54). Offspring production per female differed significantly between colonization stands ($F_{5, 14}$=3.48, p<0.03) but not between trees ($F_{9, 14}$=0.13, p>0.99; whole model R^2=0.52).

Once tree and colonization characteristics were accounted for in the model, the total number of offspring differed significantly between logs that had originated in thinned and unthinned stands (Table 4.1). More offspring were produced in logs that had originated from unthinned stands than in those originally from thinned stands (Figure 4.1a). Total offspring production was lower in logs with phloem that had higher moisture

Table 4.1. Analyses of log and tree characteristics on number of emerging *I. pini* and number of offspring per female. 'Treatment Origin' refers to the treatment (thinned or unthinned) of the stand that each experimental tree originated from. 'Development Treatment' refers to the treatment (thinned or unthinned) of the stand that the beetles were developing in. Shown are final models after non-significant tree and settlement characteristics have been removed. Log diameter, last year's growth rate, harem size and mean maximum stand temperature were removed from both models, and date of male colonization and mean female parent size were removed from the model evaluating total offspring production per female. PRC refers to the partial regression coefficient.

Offspring Production	Source	Whole Model R^2	DF	PRC	F Ratio	Prob > F
Total number of offspring	Treatment Origin	**0.81**	1, 19		11.95	0.003
	Development Treatment		1, 19		0.07	0.791
	Development Treatment*Treatment Origin		1, 19		0.25	0.624
	Phloem Moisture Content (g moisture/g phloem)		1, 19	-0.82	6.80	0.017
	Phloem Thickness (mm)		1, 19	-2.48	6.16	0.023
	Male Colonization Density (no. males/100cm^2)		1, 19	51.87	4.41	0.049
	Mean Date of Male Colonization (Julian date)		1, 19	-0.10	43.53	<.0001
	Mean Female Size (mm)		1, 19	0.24	4.01	0.060
Total number of offspring per female	Treatment Origin	**0.60**	1, 25		9.27	0.005
	Development Treatment		1, 25		0.37	0.547
	Development Treatment*Treatment Origin		1, 25		0.51	0.482
	Phloem Moisture Content (g moisture/g phloem)		1, 25	-0.32	5.05	0.034
	Phloem Thickness (mm)		1, 25	-1.08	6.12	0.021
	Mean Date of Male Colonization (Julian date)		1, 25	-0.03	23.93	<.0001

