

Chapter 6

Interactions between fire, bark beetles, and tree mortality

6.1 INTRODUCTION

Coincident with our bark beetle research program, prescribed fires began to be implemented at Itasca as a management tool to promote regeneration of red pine. Within six weeks following controlled burns in April 1998, we observed that numerous red pines within the burned area were being attacked by *Ips* bark beetles. Some of the attacked trees had sustained significant crown damage from the fire and were probably destined to die in 1998 with or without bark beetles. However, other infested trees were merely scorched on the outer bark of the lower bole, and had not sustained any crown damage from the fire, yet appeared to be endangered by the subsequent beetle attacks. Some of these trees died as an apparent result of the beetle attacks (Chapter 5). Many of the scorched red pines that were under attack exhibited copious resin flow around the sites of beetle attack. This was unusual because *Ips* bark beetles have low tolerance for pine resin and do not normally infest trees that are exuding resin. Evaluating the consequences of fire for bark beetle infestations was not part of our original research objectives. However, these observations, and a preliminary review of the literature, suggested the possibility for complex interactions between fire and bark beetles at Itasca that may be at least as important to forest management decisions as interactions between windstorm and bark beetles. Therefore, we include this chapter describing what we have been able to infer about interactions between fire, bark beetles, and tree mortality.

Fire management practices are changing in many forests throughout the world, partly in response to increased recognition of the undesirable effects that fire suppression can produce in some forests, such as loss of keystone tree species (Keane et al. 1990, Tomback et al. 1995, Williams 1998). In addition to its possible beneficial effects in promoting tree regeneration, prescribed fires may have some other benefits for forest ecosystems. In some cases, fires can reduce pest outbreaks (Hadley and Veblen 1993, Mutch et al. 1993, Herr et al., 1994, Jurgenson et al. 1997, Kipfmüller and Baker 1998). One mechanism by which fires can reduce

pest outbreaks is by direct effects on insect populations (Sgardelis et al. 1995). For example, ground fires in mid-April in Itasca, might tend to kill bark beetles, which are in diapause within the forest litter at that time (Chapter 4). Indeed, fire has long been employed in agricultural and range systems to directly reduce populations of damaged insects (Miller 1978, Fellin 1980, Miller and Wagner 1984, Brennan and Harmann 1994). Fire can be an effective tool in controlling seed or cone-infesting insects (Miller 1978) and has sometimes been used as a strategy to reduce populations of bark beetles (Smith et al. 1983, Stock and Gorley 1989). However, some insect populations rebound rather quickly after fire (Collet 1998, Greenberg and MacGrane 1996) perhaps because fires also reduce populations of predators such as *Thanasimus dubius*, which also tend to overwinter in forest litter.

The net effect of fires on forest pests is difficult to predict because tree defenses may be compromised by the fire and because reductions in the insect population due to mortality may be more than compensated by increases in immigration into the burned area (McCullough et al. 1998). Forest fires produce volatiles that are highly attractive to some insect pests and may draw insects from kilometers away (Muona and Rutanen 1994, Holsten et al. 1995, Hart 1998, Schmitz and Blekmann 1998). In particular, some bark beetles show a clear preference for colonizing burned trees (Dixon et al. 1984, Gara et al. 1984, Geiszler et al. 1984, Ehnstrom et al. 1995, Markalas 1991). So in some forest systems, fire can exacerbate damage from forest insects (Geiszler 1980, Gara et al. 1984, Geiszler et al. 1984, Baylis and James 1986, Rasmussen et al. 1996). It is not known why insects are attracted to scorched trees. It may be that they are searching for trees that have been killed outright by the fire and occasionally make mistakes by attacking live trees. It is also possible that fire causes physiological trauma in trees that changes their nutritional quality or limits their defensive responses against attack. Fire damage increases the nutritional quality of lodgepole pine bark for mammals (Jakubas et al. 1994). Any effects of fire

on resin flow in pine trees would be of special significance because resin is the primary defense of pine trees against bark beetles and their associated pathogens (Reeve et al. 1995).

The literature indicates that forest fires can both decrease and increase damage from forest insects. Presumably the outcome depends upon the nature of the fires as well as the species of trees and insect that are involved. It is well known that insects attacks can influence future fires by killing trees and increasing combustible fuels (Geiszler et al. 1980, Wood 1982, Raffa and Berryman 1987).

6.2 METHODS

Response of Itasca bark beetle populations to fire. We used pheromone-baited funnel traps to sample the abundances of *Ips* species and their specialist predators, including *Thanasimus dubius* (Coleoptera: Cleridae) in 23 locations scattered throughout the old growth pine forests of Itasca State Park (Chapter 3). Sampling was conducted in 1997 and again in 1998. Ten sample sites in old growth pine forests were within the prescribed burn conducted in April 1998. Each site was sampled with an array of three traps separated by ~15 m and configured as an equilateral triangle. Within a site, each trap was baited with either ipsdienol + lanierone (produced and preferred by *I. pini*), ipsenol (produced and preferred by *I. grandicollis*), or ipsdienol + ipsenol (produced and preferred by *I. perroti*). Traps were implemented by 1 July in 1997 and 5 May in 1998 and emptied every two weeks through late September in both 1997 and 1998. Pheromone lures were rotated around the array each time the traps were checked to control against spurious effects of trap position. We counted and identified all the *Ips* and *T. dubius* that were captured. Abundance levels were analyzed with an ANOVA model on log transformed data that included burn, date of sampling, burn x date, and site nested in fire.

