

Executive summary

From June 1997 through September 1999, we conducted a study of interactions between bark beetles and pine trees in the old growth pine forests of Itasca State Park. The program was initiated in response to severe windstorms in 1996-97 that blew down many large pine trees and led to a dramatic increase in populations of bark beetles within the park. Under some conditions, epidemic populations of bark beetles can overwhelm tree defenses and produce extensive mortality in healthy trees. Consequently, the windstorms created a significant risk for the high-value old-growth forests of Itasca State Park. The objective of our research was to expand knowledge of the bark beetle communities in Itasca State Park, assess patterns of tree resistance and host suitability within the park, evaluate the extent to which bark beetles impact tree survivorship at Itasca, and provide guidance for future management decisions. A complementary research program directed by Dr. Stephen Teale, State University of New York at Syracuse, addressed related issues including the efficacy of beetle control programs.

THE BARK BEETLE COMMUNITY

Pine trees at Itasca Park can be colonized by more than 10 species of bark beetles (Scolytidae), of which the most common are *Ips pini*, *I. grandicollis*, and *I. perroti*. These three species differ in their relative abundance and life history. Flying adults of *I. grandicollis* are most abundant in May and most of the population seems to have only one generation per year. In contrast, *I. pini* has 2-3 generations per year at Itasca, and flying adults are most abundant in early September. *I. perroti* has 1-2 generations per year at Itasca and flying adults are most abundant in August. During 1998, across 24 trapping stations scattered through the old growth pine forests at Itasca, average cumulative captures for *I. pini*, *I. grandicollis*, and *I. perroti* were 142, 30, and 16 beetles • trap array⁻¹ • year⁻¹. By virtue of having multiple generations per year, *I. pini* has the greatest capacity for rapid increases in population size following blowdowns. Other things being equal, late summer populations of *I. pini* probably represent the greatest threat to pine trees at Itasca. However, the early season flight of *I. grandicollis* may be the greatest threat to trees that have been

weakened by winter damage or spring fires. Both *I. pini* and *I. grandicollis* tend to increase in abundance when windstorms blow down suitable host trees. In 1997, the local abundance of *I. pini* was about three-fold higher within sites that sustained blowdowns, but was no higher than background levels at sites 200-300 m away from the blowdowns. In 1998, the abundance of *I. grandicollis* was elevated by about two-fold within blowdowns and at sites 200-300 m away from blowdowns. The restricted spatial scale of population responses to blowdowns indicates that beetle control programs or risk mitigation measures in response to blowdowns could be effective when conducted on a scale of hectares and need not be conducted across many square kilometers. One other practical implication is that forests outside the park suffer little risk of outbreaks due to beetle populations within the park, and vice versa.

Except that they both responded to blowdowns, there was little correlation between the local abundance of *I. grandicollis* and *I. pini*, suggesting that different factors influence their populations, possibly predators. The community includes several specialist predators that might act as natural controls on the abundance of *Ips*. In order of decreasing abundance, these include *Thanasimus dubius* (Coleoptera: Cleridae), *Platysoma cylindrica*, and *P. parallelum* (Coleoptera: Histeridae). All of these predators appear to be univoltine (one generation per year) with the flying adults being most common in May and June. The absence of predators later in the summer must contribute to increased population growth in *I. pini*.

The abundance of predators was positively correlated with the abundance of *I. grandicollis* (perhaps because *I. grandicollis* are the most abundant prey when *T. dubius* adults are feeding and reproducing in May) but negatively correlated with the abundance *I. pini* (perhaps because *T. dubius* predation limits the abundance of *I. pini*). Interspecific competition is another potential control on bark beetle abundance. The three *Ips* species rely on the same food resources, which are frequently limiting. If *I. pini* is the most significant forest pest at Itasca, *I. grandicollis* and *I. perroti* can be thought of as natural control agents of *I. pini*. Alternatively, if *I. grandicollis* is equally likely to attack live trees, then mass-trapping of *I. pini* may allow compensating increases in the

abundance of *I. grandicollis* (because of relaxed competition from *I. pini*) and provide no net benefits in reducing tree mortality.

Three-trap arrays baited with three different combinations of commercially available pheromone blends provide an efficient means of quantifying the abundance of *Ips* and their predators at Itasca. In Chapter 3, we recommend a simple, inexpensive sampling program to monitor year-to-year trends in bark beetle populations at Itasca. This would provide a valuable tool for assessing current risks from bark beetles and adjusting the timing of forest management practices as appropriate. The logistics of this program would be especially easy because of the availability of traps and trained personnel at Itasca.

Appendix 7 is the result of a literature search for scientific papers related to *Ips* bark beetles.