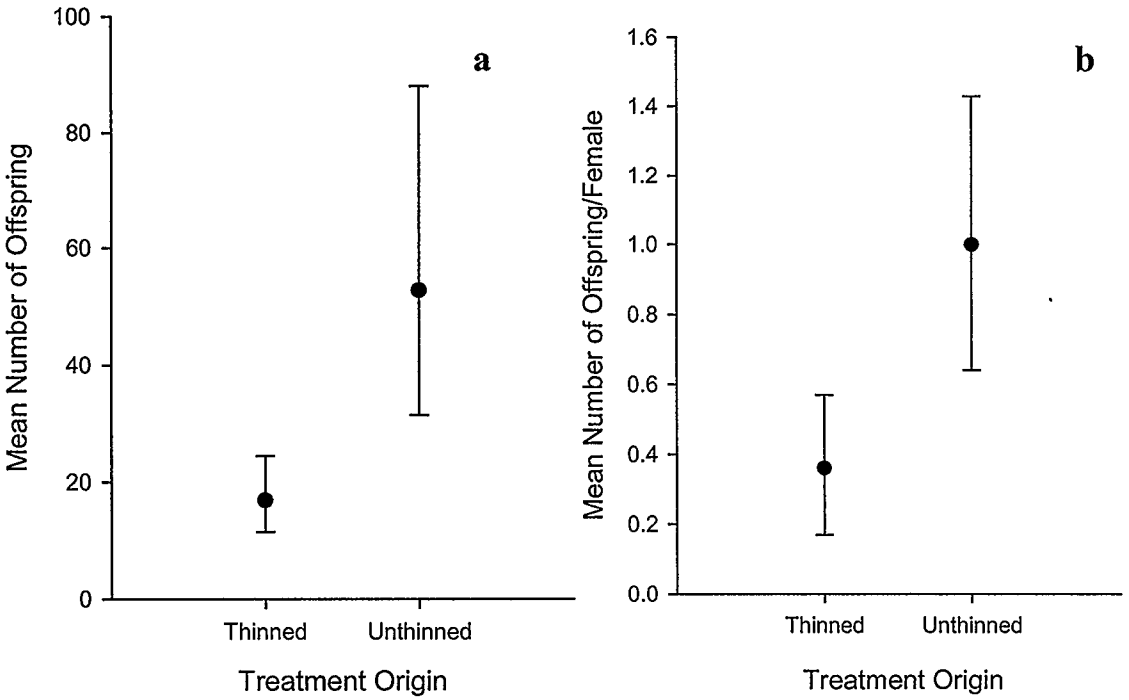

Figure 4.1. The effect of treatment origin of a log on a) the number of offspring produced per log and b) the number of offspring produced per female. Data shown are backtransformed LSMs with 95% CI. See Table 4.1 for statistical model.

content and thicker phloem. Offspring production was also reduced in logs that had lower male colonization densities and in logs that were settled later. Larger females also tended to have greater offspring production, though not significant at p=0.05 (Table 4.1).

Again, upon inclusion of tree and colonization characteristics in the model, the number of offspring produced per female differed between treatment origins (Table 4.1). Females breeding in logs from unthinned stands produced more offspring than those in logs from thinned stands (Figure 4.1b). Females produced more offspring per capita when breeding in trees with thinner phloem and in trees with less phloem moisture. In logs that were settled later, offspring production per female was lower (Table 4.1).

Timing of Offspring Emergence

To analyse treatment level effects on the time of offspring beetle emergence I used ANCOVA square root arc-sine transformed percent offspring, which was weighted by the total number of parents collected. The interaction between development treatment and treatment origin was significant ($F_{1, 13}$=16.1, p<0.002). Overall, when developing in unthinned stands, a greater percentage of offspring had emerged in the field from logs that originated from thinned stands. However, the effect tended to be the opposite when developing in thinned stands, where a greater percentage of offspring, on average, had emerged from logs originating from unthinned stands by 14 September (Figure 4.2a). Tree effects were not significant ($F_{9, 13}$=2.18, p>0.09) and there was not a significant effect of colonization stand ($F_{5, 13}$=0.45, p>0.81). The percent of offspring that had emerged by the end of the season did not depend on when the logs were colonized ($F_{1, 13}$=0.62, p>0.44; whole model R^2=0.75).