Effects of prescribed fire on resin flow. We measured the resin flow of 120 mature red pines, 10 trees in each of 12 sites, in August 1997 and July and August 1998 (see Chapter 2 for detailed protocol, description of study sites, and other measurements of the same trees). Two study sites were within the area of the April 1998 prescribed burn. All 10 trees at one site and five trees at the second site were damaged by the fire. Fire damage

was assessed as height of highest bark charring (range = 0.35 to 11.54 m, mean \pm SE = 4.57 \pm 0.91 m). The change in resin flow from 1997 to 1998 was calculated for each tree as $\Delta \text{Resinflow} = \sqrt{\text{Resin98}} - \sqrt{\text{Resin97}}$, where $\sqrt{\text{Resin98}}$ and $\sqrt{\text{Resin97}}$ equal the square root of resin flow (g) in 1997 and 1998. (Square root transformations corrected for mild heteroscedasticity of the data and permitted the application of parametric statistics.) Change in resin flow was analyzed with an ANOVA model that included burn, date of sampling in 1998, burn x date of 1998 sampling, crown class, crown class x burn, and burn nested in tree and crown. The relationship between char height and change in resin flow was evaluated with a linear regression.

Effects of experimental scorching on resin flow and beetle attacks. During 1999, we conducted additional experimental studies of the effects of fire on resin flow. We used a large propane torch to burn one side of 40-year-old red pines from a height of 0.5 - 1.5 m on the bole. Within the one meter treatment area, we exposed each of three equally spaced targets to 60 seconds of flame. This treatment had the effect of raising cambium temperatures beneath the bark to about 50 °C and produced scorching damage on the surface of the bark that matched that of many trees within the prescribed burn at Itasca. In most naturally scorched trees, as in our experimental trees, the scorching is largely restricted to one side of the tree (corresponds to the downwind side in a surface forest fire). We measured resin flow of the experimentally scorched trees, and a matched set of control trees, 1 d prior to fire treatment, 3 d after treatment, 9 d after treatment, and 60 d after treatment. Experimental and control trees were intermixed within 1 ha of homogenous, even-aged forest. We also measured the resin flow in 10 red pines that were scorched during May 1999 in a small wildfire in the same forest. Immediately after the fire treatment, we placed pheromone baits (ipsdienol or ipsenol) on 13 of 30 trees within each treatment and began to monitor beetle landings using sticky traps (30 cm of plastic wrap, sprayed with Tanglefoot) wrapped around the circumference of trees at 2 m height. On 25 August 1999, we carefully examined all the study trees to count the number of beetle attacks and evaluate their progress. These studies were conducted at our study sites near Colfax, WI.

6.3 RESULTS AND DISCUSSION

Abundance of *Ips* in burned forests. We captured 3697 *I. pini*, 872 *I. grandicollis*, 408 *I. perroti*, and 1759 *T. dubius* in 1998 (Chapter 3, Appendix 4). Compared to unburned sites, the abundance of *I. pini* in burned sites was significantly higher during May of 1998, significantly lower during late July and early August, and no different in September (Fig. 6.1). The abundance of *I. grandicollis* and *I. perroti*

was no different between burned and unburned sites. The abundance of *T. dubius* was significantly increased in burned sites, especially during May. Because the fire was conducted prior to the time when most beetles had not emerged from their overwintering sites in the forest litter, the ground fire must have directly killed many insects.

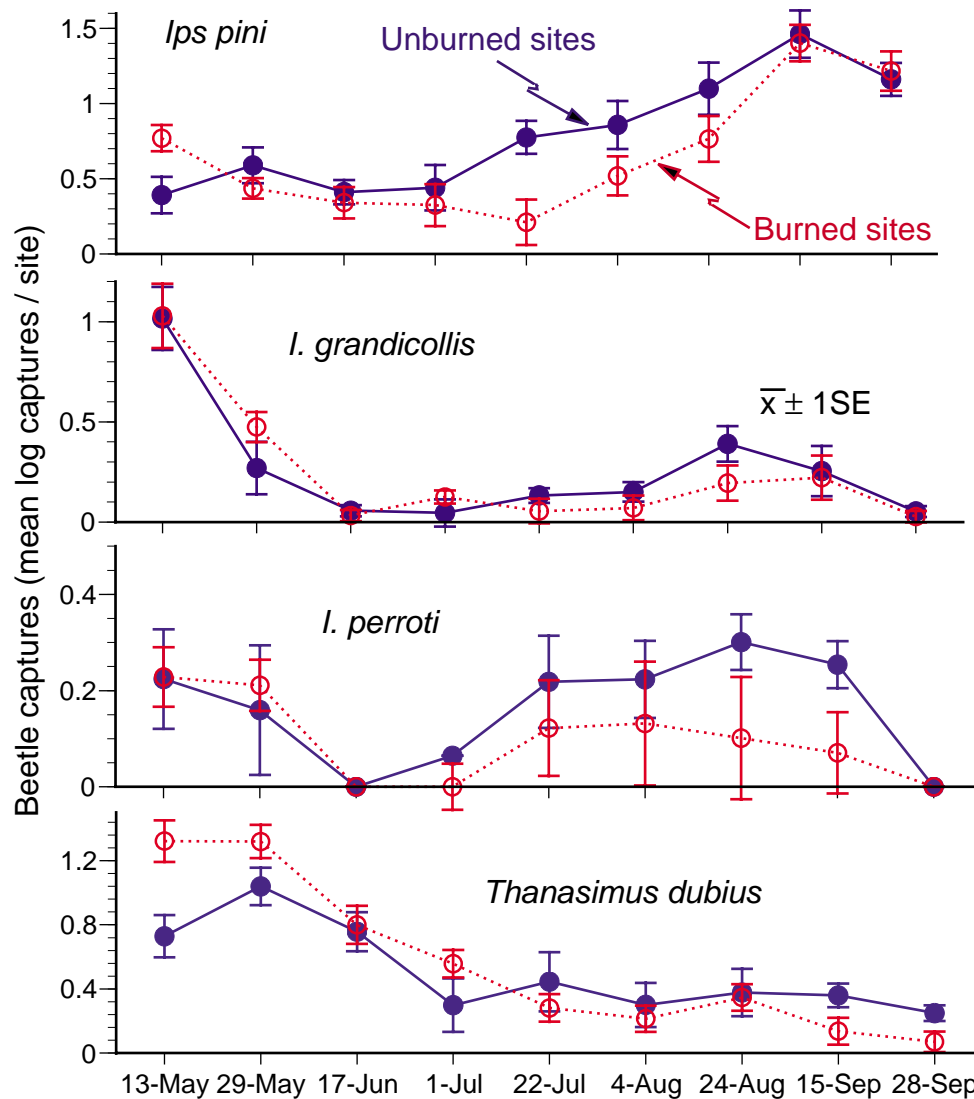


Figure 6.1. Captures during 1998 of bark beetles at sites within old-growth pine forests that were and were not exposed to prescribed fire in April 1998.