NUTRITIONAL SUITABILITY OF PINE TREES FOR BARK BEETLES

Downed trees of red pine, white pine, and jack pine can all provide excellent habitat for bark beetles. Increases in population size of up to 10-fold per generation are possible (Fig. 1.2). Thus, a local population of 1000 *I. pini* could increase to 1,000,000 *I. pini* over three generations from May to October. A single downed tree could produce as many as 80,000 bark beetles. These data substantiate the concern that blowdowns can lead to rapid dramatic increases in the abundance of bark beetles.

VARIATION IN TREE DEFENSES AMONG SPECIES AND SITES

The primary defense of pine trees against bark beetles is oleoresin, a mixture of monoterpenes and resin acids that flows from wounds and provides a chemical and physical barrier to colonization by beetles. Measurements of resin flow from standardized wounds provide a means for evaluating tree resistance to beetle attack. Of the three species of pine in Itasca, jack pine has extremely low resin flow (most trees have no measurable resin flow) and appears to be most vulnerable to beetles (Fig. 1.1). On average, white pine and red pine have much higher resin flow than jack pine.

Because of the special importance of old growth red pine at Itasca, we explored in detail the patterns of variation in red pine defenses against bark beetles. There was extensive variation among 12 old growth stands of red pine in resin

flow and all measurements of tree growth, tree morphology, and stand attributes (Figs. 2.7-2.9). The old growth forest at Itasca is a mosaic of red pine stands that differ in their constitutive defenses against bark beetles and many other attributes as well. We used regression analyses to identify the simplest combinations of parameters that could predict spatial patterns in constitutive resin flow (Fig. 2.10, Tables 2.1-2.2). Average resin flow at a site can be predicted as $Resin = 0.031 \cdot DBH - 0.013 \cdot BA$, where DBH = diameter at breast height in cm and BA = basal area of the stand in m^2 / ha . This relationship explained 74% of the variation among sites in average resin flow. Thus, old growth stands of red pine that are least defended against bark beetles are those with relatively small trees and a high basal area. Such sites deserve the most careful consideration for management strategies to minimize risk from bark beetles (e.g., by removing, debarking, or burning the trunks of large pine trees that have blown down before they can produce bark beetles).

In addition to variation among sites, there were strong differences within sites between trees that were classified *a priori* as belonging to codominant or intermediate crown classes (resin flow averaged 43% higher in codominant vs. intermediate trees; Fig. 2.7). Thus, within a stand, trees of intermediate crown class are least defended against bark beetles.

EFFECTS OF TREE AGE ON GROWTH AND ANTI-HERBIVORE DEFENSES

It has been hypothesized that the old-growth stands of red pine at Itasca are approaching senescence and, as a consequence, have declining levels of defense against insects and pathogens. If so, tree mortality from beetles might be expected to accelerate over the next two or three decades, in which case appropriate management strategies might be different than if the forest could realistically persist through another century.

Overall, there was only a weak tendency for declining growth rates in mature red pines at Itasca (Fig. 2.5). Average radial growth rates held near 1 mm / year for most of this century. A depression in growth rates from 1989-91 corresponds to a drought. There was a slight tendency for older trees to have lower growth rates, but there were no effects of age on physiological stability as measured by interannual variation in growth rate, nor were old trees more likely to be in growth decline than young trees (Fig. 2.6). Furthermore,

older trees suffered less impacts from drought and had higher resin flow than younger trees. These data indicate continuing growth and high defense in even the oldest red pines at Itasca. There was no suggestion of physiological senescence in even the oldest trees in our sample (up to 220 years old). In the absence of mortality from windstorms, bark beetles, fires, lightning, icestorms, and other disturbances, it seems realistic to expect that many mature red pines in Itasca could live for another century or more. This is very positive news for park management. One consequence is that it becomes appropriate to minimize any manageable risks of tree mortality. Given the long potential lifespan of these trees, even very small changes in mortality risk can have dramatic impacts on the lifetime of the forest (see Figs. 5.7 and 6.9 in Chapters 5 and 6).

We further tested the effects of tree age on anti-herbivore defenses by comparing resin flow in mature red pines at Itasca (100 - 220 years old) with young red pines (30 - 80 years old). Mature red pines had dramatically higher resin flow (about two-fold) than younger red pines growing on similar sites in the same area (Figs. 2.11-2.12). These results reinforce the conclusions that mature red pines at Itasca are not senescing and are not poorly defended against bark beetles.

