

IMPACTS OF DROUGHT AND BARK BEETLES ON RED PINE FORESTS OF THE ANOKA PLAINS, MINNESOTA

Preliminary report of 9 March 2003

Electronic version at: <http://www.dartmouth.edu/~mpayres/pubs/Anoka/>

Matthew P. Ayres¹, Bruce D. Ayres², Mike Peltier³, and Jana Albers⁴

¹ Biological Sciences, Dartmouth College, Hanover, NH 03755.
603 646-2788, Matt.Ayres@Dartmouth.Edu, <http://www.dartmouth.edu/~mpayres/>

² Great Lakes Institute of Pine Ecosystem Research, 310 W. 3rd Ave., Colfax, WI 54730
715 962-3608, woodsrun@wwt.net

³ Sand Dunes State Forest, Minnesota Department of Natural Resources, Zimmerman, MN

⁴ Minnesota Department of Natural Resources, Grand Rapids, MN

Executive Summary

Red pine, the state tree of Minnesota, was an important element of pre-settlement forests, and a significant timber species during the early 20th century. Red pine has been widely propagated since the late 1950s and has proven its value in terms of growth, pest resistance, soil conservation, wildlife, biodiversity, aesthetics, recreation, and timber value. Also, it facilitates a silvicultural system with regular selective harvests over a long rotation time, which allows for growing economic returns to landowners and the forest products industry while simultaneously favoring forested landscapes that include more large trees and old-growth stands than the region has known since the early 1900s. Because it is only now that the first rotation of plantings are maturing into forests, land managers have surprisingly limited experience on which to base management decisions. For example, there is limited ability to know when, or where, there will be consequential mortality of adult trees from drought and bark beetles, and what, if anything, can be done to mitigate the undesirable impacts. Motivated by the most recent drought, we conducted studies to address the following questions: (1) Why is red pine mortality associated with drought and bark beetles more common in the Anoka plains of east central Minnesota than in nearby, apparently similar, forests; e.g., the Colfax region of west central Wisconsin? (2) Are there predictable patterns in tree mortality within a region that are related to soil type? (3) Do bark beetle infestations tend to become self-perpetuating eruptions following a drought?

The Anoka Plains and the Colfax region, separated by ~ 90 miles, both contain extensive red pine forests that experience similar climates and grow on sandy soils derived from glacial outwash. The Anoka Plains have received an average of 6% less annual precipitation, which seems inadequate by itself to explain the history of recurrent droughts and forest disturbance. However, analyses of river discharge data indicated that the sandy soils of Anoka are different enough from the loamy sands of Colfax to strongly affect the probability of droughts. In ~20 years since 1930, the median weekly discharge rate from rivers that drain the Anoka plains have dropped below 30% of the long-term average. This compares to only 1 year that rivers draining the Colfax region have been so low. Droughts in 2000, 1988-89, 1976, 1964, and the 1930s were plainly evident in the river discharge data, which suggests that real-time, online, discharge data provided by the USGS can be used to recognize droughts at the time when tree water stress is maximal. The recent drought at Anoka apparently

reached its nadir in October of 2000. Some tree deaths became evident the following winter. More extensive tree mortality during the next two growing seasons was apparently due to an epidemic of the bark beetle, *Ips pini*, that was triggered by the drought. Regional differences in the rates of red pine growth and mortality are so large that optimal silvicultural practices (e.g., harvest schedules) must be different, but we know of no regionally customized guidelines that are presently available to land owners and forest managers.

Results supported the hypothesis that populations of *I. pini* are normally regulated at endemic levels by resource limitations, but can switch to an epidemic state following a resource pulse from drought-killed trees. Endemic populations of *I. pini* may function chiefly as scavengers of trees that are dying for other reasons, while epidemic populations seem to escape resource limitations by attacking, killing, and reproducing within healthy trees. Under this model, bark beetles amplify climatic effects into self-perpetuating episodes of forest disturbance. Direct death of trees from drought may be less important than drought as a factor that triggers state changes of bark beetles from endemic to epidemic. Pest systems with multiple equilibria are ideal candidates for cost-effective control, because occasional intervention can drive eruptions back to endemic levels where they will tend to be maintained by natural regulatory forces. In the case of *I. pini*, it is relatively cheap and easy to monitor local populations with pheromone-baited funnel traps to identify potential eruptions before they occur (our sampling suggested an action threshold of ~ 500 *I. pini* / stand). To our knowledge, this was the first test for eruptive population dynamics in *I. pini*. Conclusions should be regarded as tentative, but indicate the possibility for cost-effective mitigation of forest disturbance in regions such as the Anoka Plains. We suggest that a plan be developed and implemented to evaluate different possible strategies for pest monitoring and control. This could probably be done in a way that: (1) permits validation or refinement of bark beetle population models; (2) tests for possible undesirable side effects, e.g., removal of natural controls by predators; and (3) provides immediate reductions in tree mortality from beetles.