The fact that beetle abundance in burned areas increased or remained the same during May implies that there must have been significant immigration of beetles into the burned areas. The temporary decrease in *I. pini* abundance during late July and early August (Fig. 6.1) could have been due to reduced reproductive success of the first generation in burned areas, where they encountered somewhat higher numbers of predators and relatively high resin flow in some of the trees that they attacked. The overall pattern seems to be that fire had only limited and short-term effects on the abundance of bark beetles

Effects of prescribed fire on resin flow. Two to three months after the fire, resin flow was significantly increased in trees that were exposed to fire compared to those that were not (Fig. 6.2; $F_{1,116} = 6.04$, $P = 0.015$). Trees with low initial resin flow in 1997 showed the greatest increases in resin flow (Fig. 6.2), but there was no effect of crown class (codominant vs intermediate) on the change in resin flow ($F_{1,116} = 0.43$), nor was there any interaction between crown class and fire ($F_{1,116} = 0.28$). Resin flow did not differ between measurements in July and August of 1998. There was a positive relationship between char height (up to 10 m) and change in resin flow ($r^2 = 0.26$, $P = 0.004$).

Effects of experimental scorching on resin flow and beetle attacks. Three days after experimental scorching, resin flow was reduced by about 75% on the scorched side of the tree, with no effect on the unscorched side of the trees (Fig. 6.3, upper middle). Nine days after the fire, resin flow was still reduced by 50% in scorched trees relative to control trees, and the effect was evident on both sides of the scorched trees (Fig. 6.3, upper right). Thirty days after the May wildfire in Colfax, resin flow in scorched trees was almost three-fold higher than in unburned trees (Fig. 6.3, lower left). Sixty days after the experimental scorching, resin flow was about two-fold higher in scorched trees than in control trees (Fig. 6.3, lower right). Bark beetles were much more likely to attack and colonize burned trees than unburned trees (Table 6.1). Nine weeks after the scorching treatment, 11 of 30 burned trees contained *Ips* galleries compared to 0 of 30 control trees (Table 6.1). All of the trees that sustained high attack rates had been baited with a pheromone bubble cap, so presumably the attack rates were higher than they would have been without baiting, but because both burned and unburned trees were baited, it is still clear that the fire treatment increased attack rates. These patterns were also evident at

Itasca, where we observed many trees that were rapidly colonized by *Ips* within the scorched area of the lower trunk that was downwind at the time of the prescribed fires in spring of 1998 and 1999 (Fig. 6.4, left).

Feedbacks between fire, bark beetles, and tree mortality. Scorching of the outer bark that accompanies ground fires apparently produces physiological trauma to the inner bark that, for at least 9 d after the fire, compromises the ability of trees to defend themselves by exuding resin from wounds. Presumably bark beetles have evolved the ability to detect fire volatiles, fly to trees that have sustained fire damage, and preferentially attack scorched areas within those trees because their chances for reproductive success are enhanced in trees with reduced resin flow. Recently burned forests are also likely to contain trees that have been completely killed by the fire and have no defenses against beetle attack. However, it appears that bark beetles have only a limited window of opportunity to successfully colonize fire-damaged trees because red pines facultatively increase their resin flow to even higher than baseline levels within 30 d after the fire. This may be an evolved response of red pines to the increased risks of bark beetle attack that accompany fires. In many scorched trees at Itasca and Colfax,

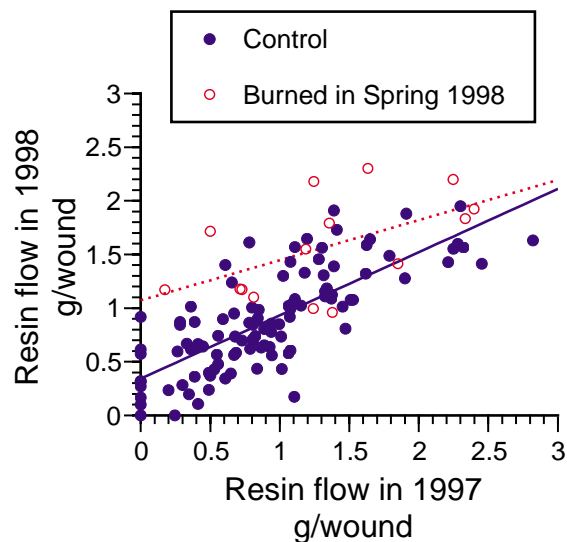


Fig. 6.2. Resin flow in 1998 vs 1997 for mature red pines that were and were not exposed to prescribed fires in the spring of 1998. Trees exposed to fire had significantly elevated resin flow by mid summer of 1998 compared to trees that were not scorched. The difference was especially pronounced in trees that relatively low baseline resin.

copious resin flow in the scorched region of the bole appeared to limit the spatial extent of girdling from bark beetle infestations (Fig. 6.4, right). Some mature red pines that were attacked by beetles following fire damage in the spring of 1998 were still alive in the fall of 1999 and were no longer under attack by beetles (see red pine in Fig. 5.2, lower).