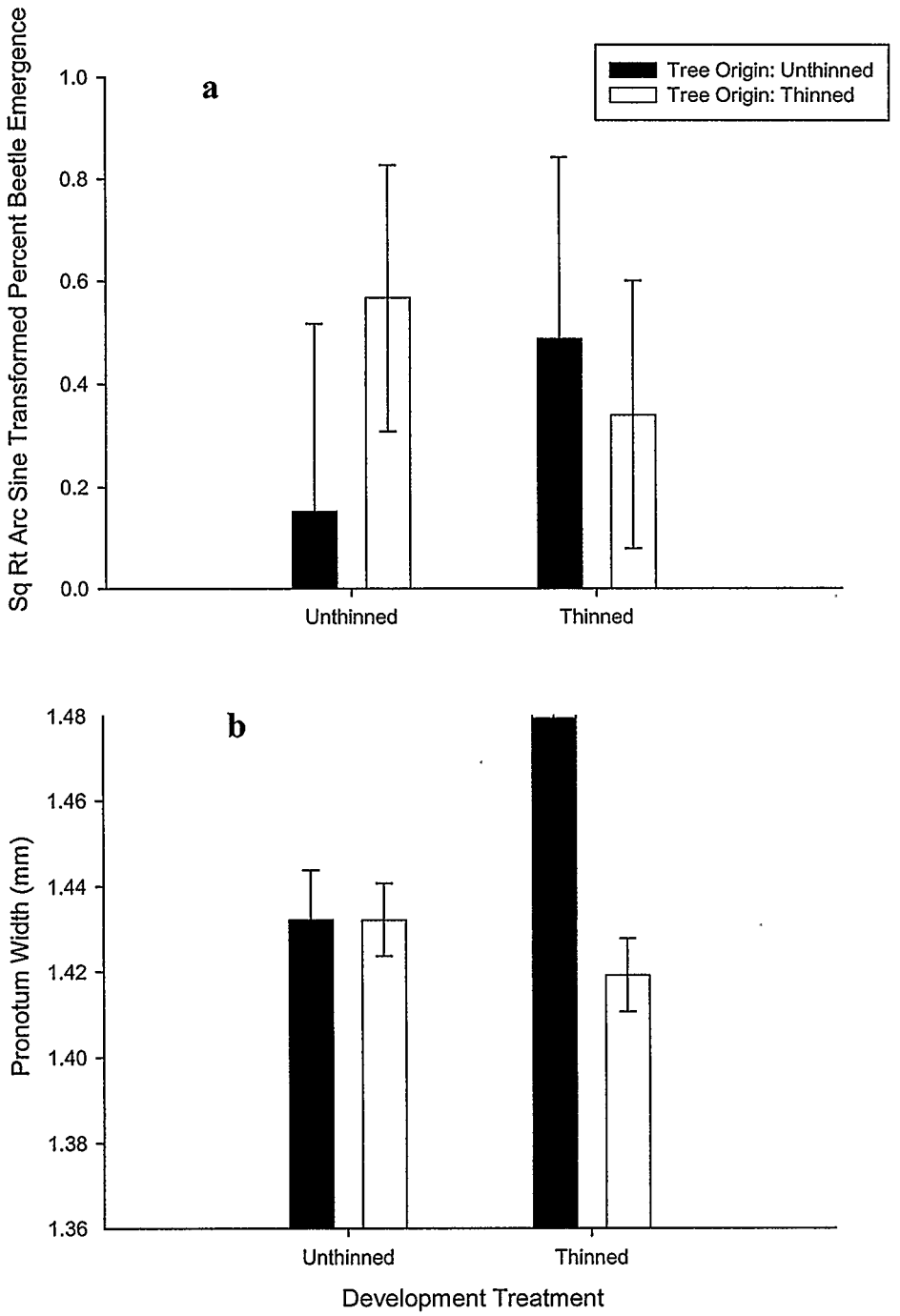

Figure 4.2. a) The effect of development treatment on the percentage of offspring that emerged by 14 September when developing in logs from thinned and unthinned stands. Square root arc sine transformed LSMs are shown with 95% confidence intervals. See Results for statistical model. b) The effect of development treatment on the size of offspring developing in trees originating from thinned and unthinned stands. Data shown are LSMs ± 1SE. Refer to Table 4.3 for statistical model.

I further investigated which tree, habitat and colonization characteristics affected offspring emergence (Table 4.2). Similar to previous analyses the responses were weighted by the total number of offspring collected per log. For offspring, the interaction between development treatment and treatment origin of the log remained significant in the same way (cf. Figure 4.2a) when log and colonization effects were included in the model for percent offspring emergence (Table 4.2). The percentage of offspring that had emerged by 15 September was higher on logs that had higher recent growth rates and on logs that had been settled earlier in the season (Table 4.2).

Offspring Size

To determine treatment and tree effects, I used an ANCOVA as above, but added in sex, the interaction between sex and development treatment, the interaction between sex and treatment origin of the tree, with the date of offspring collection as a covariate. The interaction between sex and treatment origin of the tree was removed from the final model since $p>0.05$. The effect of development treatment of offspring size differed slightly between the two sexes (Table 4.3), with males slightly larger in thinned stands whereas females showed the opposite pattern, though it was not pronounced. There was no general effect of treatment origin of the tree or the treatment in which offspring developed on offspring size. Offspring size differed between trees and males were larger than females (LSMs ± 1SE, male 1.44 ± 0.014 mm, female 1.39 mm ± 0.013). Offspring that were collected later tended to be smaller (Table 4.3).

The effects of tree, log and stand characteristics on offspring size were evaluated with ANCOVA (Table 4.3). Overall, offspring were larger when developing in logs from unthinned stands (Figure 4.2b). The effect of development treatment differed between the

Table 4.2. The results of backwards stepwise regression on the effects of log, settlement and stand characteristics on *I. pini* offspring emergence (percent of offspring that had emerged by September 15 2002). Data were square root arc sine transformed for analysis. Log diameter, phloem moisture content, phloem thickness, male colonization density, harem size/male, mean maximum stand temperature, and mean female parent size were removed from the model because $p>0.05$. Degrees of freedom for each variable is 1, 26 and the whole model $R^2=0.72$. PRC refers to the partial regression coefficient.