Introduction

At the time of European settlement, red pines (*Pinus resinosa*) were a dominant element of forests throughout the western Great Lakes region, especially in the sandy soils derived from glacial outwash (Curtis 1959, Bonnicksen 2000). Red pine and white pine (*P. strobus*) largely supported the early timber industry in this region (Walker 1998), which in turn shaped the economic and cultural development of northern Minnesota and Wisconsin (Fries 1951, Swanholm 1978, Birk 1999). Accordingly, red pine is the state tree of Minnesota. Virtually all of the mature red and white pine forests were logged by the 1930s and the associated forest products industry waned. However, red pine has been widely propagated since the late 1950s and has proven itself to be an excellent silvicultural option in that it: (1) grows well even on sites that are barely arable without irrigation; (2) resists pests and pathogens that often exert severe impacts on white pine stands (e.g., white pine weevils, blister rust, and deer browsing); (3) contributes to soil conservation, protecting the most vulnerable soil types from erosion by water (roots and duff layer) and wind (year round foliage), often stabilizing sites previously eroded by bad agricultural practices; (4) is a native species that generates wildlife habitat and promotes biodiversity; (5) produces forests with broad human appeal for aesthetics and recreation; (6) generates logs with good value and high demand; and (7) facilitates a silvicultural system with regular selective cuttings but a long rotation time, which allows for growing economic returns to landowners and the forest products industry while simultaneously favoring forested landscapes that includes more large trees and old-growth stands than the region has known since the early 1900s.

Thus red pine forests have returned to Minnesota and Wisconsin, and grow in size and value with each year. As red pine regeneration programs of the 1950s and 1960s have begun producing merchantable timber, red pine has already replaced depleted stocks of jack pine and spruce to become the major source of softwood fiber for the Lake States long established paper industry, and has re-energized the softwood lumber industry, reversing a near century of decline. In Minnesota, red pine forests accounted for 382 million acres in 2001 (compared to 71 million acres of white pine), up from 247 million acres in 1977 (Minnesota Forest Resources Information Cooperative 2003). Similarly, a 1996 forest inventory in Wisconsin reported 988 million cubic feet of red pine compared to 929 million cubic feet of white pine (Wisconsin Department of Natural Resources 1996).

The value of forest industry shipments in WI during 1996 was \$19.7 billion (compared to \$8.4 billion in 1982). Furthermore, the percentage of sawtimber volume in highest quality classifications (grades 1 and 2) increased from 28% in 1983 to 40% in 1996. As the size and value of these forests grows, so grows the importance of their management.

Since it is only now that the first rotation of plantings are maturing into 2nd growth forests, which are destined to one day become our only old growth, foresters and landowners have surprisingly limited experience on which to base some important management decisions. For example, there is little basis for knowing when or where there will be consequential mortality of adult trees from drought and bark beetles. If some soil types or regions have predictably higher mortality rates for trees, the expected half life for a cohort of trees will be reduced, which, among other things, influences the successional trajectory of a forest managed for wildlife, and changes the optimum harvest schedule of a forest managed for economic returns. There is also little basis for evaluating the costs and benefits of pest control efforts in mature stands of red pine. One of the most significant pests of mature pines in the Great Lakes region is the pine engraver beetle, *Ips pini* (Schenk and Benjamin 1969, Sartwell et al. 1971, Geiszler et al. 1984, Klepzig et al. 1991, Rasmussen et al. 1996, Kegley et al. 1997, Ayres et al. 1999, Santoro et al. 2001). *I. pini* is regarded by many forest entomologists as an occasionally eruptive species (Berryman 1987) that normally has little impact on healthy trees, but which can produce sustained outbreaks when environmental conditions such as a drought or windthrow allow the development of large populations that then become self-sustaining through continued successful mass-attacks on otherwise healthy trees. Such populations are excellent candidates for cost-effective control because occasional efforts can suppress eruptions back to low (endemic) populations levels where they then tend to be regulated by natural forces. Based on this theoretical principle, rather extensive control programs (mass-trapping) were conducted in the Sand Dunes State Forest following the drought of 1988-89 and in Itasca State Park following the windstorms of 1996-97. However, the underlying theory has not been tested for *I. pini*. If it does not hold, then bark beetle control efforts such as mass-trapping or sanitation logging would have less benefit, no benefit, or even make matters worse by delaying the onset of natural controls from predators.