Table 6.1. Number of experimentally burned and unburned trees with bark beetle attacks, oviposition galleries, and surviving *Ips* nine weeks after scorching treatments were applied. Experiment included 60 trees intermixed within a homogenous 1 ha stand of 40-year-old red pine. Half of the trees were experimentally scorched from 0.5 to 1.5 on one side of the bole on 22 June 1999.

Colonization By <i>Ips</i>	Unburned trees	Burned trees ^a
≥1 attack	11	19
≥5 attacks	2	11 **
Oviposition galleries	0	11 ***
Live <i>Ips</i> in bark	0	5 **

^a All attacks were on the burned side of the trees
** $P < .01$; *** $P < .001$; chi-square tests of the null hypothesis that frequencies did not differ between burned and unburned trees.

Nonetheless, scorching and associated beetle damage can result in irreparable loss of vascular connections between the roots and crown. Furthermore, death of the cambium precludes additional growth of wood, phloem, or bark in that region of the bole. The resulting permanent scars are referred to by foresters as “cat-faced scars” (Fig. 6.5, left). These cat-faced scars are very common in the old growth forests at Itasca. In the absence of additional fires, trees can live almost indefinitely even with large cat-faced scars. However, these scars make trees much more sensitive to damage from subsequent fires because the wood is exposed to flames without the benefit of insulation from bark. This makes it more likely that living cambium surrounding cat-faced scars will be traumatized by heat from the fire. This in turn promotes attack of the newly traumatized phloem by bark beetles. After the prescribed burns in 1998 and 1999, we observed many red pines at Itasca that contained new infestations of bark beetles localized within 20 - 50 cm of old cat-faced scars. This results in the

death of additional cambium, the loss of insulating bark (in some cases through the action of woodpeckers), an enlargement of the cat-faced scar, and increased vulnerability of the surviving cambium to heat trauma from future fires.

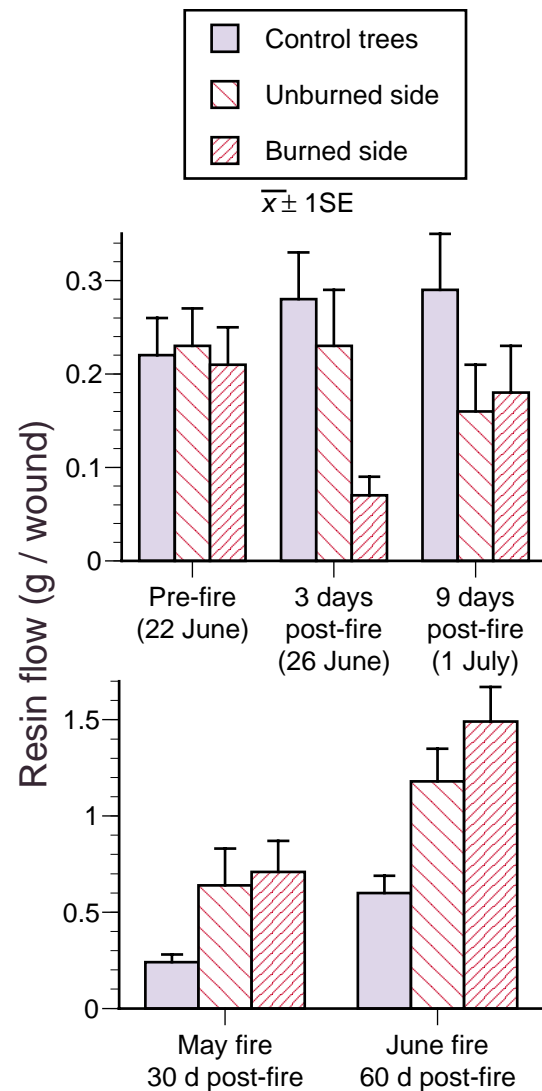


Fig. 6.3. Upper: resin flow in experimentally scorched red pines 1 d before, 3 d after, and 9 d after fire treatments. Lower: resin flow in red pines 30 d after scorching from a natural wildfire and 60 d after experimental scorching.

For images see
<http://www.dartmouth.edu/~mpayres/grants/Itasca/photos.htm>

Fig. 6.4. Left: An incipient cat-faced scar forming on a red pine in Itasca that was scorched by prescribed fire during spring 1998. *Ips* bark beetles are colonizing the scorched side of the tree that was on the downwind side of the fire. The attacks are being restricted to this region of the tree by copious resin flow around the periphery of the scorching. Nonetheless, about half the circumference of the tree has been girdled as a result of the fire and beetles. If the tree lives, this damaged area will be evident as a cat-faced scar (Fig. 6.5, left), which will increase the vulnerability of the tree to subsequent fires (Fig. 6.5, right). Right: bark beetle galleries within the phloem of a red pine that was experimentally scorched. The cambium is dead within the infested area, so further tree growth in this region of the bole would be impossible. Note how the phloem has become impregnated with resin in the region of attack, which appears to have limited the extent of the beetle galleries..

For images see
<http://www.dartmouth.edu/~mpayres/grants/Itasca/photos.htm>

Fig. 6.5. Left: Cat-faced scars in mature red pines at Itasca – probably a legacy of past fires and the localized attacks of bark beetles within scorched regions of the bole. In these trees, and many others at Itasca, the cat-faced scars bear evidence of multiple wounding events that were separated by years or decades (probably a sequence of fires followed by beetle attacks). Each wounding event tends to expand the percentage of the trunk that is girdled and increases the amount of wood that is exposed to future fires. Right: one of many trees at Itasca that died from ignition of the exposed wood in a cat-faced scar. This is the endpoint of the positive feedback cycle represented in Fig. 6.7. The downed tree will increase the local fuel load for subsequent fires and increase the probability of fire damage to adjacent trees (Fig. 6.8).