Source	PRC	F Ratio	Prob > F
Treatment Origin		0.33	0.569
Development Treatment		6.31	0.019
Development Treatment*Treatment Origin		15.97	0.001
Last Year's Growth Rate (mm)	0.90	32.72	<.0001
Mean Date of Male Colonization (Julian date)	-0.01	8.25	0.008

Table 4.3. Results of ANCOVA for offspring size (mm). Results of two models are presented, a) controls for treatment level effects and b) shows the results of backwards stepwise regression on an ANCOVA model that included tree, stand and settlement characteristics. From this model, log diameter, last year's growth rate, phloem moisture content, phloem thickness, male colonization density and harem size were removed because $p>0.05$. PRC refers to the partial regression coefficient.

	Source	Whole Model R^2	DF	PRC	F Ratio	Prob > F
a)	Treatment Origin	**0.30**	1, 384		0.77	0.380
	Development Treatment		1, 13		0.25	0.625
	Development Treatment*Treatment Origin		1, 384		0.05	0.820
	Tree (Treatment Origin)*		13, 384		7.02	<.0001
	Sex		1, 384		44.03	<.0001
	Sex*Development Treatment		1, 384		3.90	0.049
	Date Collected (Julian date)		1, 384	-0.002	13.48	0.0003
b)	Treatment Origin	**0.24**	1, 321		10.81	0.001
	Development Treatment		1, 321		2.58	0.109
	Development Treatment*Treatment Origin		1, 321		8.78	0.003
	Sex		1, 321		38.15	<.0001
	Sex*Development Treatment		1, 321		3.50	0.062
	Date Collected (Julian date)		1, 321	-0.002	10.89	0.001
	Mean Date of Male Colonization (Julian date)		1, 321	-0.003	32.71	<.0001
	Mean Female Size (mm)		1, 321	0.598	15.07	0.000
	Mean Maximum Temperature (°C)		1, 321	-0.008	5.68	0.018

two tree origins (significant interaction between development treatment and treatment origin; Table 4.3). For trees from unthinned stands, offspring were larger when developing in logs in thinned stands than in unthinned, whereas development treatment had little effect for offspring developing in logs from unthinned stands (Figure 4.2b). As before, males were larger than females and offspring that emerged later were smaller. Offspring that developed in larger logs were larger at emergence. Offspring were larger when their fathers settled earlier and when their mothers were larger. As predicted, offspring tended to be smaller when developing in stands with higher maximum temperatures (Table 4.3).

DISCUSSION

Habitat and Tree Characteristics

The effects of stand thinning on stand temperatures were as expected, but the effects on host quality were not. As others have found, thinned stands were significantly warmer than unthinned stands, and as a result more degree-days accumulated during the season in thinned stands (Wickman and Torgersen 1987, Bartos and Amman 1989, Schmid *et al.* 1991, 1992, Hindmarch and Reid 2001). Contrary to expectation, trees growing in thinned stands were not growing faster than trees in unthinned stands, nor were there differences in phloem moisture levels. Surprisingly, trees in unthinned stands had thicker phloem and more phloem nitrogen than trees in thinned stands. However, both nitrogen content and phloem thickness are positively correlated with tree diameter. Because trees remaining in thinned stands after harvest are larger, they may actually be

better quality hosts. Nonetheless, when I controlled for the effects of tree size, no positive increase in tree quality was observed after thinning (Chapter 3).

Previously, loss of phloem moisture has been implicated as one of the major costs of breeding in trees located in thinned stands for *I. pini* (Villa-Castillo and Wagner 1996). However, in my study area logs actually gained moisture during the season. The difference may be attributed to the wetter and cooler climate of my study area compared to the Arizona study area of Villa-Castillo and Wagner (1996). I also found no difference in moisture changes between thinned and unthinned stands, contrary to Villa-Castillo and Wagner (1996), even at the ends of logs where phloem lost more moisture than phloem further from the ends.

Beetle Reproduction

The observed, though not predicted, pattern that trees in unthinned stands were better hosts (thicker phloem, more phloem nitrogen) was consistent with the patterns of offspring production. Offspring were larger when developing in trees originating from unthinned stands relative to those from thinned stands (Figure 4.2a). Bark beetles tend to emerge larger from trees that have thicker phloem and more phloem nitrogen (Haack *et al.* 1985, 1987b). Furthermore, once tree and colonization characteristics were accounted for explicitly, the total number of offspring and the number of offspring produced per female was greater in logs originating from unthinned stands than from logs originally from thinned stands (Figure 4.1). Host effects on timing of emergence were less clear. In thinned stands, offspring emerged earlier on average from logs originating from thinned stands compared to those from unthinned stands, as expected (Haack *et al.* 1985),

but the result was the opposite in unthinned stands. However, overall there were important indirect effects of thinning mediated through host quality.