Objectives

We conducted studies during 2002 to address the following questions:

1. Why is tree mortality associated with bark beetles more common in the Anoka plains than in superficially similar regions, e.g., west central Wisconsin?
2. Are there predictable patterns in tree mortality within a region that are related to soil type?
3. Do bark beetle infestations tend to become self-perpetuating eruptions following a drought?

Background for Objective 1: Why regional differences?

The Anoka Plains of east central Minnesota, including Sand Dunes State Forest in Sherburne Co., contains significant stands of red pine that generally grow well but have a history of bark beetle outbreaks coincident with droughts (e.g., 1976, 1988-89, and 2000-01). The Colfax region of nearby west central Wisconsin also contains extensive stands of red pine that are comparable in age and structure to those in MN. However, tree mortality from bark beetles or drought is very rare in the Colfax region. In 15 years of studying bark beetles in red pine forests, we have only witnessed very occasional instances of individual trees that might have died from drought or bark beetles, and we have never observed the simultaneous infestation of multiple live trees. Most foresters and landowners in the Colfax region understandably ignore bark beetles in their management. These two regions have similar sandy soils derived in part or whole from glacial outwash and are near enough (90 miles) that one would expect similar temperatures and precipitation (Fig. 3). We compared these regions with respect to historical patterns in precipitation to test whether climatic patterns could account for the apparent differences in tree mortality from droughts and bark beetles. We also compared soil characteristics and river discharge patterns to test the alternative hypothesis that patterns are due to soils and drainage rather than climate. Finally, we compared regions with respect to site index for red pines and interannual variation in diameter growth to test whether trees on the Anoka Plains are more water limited for any reason.

Background for Objective 2: Site-specific patterns in tree growth and mortality?

Sites that are generally suitable for red pine in the Anoka Plains include some soils with banding, which tends to slow the drainage of soil water out of the rooting zone, and other soils that lack banding. Soils with banding appear to support higher tree growth on

average, presumably because of increased access to water, but may also increase susceptibility to drought. This could be because root systems on banded soils are shallower, due to generally higher water availability in the upper soil zones and increased mortality of those roots that extend into deeper zones subject to water saturation that limits oxygen supply. Trees with such root systems may be more susceptible to drought during dry years when water becomes depleted in the upper soil zones. Thus, red pines growing on soils with low site index (reflecting average growth) may develop deeper root systems that make them better able to survive droughts. One alternative hypothesis is that average growth is positively correlated with drought tolerance, including resistance to bark beetles. We tested these hypotheses by measuring tree growth, and tree mortality associated with a recent drought, across a range of soil types near Sand Dunes State Forest in MN. We also measured soil water profiles within each site.

Background for Objective 3: Are *I. pini* populations eruptive on the Anoka Plains?

During July 2001, more than 50 patches of red pine mortality were detected in Sherburne and Isanti Counties during aerial surveys by Minnesota Forest Health personnel. This was thought to be the result of a drought during 2000, which had ended by 2002. The eruption hypothesis assumes that populations are regulated around one of two equilibria, at endemic or epidemic levels (Fig. 1). Under this model, populations can undergo a state change from endemic to epidemic if some exogenous factor (e.g., a drought that kills some trees and produces a pulse of high quality food resources) permits populations to exceed an escape threshold beyond which further resource limitations are relaxed because they are able to employ mass-attacks to kill additional trees. In the case of bark beetles, resource limitations that regulate populations around the endemic equilibrium are expected to produce a pattern of increasing colonization density in suitable host material (fresh logs and recently killed trees) with increasing abundance of colonizing adults within the forest stand. When local abundance of colonizing adults exceed the hypothetical escape threshold, colonization density in logs is predicted to decline as some adults participate in attacks of nearby live trees. We tested these predictions (Fig. 2) with studies of multiple infestations in and around the Sand Dunes State Forest, a putative epidemic population, and multiple stands of red pine on the Colfax Plains, a putative endemic population.