Apparently, this process of sequentially enlarging scars has been important at Itasca within the lifespan of trees that live there now. Examination of the scar tissues in many old trees at Itasca reveal cases where a scar that was initially small has become episodically enlarged at intervals that can be separated by many years. We hypothesize that most of these enlargements can be dated to fires that pre-date the recent era of active fire suppression at Itasca. Enlargement of cat-faced scars increases the probability of catastrophic damage or mortality from future disturbances, especially fires.

The forests at Itasca that were burned in 1998 and 1999 contain many trees that experienced no direct crown damage from the fire but died as a result of surface fire igniting the wood at the site of old cat-faced scars and burning out the inside of the tree (Fig. 6.5, right). This same pattern of high tree mortality from low intensity surface fires igniting old scars has also been reported in old growth forests of *Pinus sylvestris* in Sweden (Linder et al. 1998).

Thus, the interaction of fires and bark beetles can lead to the initiation of scars on the lower bole of red pines (Fig. 6.6, phase I). This initiates a system of positive feedbacks where the scarred tree

is increasingly sensitive to damage from future fires, which exposes it to additional attacks by bark beetles, which further increases the sensitivity to future fires (Fig. 6.6, phase II). This process can lead to premature death of the tree when a fire eventually burns out the lower trunk (Fig. 6.6, phase III). Presumably, the average number of fires required to kill a tree after the formation of the initial scar will be greatest if the fires are of low intensity and coincide with times of low bark beetle abundance (Fig. 6.7). There is probably an additional positive feedback because the death of trees from a current fire will tend to increase the risk of scar initiation on nearby trees because a fire-killed tree will tend to (1) increase the abundance of bark beetles that can damage other trees and (2) increase fuel load within the stand, which will increase the heat experienced by nearby trees during present and/or future fires (Fig. 6.8). Because the relationship between fire, bark beetles, and tree mortality appears to involve positive feedbacks (Figs. 6.7 - 6.8), the proportion of trees that succumb to fires would be expected to increase with each additional fire, and it would be easy for forest managers to underestimate the consequences of future fires for tree mortality.

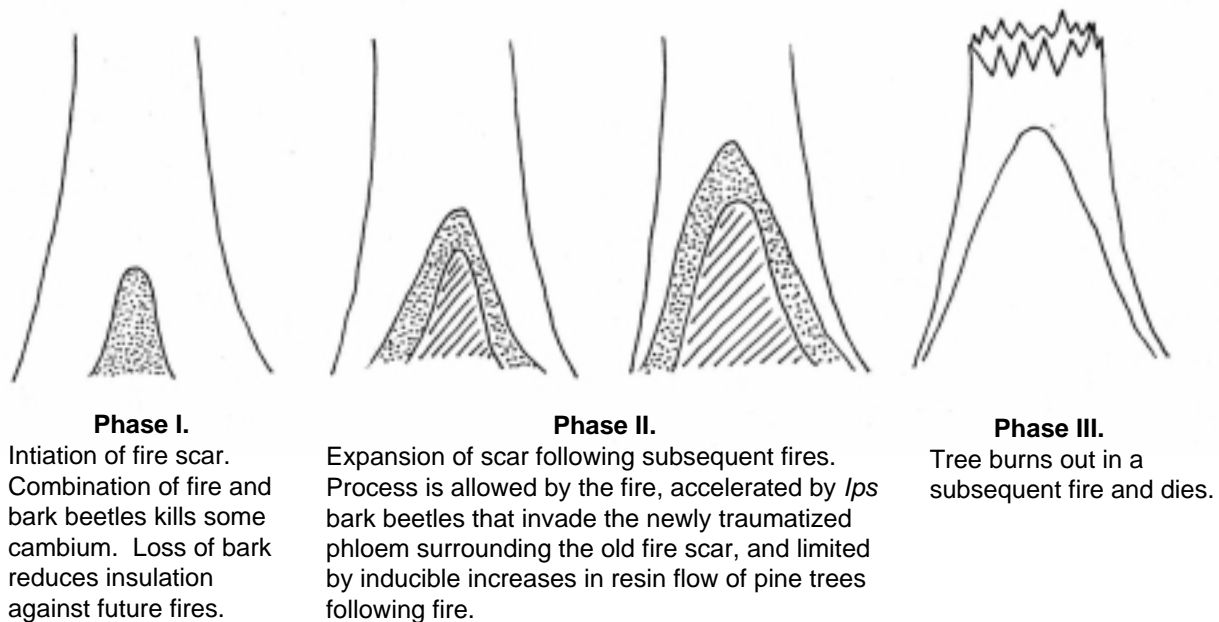


Fig. 6.6. A schematic of the process by which fire and beetles interact to produce and enlarge cat-faced scars on the lower trunk of pine trees. These scars can eventually lead to tree mortality when a surface fire ignites the exposed wood and consumes the trunk.