Although there was a treatment level correspondence between tree quality and beetle production, the relationships were less clear when characteristics of individual trees were considered. The effect of tree growth rate, previously shown to strongly enhance offspring production in *I. pini* (Reid and Robb 1999, Reid and Glubish 2001), had only a detectable, positive effect on offspring emergence time in this study. Offspring were larger if they developed in larger diameter logs, but diameter was controlled experimentally at the treatment level. However, under natural conditions, diameter could translate into a treatment effect, because live trees remaining in thinned stands are larger, on average, than those in unthinned stands (Chapter 3). Curiously, when phloem thickness of individual trees had a significant effect, it was negative: more offspring were produced when phloem was thinner, a result contrary to previous research (Haack *et al.* 1985, 1987a, b, Amman and Pasek 1986). Furthermore, the effects of treatment origin were stronger when individual tree characteristics were considered explicitly in the statistical models, indicating that thinning had some effect(s) on host quality for bark beetles for which I did not account. Thus, the mechanisms by which thinning affects beetle production via host quality remain unclear.

Host quality could affect beetle reproduction indirectly if it altered patterns of colonization by beetles. Logs originating from thinned stands were colonized earlier than those from unthinned stands (Chapter 3), and earlier colonization corresponded strongly to increased numbers and size of offspring being produced, perhaps due to detrimental effects of higher phloem moisture that increased over the season. The effects of male

colonization date may explain why treatment origin effects became significant once this (and other) covariates were included in the models. Males settled earlier on logs from thinned stands, but overall these logs were less suitable for reproduction than those from unthinned stands once colonization date was taken into account. Similarly, logs from thinned stands were colonized at higher densities (Chapter 3), and offspring number and size was positively related to breeding density, in contrast to previous work (Anderbrant *et al.* 1985, Anderbrant and Schlyter 1989). Thus it appears that adult *I. pini* may be behaving maladaptively when colonizing logs from thinned stands, because these logs reduce offspring performance. Insect herbivores do not always choose hosts where performance is highest, and this may be related to search behaviour, host plant availability or quality, among other things (reviewed in Mayhew 1997).

Direct effects of stand thinning on bark beetle development due to temperature were not evident. Because of the higher temperatures in thinned stands, I expected that offspring would emerge earlier and with smaller body size than those in unthinned stands (Atkinson 1994). Such effects are common in studies that experimentally manipulate temperature (Atkins 1967, Safranyik and Whitney 1985, Haack *et al.* 1985, Wagner *et al.* 1987). However, my results did not reveal a strong trade-off between development time and body size. Although I did detect a negative effect of temperature on offspring size, this did not translate into a general effect of thinned stands. The development stand treatment that yielded the earlier emerging offspring differed depending on whether the logs had originated from thinned and unthinned stands, further suggesting that stand temperature was not a primary factor influencing beetle development in this study. However, stand conditions during development may interact with host quality though

previous work has shown that this interaction may not occur in a consistent way with respect to temperature (Stamp and Yang 1996).

This study documents multiple interactions between biotic and abiotic conditions that significantly influence development in an herbivorous insect. Overall, the host tree effects (indirect) appear more important than the stand effects (direct) on development of *I. pini* offspring. Although thinned stands were warmer, and offspring developing at higher temperatures emerged at a smaller final size, this did not translate into a general effect of thinning. When developing in logs from unthinned stands, more offspring were produced and offspring emerged at larger body size, consistent with the observation that trees from unthinned stands were of higher quality. However, *I. pini* preferred to colonize trees from thinned stands, suggesting that the cues used during habitat search may be disconnected from the consequence of those choices.

CHAPTER 5: GENERAL CONCLUSIONS

Forest thinning altered bark beetle abundance, reproduction and development significantly. *Ips pini* were an order of magnitude more abundant in thinned stands than in unthinned stands up to seven years after forest harvest. Furthermore, experimental logs in thinned stands were colonized by male *I. pini* at significantly higher densities than logs in unthinned stands. In contrast, another species of secondary bark beetle, *Trypodendron lineatum*, was more abundant in unthinned stands and the abundance of a bark beetle predator, *Thanasimus undatulus,* did not change as a result of thinning. *Ips pini* tended to colonize trees that originated from thinned stands yet performed better when reproducing and developing in trees from unthinned stands. Below I review the changes in stands and trees that result from forest thinning and summarize how these changes influence plant-insect interactions directly and indirectly via alterations in abiotic conditions, host plants and predation pressure.