Methods

Objective 1: Regional comparison of precipitation, soils, river discharge, and tree growth

We identified 10 weather stations within about 50 km of our study sites near Anoka, MN (Fig. 5) and Colfax, WI (Fig. 6). Monthly climate records since 1940 were downloaded for each site from the National Oceanic and Atmospheric Association (NOAA 2003). We calculated annual growing season precipitation for each site as the total from 1 October of the previous year through 30 September of the growing year. We calculated indices of summer and winter temperatures as average daily temperature for June-August and December-February, respectively.

We identified two United States Geological Service gaging stations in each region with on-line, long term records of daily discharge rates: Elk River near Big Lake, MN (USGS 2003a), Rum River near St. Francis, MN (USGS 2003b), Red Cedar River at Menomonie, WI (USGS 2003c), Hay River at Wheeler, WI (USGS 2003d). The location of these gaging stations is indicated on Figs. 5-6, and, in higher resolution, at the USGS web sites in the bibliography. We downloaded the full history of daily discharge rates for each station, which went back to 1930 in most cases. Daily discharge rates showed frequent brief surges that corresponded to precipitation events, but also indicated a tendency to return towards a moving baseline that reflects the rate of groundwater input and might be interpretable as a measure of regional soil water availability for trees. We estimated this moving baseline for each station for each week of the data record (as the median of 7 daily records). The weekly interval was selected as being a time period that is physiologically relevant to trees; i.e., a week of severe water deficits would be expected to evoke drought stress in trees. To look for drought signals over the full 70 year record, we calculated the annual minimum of median weekly discharge for each station and plotted the time series and frequency distributions. These data were compared against historical reports of droughts in both regions. Weekly discharge rates were plotted for 3-4 year intervals that encompassed putative droughts at Anoka. We also plotted the frequency distributions of median weekly discharge rates ($n \sim 3600$ weekly values for each site).

We used USDA soil surveys for Sherburne County, MN and Dunn County, WI to compare the attributes of the soils supporting the red pine stands that we studied. We calculated site indices for red pine at a sample of 30-50 year-old red pine stands in each region (see below). We extracted increment bores from red pines in both regions, including a sample of

60-100 year-old trees, to test for regional differences in the effects of water availability on annual diameter growth.

Objective 2: Site specific patterns in tree growth and mortality

We selected 8 red pine stands near Sand Dunes State Forest to include a spectrum of soil types and a range of tree mortality following the drought of 2000 (Fig. 3). We also chose 5 sites near Colfax, WI (separated by 1 - 10 km) that included a spectrum of soil types in this region. At each site, we measured tree heights with a laser hypsometer, diameter at breast height of 5 trees / site, and basal area with an English BAF 10 prism (3 measurements / site). We extracted and mounted increment cores at 1 m height from 3 trees at each site. Site index was calculated from age and height following Lundgren and Dolid (1970). On 23-27 August, 2002, we collected one soil core from each site (3/4" diameter to 90 cm depth). Cores were sectioned into 14 cm lengths, weighed immediately, then dried and re-weighed to obtain water content as percent mass. At the same time, we surveyed 600-1000 trees at each site to estimate percent mortality during 2000, 2001, and 2002. Trees with no needles produced during the last year, and few dead needles still remaining on the tree, were judged to have died during 2000. Those with no live foliage, but holding needles produced during 2001 were judged to have died during 2001, and those with red foliage and current beetle attacks were classified as dead in 2002. These categories seemed to be quite discrete.

Objective 3: Test for eruptive behavior in populations of *Ips pini*

We used 12-unit Lindgren funnel traps to estimate the abundance of *Ips* bark beetles at each study site during the early summer flight period in 2002 (4 weeks of sampling from 26 May to 25 June). This sampling was timed to capture beetles that had successfully overwintered and were destined to reproduce during the summer. At each site, we deployed an array of four funnel traps, configured as an approximate square of $\sim 20 \times 20$ m. Two traps per site were baited with the pheromone signal of *Ips pini*, ipsdienol + Lanierone, one was baited with the pheromone signal of *I. grandicollis*, ipsenol, and one was baited with the pheromone signal of *I. perroti*, ipsenol and ipsdienol (Ayres et al. 2001). Pheromone lures were bubblecaps purchased from PheroTech: elution rates of 0.2 mg / d for ipsdienol (racemic) and ipsenol, and 0.01 mg / d for Lanierone. Traps were emptied weekly and, at the same time, lures were rotated among traps to guard

against spurious effects from trap position. Later, trap captures were counted and identified.