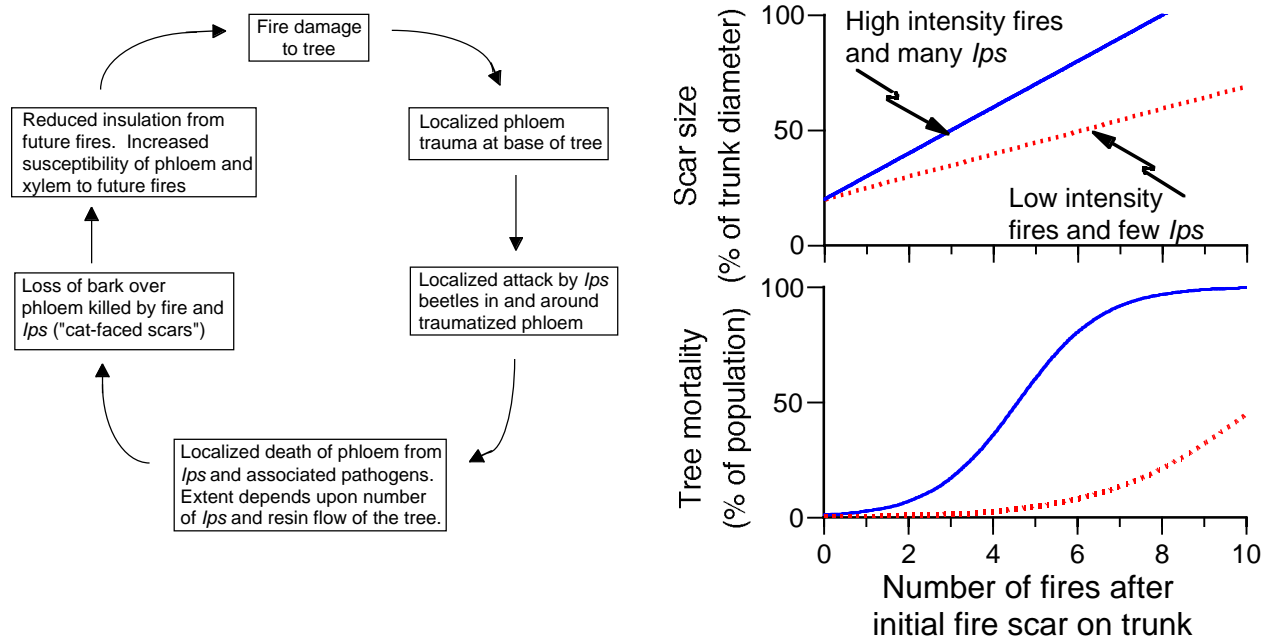


Fig. 6.7. Left: a flowchart of the positive feedback system by which fire and beetles interact to produce and enlarge cat-faced scars on the lower trunk of pine trees. The eventual outcome is for a fire to ignite the exposed wood, consume the trunk, and kill the tree. Right: the number of fire-beetle cycles from initial scar formation until the death of the tree is hypothesized to depend upon fire intensity and the abundance of bark beetles during the weeks immediately following the fire. This positive feedback system creates a risk that tree mortality from prescribed burns will tend to increase with each subsequent burn.

We expanded the simple demographic model from Chapter 5 to evaluate the potential effects of changes in tree mortality rates that might be associated with the interacting effects of prescribed fires and bark beetles on the survivorship of old growth pines in Itasca. With the mortality rates that we used in Chapter 5, a hypothetical pine forest would be reduced to half in about 65 years. It was beyond the scope of this study to develop rigorous estimates of these mortality rates for Itasca, but we used rates that matched our data and intuition for Itasca. Furthermore, a half-life of 65 years seems realistic to us. Prescribed fires will tend to decrease the survivorship of red pine adults at Itasca through (1) the direct effects of killing trees, (2) indirect effects of increasing short term attack rates by bark beetles, and (3) producing scars that increase future susceptibility to fires and beetles. These processes imply an increase in all four parameters that determine mortality rates in Fig. 6.9 ($M1$, $M2$, and $M3$). In the absence of demographic data for mature red pines subjected to surface fires, we can only guess at the magnitude of these increases, but a doubling or tripling of mortality rates does not seem

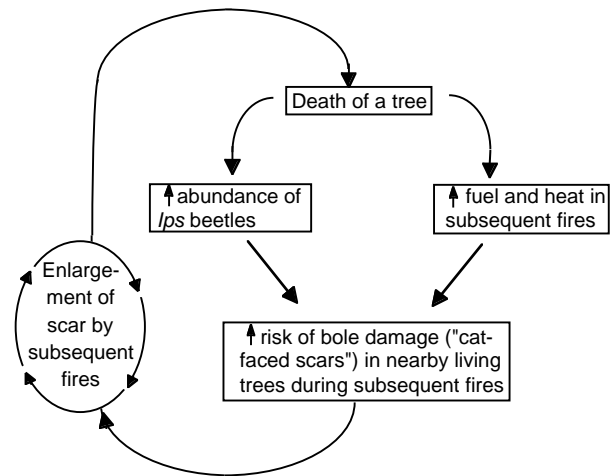


Fig. 6.8. A flowchart of the positive feedback system by which the death of one tree from fire can contribute to the death of nearby trees. When a tree dies, it can provide food that increases the population of bark beetles and fuel that increases the heat of future fires, both of which increase the probability that scars will be initiated on nearby trees. The loop at left is depicted in Figs. 6.6 - 6.7. This positive feedback loop creates a risk that tree mortality from prescribed burns will tend to increase with each subsequent burn.

improbable. For example, if direct mortality from fires of unwounded trees is 10 trees per 1000 and fires are applied every five years, this corresponds to an increase of 2.5 / 1000 in $M1$, as in the middle scenario of Fig. 6.9. Similarly, if fire induces beetle attacks in 50 trees / 1000 (compare to 11 / 30 trees in Table 6.1), and half of them are killed outright (see Chapter 5), then $M2$ and $M3$ would increase to 10 / 1000, as in the middle scenario of Fig. 6.9.

The model depicted in Fig. 6.9 clearly illustrates that even modest increases in tree mortality rates, which should be expected with the implementation of prescribed fires, could have rather dramatic impacts on the future of old growth forests at Itasca. The model should not be taken as a forecast of tree mortality patterns at Itasca, but as a starting point for the development of models that can guide management decisions by incorporating the processes through which fire and beetles interact to influence tree survival. Demographic models such as these should be refined, parameterized, and evaluated in concert with the development of fire management practices at Itasca. Presumably the optimal fire management strategy is one that carefully balances the costs of reduced survivorship in mature trees against the benefits of possible improvements in red pine regeneration and forest aesthetics.

6.4 MANAGEMENT RECOMMENDATIONS TO MINIMIZE TREE MORTALITY ASSOCIATED WITH PRESCRIBED FIRES

Recommendations that follow from Fig. 6.7.