AGE STRUCTURE OF RED PINE FORESTS AT ITASCA

Among 11 stands of mature red pine at Itasca, the oldest median age of establishment was 1819 and the youngest was 1902. Five of 11 stands were even-aged, suggesting that they originated as the result of stand-clearing wildfires, and six contained trees of mixed ages, indicating that stand-clearing fires have not always been required for the regeneration of red pine at Itasca. At these latter sites, we found adjacent trees that differed in age by as much as 50 - 140 years. This is more positive news because it implies that red pine regeneration is possible without the elimination of mature trees.

REGIONAL PATTERNS IN THE SUSCEPTIBILITY OF RED PINE TO BARK BEETLES

Because the forests at Itasca are very near the western distribution limits of red pine, Itasca forests might be chronically stressed and generally susceptible to insects and pathogens. We tested this hypothesis by comparing resin defenses of red pines in Itasca with those growing in a region of

west-central Wisconsin where growth rates are near the maximum for red pines anywhere. For comparably aged red pines, resin flow averaged nearly twice as high in Itasca as in Wisconsin (Fig. 2.13). These results are contrary to the hypothesis that trees growing on marginal sites, such as Itasca, tend to be less defended against bark beetles than trees on high quality sites. However, results are completely consistent with a physiological model that predicts secondary metabolism will increase in environments where water deficiencies limit growth more than photosynthesis (Fig. 2.14). It appears that the low growth of red pines at Itasca is associated with increased resin flow and reduced risks from bark beetles, which should increase the potential longevity of the forest. A counterpoint to this good news is that the same physiological model predicts that tree defenses at Itasca could be compromised during droughts. We lack any basis for speculating on the severity of drought that would be required to increase tree risks from bark beetles.

All available data indicate that (1) red pine in Itasca are not chronically susceptible to bark beetles compared to red pine growing on better sites and (2) old red pine at Itasca are not chronically susceptible to bark beetles because of reduced resin flow, declining growth, and senescence. Mortality of Itasca red pines from bark beetles is apparently the product of long exposure to low risks rather than an indication of a forest that is in rapid decline or chronically vulnerable to insects.

EFFECTS OF WINTER TEMPERATURES ON BARK BEETLES

The ability to survive annual temperature minima can be a critical determinant of insect abundance. If winter conditions are a significant source of mortality for *Ips*, then it would be possible to predict population abundance in the upcoming summer as a function of winter temperatures and snow cover, and such models could have high utility for anticipating and mitigating risks of tree mortality from bark beetles. This component of our research was designed to measure the lower lethal temperature of *Ips* spp., identify their overwintering sites, and develop a model to predict winter mortality of *Ips*. The lower lethal temperature for adults of *I. pini*, *I. grandicollis*, and *I. perroti* averaged -12.6, -15.2, and -14.4 °C, respectively (Table 4.1). Larvae and pupae are less cold tolerant than adults and are obliged to

remain within the phloem of their host trees (where they are poorly buffered from temperature extremes). Apparently, the only life stages that can survive most winters are the adults that reach overwintering sites in the forest litter.

We collected microclimatic data to develop a mathematical model that estimates temperatures within the overwintering habitat of *Ips* adults (Eq. 4.1). This allowed us to identify winter conditions that can kill bark beetles (Fig. 4.2). For example, during a cold snap where minimum air temperatures reach -35°C , with no snow cover, we expect about 65% mortality in *Ips* adults (Fig. 4.3). Such conditions are less common at Itasca than we had expected. Based on climate records from nearby Bemidji, MN, winter mortality of *Ips* adults reached a maximum of only 33% from 1947 - 1992 (compare to a maximum of 71% in west central Wisconsin during the same years; Fig. 4.4). From the perspective of *Ips* bark beetles, Itasca has relatively benign winters because snowfall usually insulates the upper soil well before the coldest annual air temperatures (Figs. 4.6-4.7). Fig. 4.3 provides a tool for predicting *Ips* mortality under any combination of winter air temperature and snow cover.

DO BARK BEETLES KILL TREES AT ITASCA?

Ips infestations at Itasca could be restricted to trees that are destined to die soon anyway. If so, the abundance of *Ips* would have no consequences for the demography of pine forests at Itasca and could be ignored in management decisions. We tested whether or not *Ips* kill red pines at Itasca by surveying for trees that were infested by bark beetles, monitoring the fate of those trees, and evaluating whether the infested trees were in declining physiological condition prior to being infested by beetles. In 1998, we examined about 4000 mature red pines and located 41 that were infested by bark beetles (see photos in Figs. 5.1 and 5.3). In 1999, we searched the same area and found 39 other trees that had come under attack. *Ips pini* and/or *I. grandicollis* accounted for most of the infestations. Of 41 red pines infested during 1998, 21 were dead, or very nearly so, by the end of the next growing season (Fig. 5.3). Of the 17 trees that were still alive, six were sustaining continuing attacks in 1999, and 11 were apparently free of new attacks (Table 5.1). In our judgement, some of the trees in this latter group might survive for decades longer. However, all attacked trees sustained irreparable damage to their vascular

system, lost significant portions of their crown, and were destined to be more vulnerable to future insects, pathogens, fire, and windstorms. Thus, beetle infestations led to rapid mortality in about half of the attacked trees and increased the probability of mortality for the remainder.