At each site, we also measured beetle colonization densities in logs. In late May, two trees were felled at each site, and 5, 50-cm long logs were removed from the mid-bole of each tree. At this time, 5 logs (2 or 3 from each source tree) were spread over each site (one log near each funnel trap, and one in the center of the trapping area). The other five logs were covered with a tarp, to prevent beetle colonization, until 15-20 July, when they were placed in the same locations as the first set of logs to provide a resource for colonization by the 2nd generation of *I. pini*. At this time, the first set of logs were consolidated and covered with a tarp to prevent further colonization by beetles. On 22-27 August, we measured the colonization density by *Ips* of each trap log. We carefully removed a 40 x 22 cm section of bark from the upper surface of each log and counted the number of oviposition galleries, each representing one adult female that entered the log and began laying eggs. For each site, we calculated average experienced attack density, *ExpAD*, as:

$$ExpAD = \frac{\sum_{i=1}^{imax} (n_i \cdot \frac{n_i}{area_i})}{\sum_{i=1}^{imax} n_i} \quad \text{Eq 1}$$

where *I* = index for each log within a site, *imax* = the number of logs within a site, *n_i* = number of attacking females per log, and *area_i* = dm² of area sampled within each log. This calculates the density experienced by an average ovipositing female within each site, which is more appropriate than the average density per log for estimating effects of intraspecific competition on population growth rate. It turned out that by the time of our measurements in late August, the logs colonized during June were too damaged by wood borers and other phloem-feeding insects to measure *Ips* colonization densities. Hence, our subsequent analyses were restricted to logs colonized after 15 July. When we examined the logs in late August, we collected samples of adult *Ips* from the trap logs for identification. Not all of these have been examined yet, but it appeared that most, or all, were *I. pini*, which is as expected since the *I. pini* always has multiple generations per year in this region, while *I. grandicollis* and *I. perroti* typically just have a single generation (Ayres et al. 2001).

Results and Discussion

Objective 1a: Regional comparison of precipitation and temperature

Since 1940, annual precipitation near Anoka averaged about 6% less, with slightly greater inter-annual variation, than near Colfax: average mean ± average SD = 29.5 ± 6.3 inches / year vs 31.9 ± 5.5 inches / year (Table 1). Average summer temperatures were slightly warmer near Anoka (68.7 vs. 67.7 °F) and average winter temperatures were slightly cooler (14.5 vs. 15.3 °F) (Table 1). Neither Table 1 nor Fig. 7 indicated that the Anoka sand plains near Sand Dunes State Forest receive less precipitation than areas 20-30 miles further north, south, east, or west. Stations at Santiago and Elk River, about 10 miles north and south, respectively, of Sand Dunes State Forest (Fig. 5), have received annual precipitation that is representative for the broader area (Table 1, Fig. 7). In general, there was little variation in annual precipitation among sites within a region. The time series of annual precipitation since 1930 showed clear inter-annual variation in both regions, and some of the historical droughts were evident in the Anoka time series (Fig. 7); e.g., precipitation lows during 1976, 1987-88, and 2000 correspond to times of drought as evidenced by tree mortality and, sometimes, peat fires. Droughts reported in 1980-81 and 1965 were less evident in the Anoka precipitation data, and the extended drought of the mid 1930s (“Dust Bowl”) was not very conspicuous. The precipitation time series for Colfax (Fig. 7, lower) was qualitatively similar to that of Anoka. In Fig. 7, there appear to be fewer years at Colfax vs. Anoka that stand out as having conspicuously lower precipitation. On the other hand, comparison of frequency distributions (Fig. 8) indicate that the interannual variation in precipitation was quite similar between regions. In general, interannual precipitation patterns were well correlated between the regions; i.e., dry years in Anoka also tended to be dry years in Colfax (Fig. 9).

Objective 1b: Regional comparison of river discharge

River discharge data showed very clear signals of all the reported droughts near Anoka (Fig. 10). Interannual variation in minimum weekly discharge rates were highly correlated between Rum River and Elk River, indicating that minimum weekly discharge is primarily driven by regional climatic patterns, rather than local land use, or local precipitation events. In both watersheds, an empirical drought threshold of < 30% of the long term average in weekly discharge rates did a good job of identifying drought