- Limit fire intensity to minimize the number of new scars that are initiated with each fire.
- Limit fire intensity in areas with scarred trees.
- Increase duration between fires as much as possible, especially in areas with scarred trees.
- Conduct burns when existing scars will be on the upwind side of trees rather than the downwind side of trees.
- Limit intensity and frequency of fires in stands where pine trees have low resin flow.
- Implement a low cost program for monitoring *Ips* population abundance (see Chapter 3) and use these data to:
 - burn in years with relatively low abundance of *Ips* (e.g., following summers of low abundance of *Ips* and winters with high mortality of *Ips*); and
 - burn in park regions where the local abundance of *Ips* is low; avoid areas where the local abundance is high, such as in the vicinity of recent blowdowns.

- Conduct sampling after controlled burns to (1) estimate the probability of new scars, (2) map the location of scarred trees, (3) monitor scar expansion on previously scarred trees, (4) record any tree deaths, (5) estimate the probability of tree death from fire as a function of previous scar size, and (6) map the location of red seedlings and saplings that would be vulnerable to future ground fires.

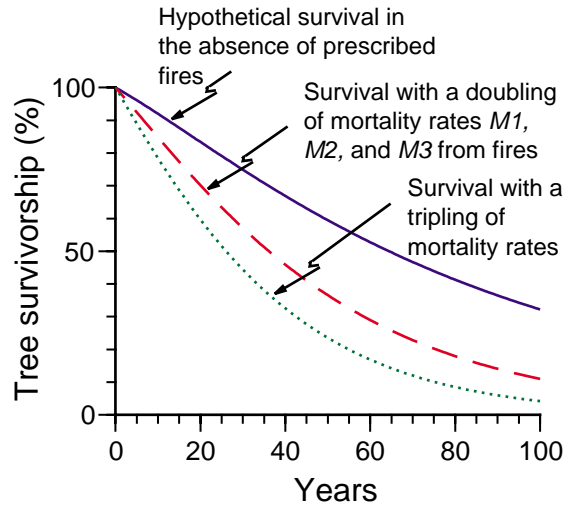


Fig. 6.9. Survivorship curves for a hypothetical population of red pines with annual mortality rates from bark beetles and other causes as estimated in Chapter 5, compared to scenarios with increased mortality rates that might be associated with the interacting effects of prescribed burns and bark beetles. The baseline model assumes constant annual mortality rates in unwounded trees of 5 trees / 1000 from bark beetles (= parameter $M1$) and 2.5 trees / 1000 from other causes ($M2$). The model further assumes that 5 trees / 1000 are wounded from bark beetles or fire per year ($M3$) and that these sustain an annual mortality rate of 50 trees / 1000 ($M4$). With a doubling of $M1$, $M2$, and $M3$, the hypothetical tree population would be reduced to half in 37 years instead of 65 years. With a tripling, it would be reduced to half in 27 years.

Recommendations that follow from Fig. 6.8

- Keep duration between fires long enough to avoid high *Ips* populations from last fire.
- Limit *Ips* increases in trees killed by fires by debarking, flaming, or mass trapping. However, this may have undesirable side effects of reducing the abundance of *Ips* predators and lowering the naturally high biodiversity associated with dead trees, so previous recommendation is preferred except perhaps in cases where there are clusters of downed trees.
- Monitor duration and spatial scale of *Ips* population increases associated with fires in general and downed trees in particular.
- Map the location of downed trees.
- Attempt to limit fire intensity in areas with downed trees.
- Increase duration between fires in areas with downed trees.

