Introduction

In 1994-96, the old growth pine forests in Lake Itasca State Park sustained a sequence of heavy blowdowns from windstorms. The downed trees provided abundant food resources for *Ips* bark beetles and led to a dramatic increase in the abundance of *Ips*. Under some conditions, it is thought that *Ips* are capable of attacking and killing trees that would otherwise survive. Limitations in soil water availability, such as characterize forests near the edge of the Great Plains in western Minnesota, have been hypothesized to exacerbate the risk of tree mortality from bark beetles. Thus, bark beetles pose a potentially severe risk for the remaining old growth forests of Lake Itasca State Park. The objective of this research was to assess that risk, evaluate potential strategies to mitigate the risk, and develop biologically sound models to guide the management of this unique and irreplaceable forest ecosystem. Although there was a substantial pre-existing knowledge base regarding interactions between pine trees and bark beetles, this research was unique in being among the first scientific study of bark beetles in old growth pine forests of the Great Lakes region. Because Lake Itasca represents one of the last remaining patches of primary forest from this once extensive forest type, results also have considerable significance in advancing our understanding of the natural workings of unaltered forest ecosystems. Our research is presented in six chapters.

CHAPTER 1. PATTERNS OF HOST SUITABILITY AMONG PINE SPECIES.
Itasca State Park contains red pine, white pine, and jack pine. All are potential hosts of *Ips* bark beetles, but their relative quality for bark beetles is not known. This chapter compared the anti-herbivore defenses and nutritional suitability of the three species, which has significance for evaluating the consequences of blowdowns in pine stands with different species composition.

CHAPTER 2. GROWTH AND ANTI-HERBIVORE DEFENSES OF RED PINE AT ITASCA STATE PARK.
The physiology of pine trees, and their resistance to bark beetle attack, could be influenced by variation in tree age, water availability, nutrient availability, competition with nearby trees, and other environmental effects. If so, there would be predictable patterns in the susceptibility of pines to beetle attack that could be used to assess risks and guide strategies for monitoring and control. In this component of the research, we tested whether or not mature red pines at Itasca are in a state of declining growth and weakened defenses. We also assessed variation in growth and anti-herbivore defenses among stands to evaluate whether or not there are some stands within the park that have particularly high susceptibility to beetles, and to characterize attributes of such stands for the purposes of developing a system for risk-rating. Finally, we compared the anti-herbivore defenses of red pines in Itasca with red pines growing in sites that are more favorable for tree growth. This allowed us to test if the forests at Itasca are chronically stressed and generally susceptible to insects and pathogens.

CHAPTER 3. BARK BEETLE COMMUNITIES AT ITASCA STATE PARK
Itasca Park potentially harbors three different species of *Ips* bark beetles and a guild of specialist predators that prey upon the bark beetles. We conducted sampling of pine forests with different disturbance histories to evaluate which of the bark beetle species are most common at Itasca, which are most responsive to windstorm disturbance, and whether or not predation and/or competition are likely to function as natural control agents on bark beetle populations. This research was also designed to characterize seasonal patterns of abundance in the various species and assess the efficacy of different pheromones as trap lures.

CHAPTER 4. COLD TOLERANCE AND WINTER MORTALITY OF BARK BEETLES AT ITASCA STATE PARK.
Winter temperatures could be a critical determinant of bark beetle population size at Itasca. If so, then it should be possible to reliably predict population abundance in the upcoming summer as a function of winter temperatures and snow cover. Such models could have high utility for management decisions. This component of the research was designed to: (1) measure the lower lethal temperature of the different species and life stages of *Ips*; (2) identify overwintering sites of *Ips*; and

(3) develop a model that incorporates knowledge of cold tolerance, overwintering sites, and microsite temperatures to predict winter mortality of *Ips* using easily measured climatic parameters.

CHAPTER 5. DO BARK BEETLES KILL TREES AT ITASCA STATE PARK?

Forest entomologists are mixed in their opinions of whether or not *Ips* bark beetles are a significant source of mortality for pine trees in the Great Lakes region. Most dying trees are infested by *Ips*, but this could be because *Ips* cause the death of the tree or simply because *Ips* are efficient at locating and colonizing trees that are dying for other reasons. Which of these scenarios is true has important implications for forest management at Itasca State Park. If *Ips* infestations are restricted to trees that are destined to die with or without the presence of bark beetles, then the abundance of *Ips* has no consequences for the demography of pine forests at Itasca, and there is no compelling reason to monitor bark beetle populations, control them, or make any management decisions based upon the abundance of bark beetles. Alternatively, if *Ips* commonly attack and kill trees that are otherwise healthy, then bark beetles may deserve careful consideration in forest management decisions. We addressed this question by surveying the population of red pines at Itasca for trees that were infested by bark beetles, monitoring the fate of those trees, evaluating whether or not the infested trees were in declining physiological condition prior to being infested by beetles, and developing a simple demographic model to evaluate the potential contributions of mortality from bark beetles on the long term survivorship of red pine forests at Itasca.

CHAPTER 6. INTERACTIONS BETWEEN FIRE, BARK BEETLES, AND TREE MORTALITY

During our bark beetle research at Itasca, prescribed fires began to be implemented as a management tool. Our observations following the fires, and a preliminary review of the literature, suggested the potential 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 extended our research by (1) comparing bark beetle abundance in forests that were and were not exposed to prescribed fires, (2) monitoring the fate of trees that were infested by bark beetles after the fire, (3) testing the effects of bark scorching on the resin defenses of trees against bark beetles, (4) characterizing the processes by which fire and bark beetles can interact to influence tree mortality, and (5) expanding the demographic model for pine survivorship from Chapter 5 to incorporate the potential effects of fire and suggest an analytical framework for assessing the costs and benefits of prescribed fire for the long term management of pine populations at Itasca.