None of the trees that were infested by bark beetles showed a pattern of declining growth in the years immediately preceding the infestation nor any systematic differences from their paired control trees at any time from 1935 - 1996 (Figs. 5.4-5.5). In fact, bark beetle infestations included some of the fastest growing trees in the park (Fig. 5.6). Apparently, bark beetles at Itasca commonly kill red pines that could otherwise live for decades. With an annual mortality rate of 0.5% from bark beetles (as suggested by our surveys), and no regeneration of trees, the Itasca population of red pines would be halved by beetle attacks in 139 years. The expected half life of the forest declines to 65 years if we include a modest level of background mortality from other causes (0.25% / year) and assume that the mortality rate increases in trees that have survived past beetle attacks (to 5% / year). If the same hypothetical forest lacked bark beetles, it would have a half life of 277 years. Bark beetle attack rates such as we observed at Itasca can have surprisingly large effects on forest longevity (Fig. 5.7).

INTERACTIONS BETWEEN FIRE, BARK BEETLES, AND TREE MORTALITY

Prescribed fires were implemented at Itasca during 1998 and 1999. We extended our research to consider fire because it appeared that interactions between fire and bark beetles may be at least as important to forest management as interactions between windstorm and bark beetles. Prescribed fires might reduce bark beetle abundance by killing beetles or increase local abundance by producing volatiles that attract beetles. In fact, the 1998 fire had only limited effects on the abundance of bark beetles (slight increases in *I. pini* during May and slight decreases during mid-summer; Fig. 6.1). However, fire produced a short-term reduction in the resin defenses of red pine and triggered rapid colonization of the scorched trunks by bark beetles (Figs. 6.3 - 6.4, Table 6.1). Within 10 - 30 days, the resin flow in scorched trees increased to higher than baseline levels (Figs. 6.2 - 6.3), which restricted the extent of beetle galleries and probably saved many scorched trees from being killed by bark beetles (Fig. 6.4). Nonetheless,

these attacks kill the phloem, interrupt vascular connections, and partially girdle the tree (permanently). The cambium in the infested area also dies, which precludes additional growth of bark or wood and ensures that a scar will form. This is probably the dominant process by which so-called “cat-faced scars” have been produced on mature red pines at Itasca (Fig. 6.5 - 6.6).

Following the prescribed burns in 1998-99, we found dozens of red pines with incipient scars forming as a result of beetles attacking the scorched lower trunks (Fig. 6.4). We also found many red pines with pre-existing cat-faced scars, whose living bark was being colonized by beetles around the periphery of the old scar. This appeared to be the result of greater heat trauma to the living tissue around the region of the trunk that lacked insulating bark. Finally, the prescribed fires directly killed many red pines when the wood that was exposed at pre-existing scars was ignited by the fire (Fig. 6.5). Fires and beetles can produce a positive feedback loop in which fires promote beetle attack, which increases susceptibility to future fires and future beetles, and which eventually leads to the death of the tree (Fig. 6.7). There can be additional positive feedback at the level of the forest, because a tree that dies in one fire increases the fuel load for future fires and therefore increases the probability of fire and beetle damage to adjacent trees (Fig. 6.8).

Because the relationship between fire, bark beetles, and tree mortality appears to involve positive feedbacks, the proportion of trees that succumb to fires would be expected to increase with each additional fire, and it would be easy to underestimate the consequences of future fires for tree mortality. For example, a doubling of tree mortality rates as a result of increased fire frequency could reduce the half-life of the forest from 65 years to 37 years (Fig. 6.9). We suggest that fire management practices at Itasca be developed in concert with the refinement and parameterization of demographic models of tree survivorship. Presumably, the optimal fire management strategy is one that balances the costs of reduced survivorship in mature trees against the benefits of increased regeneration.

Chapter 6 concludes with a list of specific recommendations for minimizing tree mortality associated with fire and bark beetles.

Appendices 1-5 provide additional raw data. Appendices 6 and 7 are two papers from this research that have been accepted for publication in peer reviewed journals (*Environmental Entomology* and *Forest Ecology & Management*). Three additional appendices in Volume II of this report are the result of literature searches for scientific papers related to *Ips* bark beetles, fire and insects, and fire and pine forests, respectively; they include citations and abstracts for about 250 papers.