6.5 REFERENCES CITED

- Baylis, N. T., R. C. De, and D. B. James. 1986. Observations of damage of a secondary nature following a wild fire at the otterford state forest south africa. *South African Forestry Journal* :36-37.
- Brennan, L. A. and S. M. Hermann. 1994. Prescribed fire and forest pests - solutions for today and tomorrow. *Journal of Forestry* 92:34-37.
- Collett, N. G. 1998. Effects of two short rotation prescribed fires in autumn on surface-active arthropods in dry sclerophyll eucalypt forest of west-central victoria. *Forest Ecology & Management*. 107:253-273.
- Dixon, W. N., J. A. Corneil, R. C. Wilkinson, and J. L. Foltz. 1984. Using stem char to predict mortality and insect infestation of fire-damaged slash pines *Pinus elliottii*. *Southern Journal of Applied Forestry* 8:85-88.
- Ehnstrom, B., B. Langstrom, and C. Hellqvist. 1995. Insects in burned forests-forest protection and faunal conservation (preliminary results). *Entomologica Fennica* 6:109-117.
- Gara, R. I., D. R. Geiszler, and W. R. Littke. 1984. Primary attraction of the mountain pine beetle *Dendroctonus ponderosae* to lodgepole pine *Pinus contorta* in Oregon USA. *Annals of the Entomological Society of America* 77:333-334.
- Geiszler, D. R., R. I. Gara, C. H. Driver, V. F. Gallucci, and R. E. Martin. 1980. Fire, fungi (*Phaeolus schweinitzii*) and beetle (*Dendroctonus ponderosae*) influences on a lodgepole pine (*Pinus contorta*) ecosystem of south central Oregon USA. *Oecologia* 46 :239-243.
- Geiszler, D. R., R. I. Gara, and W. R. Littke. 1984. Bark beetle infestations of lodgepole pine, *Pinus contorta* var *murrayana*, following a fire in south central Oregon USA. *Zeitschrift Fuer Angewandte Entomologie* 98 :389-394.
- Greenberg, C. H. and A. McGrane. 1996. A comparison of relative abundance and biomass of ground-dwelling arthropods under different forest management practices. *Forest Ecology & Management*. 89: 31-41.
- Hadley, K. S. and T. T. Veblen. 1993. Stand response to western spruce budworm and douglas-fir bark beetle outbreaks in the Colorado front range. *Canadian Journal of Forest Research* 23 :479-491.
- Hart, S. 1998. Beetle mania: an attraction to fire. *BioScience*. 48:3-5.
- Herr, D. G., L. C. Duchesne, R. Tellier, R. S. Mcalpine, and R. L. Peterson. 1994. Effect of prescribed burning on the ectomycorrhizal infectivity of a forest soil. *International Journal of Wildland Fire* 4:95-102.
- Holsten, E. H., R. A. Werner, and R. L. Develice. 1995. Effects of a spruce beetle (Coleoptera: Scolytidae) outbreak and fire on Lutz spruce in Alaska. *Environmental Entomology* 24: 1539-1547.
- Jakubas, W. J., R. A. Garrott, P. J. White, and D. R. Mertens. 1994. Fire-induced changes in the nutritional quality of lodgepole pine bark. *Journal of Wildlife Management* 58 :35-46.
- Jurgensen, M. F., A. E. Harvey, R. T. Graham, D. S. Page-Dumroese, J. R. Tonn, M. J. Larsen, and T. B. Jain. 1997. Impacts of timber harvesting on soil organic matter, nitrogen, productivity, and health of inland northwest forests. *Forest Science* 43:234-251.
- Keane, R. E., S. F. Arno, J. K. Brown, and D. F. Tomback. 1990. Modelling stand dynamics in whitebark pine *Pinus albicaulis* forests. *Ecological Modelling* 51:73-96.
- Kipfmuller, K. F. and W. L. Baker. 1998. Fires and dwarf mistletoe in a Rocky Mountain lodgepole pine ecosystem. *Forest Ecology & Management* 108:77-84.
- Linder, P., P. Jonsson, and M. Niklasson. 1998. Tree mortality after prescribed burning in an old-growth scots pine forest in northern sweden. *Silva Fennica*. 32: 339-349.
- Markalas, S. 1991. Insects attacking burnt pine trees *Pinus halepensis*, *Pinus brutia*, and *Pinus nigra* in Greece. *Anzeiger Fuer Schaedlingskunde Pflanzenschutz Umweltschutz* 64 :72-75.
- McCullough, D. G., R. A. Werner, and D. Neumann. 1998. Fire and insects in northern and boreal forest ecosystems of North America. *Annual Review of Entomology* 43:107-127.
- Miller, W. E. 1978. Use prescribed burning in seed production areas to control red pine cone beetle. *Environmental Entomology* 7:698-702.
- Miller, W. E. and M. R. Wagner. 1984. Factors influencing pupal distribution of the pandora moth (Lepidoptera: Saturniidae) and their relationship to prescribed burning. *Environmental Entomology* 13:430-431.
- Muona, J. and I. Rutanen. 1994. The short-term impact of fire on the beetle fauna in boreal coniferous forest. *Annales Zoologici Fennici* 31:109-121.
- Mutch, R. W., S. F. Arno, J. K. Brown, C. E. Carlson, R. D. Ottmar, and J. L. Peterson. 1993. Forest health in the Blue Mountains a management strategy for fire-adapted ecosystems. U S Forest Service General Technical Report PNW-310:1-14.

- Raffa, K. F. and A. A. Berryman. 1987. Interacting selective pressures in conifer-bark beetle systems a basis for reciprocal adaptations. *American Naturalist* 129:234-262.
- Rasmussen, L. A., G. D. Amman, J. C. Vandygriff, R. D. Oakes, A. S. Munson, and K. E. Gibson. 1996. Bark Beetle and Wood Borer Infestation in the Greater Yellowstone Area During Four Postfire Years. USDA Forest Service Intermountain Research Station Research Paper 487:1-10.
- Reeve, J. R., M. P. Ayres and P. L. Lorio, Jr. 1995. Host suitability, predation, and bark beetle population dynamics. Pages 339-357 in Cappuccino, N. and P. W. Price, editors. *Population dynamics: New approaches and synthesis*. Academic Press, San Diego, CA.
- Schmitz H and Bleckmann H. 1998. The photomechanic infrared receptor for the detection of forest fires in the beetle *melanophila acuminata* (coleoptera: buprestidae). *Journal of Comparative Physiology A- Sensory Neural & Behavioral Physiology*. 18: 647-657.
- Sgardelis, S. P., J. D. Pantis, M. D. Argyropoulou, and G. P. Stamou. 1995. Effects of fire on soil macroinvertebrates in a Mediterranean phryganic ecosystem. *International Journal of Wildland Fire* 5:113-121.
- Smith, D., R. Mrowka, and J. Maupin. 1983. Underburning to reduce fire hazard and control *Ips* beetles in green thinning slash. *Fire Management Notes* 44:5-6.
- Stock, A. J. and R. A. Gorley. 1989. Observations on a trial of broadcast burning to control an infestation of the mountain pine-beetle *Dendroctonus-ponderosae*. *Canadian Entomologist* 121:521-523.
- Thomas, T. L. and J. K. Agee. 1986. Prescribed fire effects on mixed conifer forest structure at Crater Lake, Oregon USA. *Canadian Journal of Forest Research* 16:1082-1087.
- Tomback, D. F., J. K. Clary, J. Koehler, R. J. Hoff, and S. F. Arno. 1995. The effects of blister rust on post-fire regeneration of whitebark pine: the Sundance burn of northern Idaho (U.S.A.). *Conservation Biology* 9:654-664.
- Williams, C. E. 1998. History and status of table mountain pine-pitch pine forests of the southern Appalachian Mountains (USA). *Natural Areas Journal* 18:81-90.
- Wood, S. L. 1982. The bark beetles and ambrosia beetles of North America and Central America (Coleoptera: Scolytidae) a taxonomic monograph. *Great Basin Naturalist Memoirs* 6:1-1359.