Effects of Thinning on Forest Stands

Forest thinning changed the biotic and abiotic environment of forest stands that persist up to seven years after harvest. As a result of tree removal during harvest, thinned stands were less dense, simplifying the physical structure of the stands. Thinning shifted species composition towards a more uniform distribution dominated by lodgepole pine trees. Thinned stands were windier than their unthinned counterparts. These three conditions likely increased input of freshly downed lodgepole pine trees in thinned stands. Finally, after thinning, stands were warmer, and as a result more degree-days accumulated.

Effects of Thinning on Trees

The effects of thinning on trees growing in thinned stands were not as I had predicted. Trees remaining after harvest in thinned stands were larger on average than those in unthinned stands. However, this effect was not due to an improvement in the growth rates of trees in thinned stands after a reduction in competition, as recent growth rates did not differ between trees growing in thinned and unthinned stands. In addition, contrary to my expectation, trees growing in thinned stands had thinner phloem and less phloem nitrogen than trees in unthinned stands. Phloem moisture content did not differ between trees growing in thinned and unthinned stands. In sum, trees in thinned stands did not improve in terms of growth or vigour after thinning harvest.

Abiotic Effects on Bark Beetles

The reduction in stand density after thinning positively effected *I. pini.* Beetles were more abundant in less dense stands, possibly because the more open, less cluttered, thinned stands facilitated habitat search (Hindmarch 1999). This is corroborated by the fact that *I. pini* colonized almost none of the logs placed in unthinned stands. Additionally, *I. pini* likely benefited indirectly from the altered abiotic conditions within thinned forest stands. The combination of enhanced wind speeds, more widely spaced trees and the shift in tree-species composition to stands that were dominated by lodgepole pine trees likely increased habitat availability in thinned stands. The effects of increased temperatures in thinned stands on the development of *I. pini* were equivocal and inconsistent between logs originating from thinned or unthinned stands, suggesting that this effect is of minimal import for beetle development.

Host Plant Effects on Bark Beetles

Despite the increased quantity of freshly downed lodgepole pine trees available in thinned stands, it did not affect *I. pini* abundance by itself. However, *I. pini* would probably not continue to be an order of magnitude more abundant in thinned stands than in unthinned stands without continued input of fresh host material.

Overall, male *I. pini* tended to colonize trees from thinned stands. Consistent with my prediction, beetles preferred to settle on trees that were growing more vigorously before they died (Reid and Robb 1999, Reid and Glubish 2001). Consistent with my prediction, males preferred to colonize logs with thicker phloem, although thick phloem was not a characteristic of trees growing in thinned stands in my study. However, because trees in thinned stands tend to be larger, and trees with larger diameters have thicker phloem (this study, Reid and Glubish 2001), this may represent an effect of thinning that would occur under natural conditions of beetle colonization. That males preferred to colonize large diameter logs corroborates this. Finally, males preferred to colonize trees with low phloem nitrogen content, a characteristic of trees from thinned stands, however unexpected and difficult to explain.

Males in high quality logs (thicker phloem, more phloem nitrogen) attracted more mates. Curiously, males also attracted more mates on smaller diameter logs. Regardless of the reasons behind larger harem sizes, all of the traits linked to enhanced mate attraction are characteristic of trees from unthinned stands. Thus, although males may prefer to colonize logs from thinned stands, they ultimately attract fewer mates on logs with such characteristics.

Furthermore, females breeding in trees from thinned stands fared relatively poorly compared to females breeding in trees from unthinned stands. Although females in trees from thinned stands laid their first eggs sooner, they also had shorter galleries and laid fewer eggs, which led to smaller clutch size for males in trees from thinned stands. These results are consistent with the observed (though not expected) result that trees from unthinned stands were better quality hosts. These treatment effects remain even when other tree characteristics were controlled in statistical models, suggesting that there is some effect of thinning for which I did not account, possibly constitutive defensive content in phloem.

Females tended to lay their first eggs sooner in larger trees, which may account for the observation that females in trees from thinned stands also laid their first eggs earlier, because trees in thinned stands are larger. Contrary to my prediction and previous work (Reid and Robb 1999, Reid and Glubish 2001), breeding in trees with higher recent growth rates was largely deleterious for females, resulting in shorter galleries. Although higher nitrogen content of phloem enhanced resource consumption, this did not translate into greater egg production, an unexpected result (Popp *et al.* 1989). The decline in male and female reproductive output when breeding in trees with thicker phloem is also contrary to my prediction based on previous work (Haack *et al.* 1985, 1987a, b, Amman and Pasek 1986), and difficult to explain considering that thick phloem is a characteristic of trees in unthinned stands, where male and female reproductive success in enhanced.

Offspring were larger and offspring production (both total and per female) was enhanced in trees from unthinned stands, indicates that trees from unthinned stands were better quality hosts. Interestingly, offspring were larger when developing in larger

diameter logs. Thus under natural conditions, beetles may benefit when developing in trees from thinned stands, because these trees are larger, on average, than trees from unthinned stands. Furthermore, offspring production was greater in logs with thinner phloem, another characteristic of trees from thinned stands. Finally, there may be an indirect benefit to developing in trees from thinned stands, because these logs tend to be colonized earlier, and trees that are colonized earlier produce more offspring and these offspring tend to be larger.

In summary, results of my experiments suggest that although *I. pini* tended to colonize trees from thinned stands, trees originating from unthinned stands are actually better quality hosts for. Several studies document such a disparity between herbivorous insect host preference and performance (reviewed in Mayhew 1997). However, when individual tree characteristics were considered, many traits linked to improved herbivore performance were characteristics of trees growing in thinned stands. Thus, under natural conditions of habitat colonization, such a divergence between choice and consequence may not be so substantial.

Predator Effects on Bark Beetles

The number of *T. undatulus* did not differ between thinned and unthinned stands, though I had predicted that *T. undatulus* might be more abundant in unthinned stands. However, the ratio of prey to predators was higher in thinned stands than in unthinned stands, possibly reducing per-capita predation pressure in thinned stands. Overall, I found a positive relationship between the abundance of *I. pini* and the abundance *T. undatulus* suggesting that there is a decelerating functional response between predators and prey in this system. Overall, at high prey densities, clerids exert diminished predation pressure

than at lower prey densities (Reeve 1997). Thus, in thinned stands *I. pini* may benefit from a reduction in predation pressure, even though predator abundance does not change after thinning.

Environmental Change and Plant-Insect Interactions

Bark beetles were affected by both the direct and indirect effects of forest thinning (Figure 1.1). The reduction in stand density, a direct result of forest harvest, was correlated with increased abundance of *I. pini*. Interestingly, changing temperature conditions had little effect on beetle abundance and development. Previous work suggests that herbivorous insects should be sensitive to subtle changes in temperature regimes, like those that result from global climate change (Bale *et al.* 2002). Along the indirect bottom-up pathway, *I. pini* likely benefited from increased host availability resulting from the altered biotic and abiotic conditions within thinned stands. However, *I. pini* may have paid a cost when breeding and developing in trees from thinned stands, which were of lower quality hosts than trees growing in unthinned stands. Thus, herbivores may pay a cost, such as decreased reproductive success, if environmental change results in a decline in host quality, either by increasing defensive capabilities or decreasing nutritional content (Amwack and Leather 2002). Considering indirect top-down effects of environmental change, the decrease in the ratio of predators to prey in thinned stands was likely beneficial to *I. pini*, because at high prey densities predators are not as effective at controlling prey populations (Reeve 1997). Regardless of the decline in host quality after thinning, herbivores remain more abundant in thinned stands. This suggests that the cost of declining host quality is offset by improvements in stand structure, an increase in host availability and/or a reduction in predation probability.

Significance

This study is the first to document the long-term effects of forest thinning on plant-insect interactions. Within a complex system, I separated the biotic and abiotic effects of thinning on herbivore abundance, reproduction and development. Moreover, this study is one of the first to look at the interacting direct and indirect changes that occur after anthropogenic environmental disturbance. Furthermore, my work draws attention to the unintended and persistent effects of the manipulation of large-scale ecosystems by humans. Forest managers must consider the impact of the increased abundance of a potentially economically important herbivore if forest thinning is to be employed as a principal harvest strategy.

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