years - better than precipitation patterns (compare Fig. 10 and Fig. 7). Discharge data from two rivers near Colfax area also showed high correlation across years (Fig. 11). The dry years of 1988-89 and the Dust Bowl were evident in the Colfax rivers, but, in contrast to the Anoka Plains, the annual minimum in weekly discharge rates never dropped below 30% of the long term average. This is consistent with the historical rarity of tree mortality from drought in the Colfax region. The frequency distributions of minimum annual discharge from the Anoka Plains differed from those of the Colfax region in tending to be skewed to the left (Fig. 12); i.e., a larger proportion of the years had low minimum discharge rates in the Anoka Plains than near Colfax. The regional differences were even more pronounced in the frequency distributions of weekly discharge rates (Fig. 13). The variance in weekly discharge was dramatically higher in the Anoka Plains than near Colfax: coefficient of variation (SD / mean) = 1.23 and 1.31 for Elk and Rum Rivers vs. 0.67 and 0.83 for Red Cedar and Hay Rivers. Thus, weekly discharge in the Anoka Plains frequently dropped below the empirical drought threshold of 30% of the average while this has almost never happened in the Colfax region (Fig. 13). Note that there were strong regional differences in discharge variability even though precipitation variability was quite similar (compare Figs. 8 and 13).

Discharge data also permitted higher resolution in identifying the timing of historical droughts (Fig. 14). For example, discharge data indicate that the recent drought reached its nadir in October-November of 2000 (Fig. 14, upper), which is consistent with observations of dead and dying trees during aerial surveys in the winter of 2000-2001. Discharge rates remained above the drought threshold during 2001 and were well above average during 2002. Discharge data indicate that the drought of the late 1980s extended through two summers, 1988-89, and followed record highs during the summer of 1986 (Fig. 14, 2nd panel), which might have exacerbated the effects by producing root mortality in saturated soils. The drought of 1976 reached its nadir in September of 1976 (Fig. 14, 3rd panel), and the drought reported from the mid 1960s appears to have reached its nadir in August of 1964 (Fig. 14, lower panel).

Objective 1c: Regional comparison of soils

Our study sites spanned four mapped soil types within each region (Table 2). Both regions include sandy soils, derived from glacial outwash, that are characterized as having excessive permeability, limited available water capacity, and low fertility. However, the pine-bearing soils of the Anoka Plains

are almost exclusively glacial outwash while the Colfax region also includes sandstone residuum derived from the sandstone that was only 30-60 cm below the surface of two study sites. There are two separate glacial histories in the Colfax lobe of the Central Plain in Wisconsin. The entire landscape was thought to be glaciated only once, covered by the farthest reach of the first Wisconsinian glacial advance, the Altonian (30,000-50,000 YBP). It was very thin in the Colfax area, and thirty thousand years later, the till left behind is only inches deep on the upland areas that were not covered and reshuffled by the outwash of a later glacial advance, the Woodfordian (ca 10,000 YBP), which stopped ~ 30 km north of our study sites (Paull and Paull 1977). Now the region includes numerous sandstone ridges (20-60 m high) covered by shallow soils (18-60 cm) made up of weathered Altonian residuum, plus loess and decayed sandstone. The soils between the ridges, especially near rivers that drained the Northern Highlands, contains extensive sandy glacial outwash of the Woodfordian glacier (Lagerge 1994). Thus, soils of the Colfax region, although tending to be sandy throughout, have two different histories, and somewhat different characteristics: tending to be relatively deep, outwash sands in the lowlands, versus shallow loams, underlain by sandstone, on the ridges. The two soils commingle and intergrade throughout the region.

The Anoka soils are classified as fine sand, loamy fine sand, or fine sandy loam. While the Colfax soils are loamy sand or loam. This suggests larger particle size and more rapid drainage through the Anoka soils compared to Colfax, which is consistent with the pattern of more variable river discharge rates from Anoka (Fig. 12), and more frequent drought (Figs. 10 vs. 11), even though precipitation is only 6% lower and no more variable (Fig. 8). Based on the soil survey data, the regions also differ in that Anoka soils tend to be more acidic and have lower available water capacity (Table 2). Somewhat surprisingly, the soil survey data revealed no differences in permeability or percentage of soil passing through sieves of four different size classes.

Objective 1d: Regional comparison of tree growth

The regional differences in red pine growth were larger than we guessed *a priori*. In Anoka, stands that were 45 - 55 years old were 52 - 66 feet tall and 7.7 - 10.9 inches diameter, while in Colfax, the stands were 4 - 15 years younger, but the trees were larger: 67 - 72 feet tall and 8.6 - 11.0 inches in diameter (Table 3). We calculated the average site indices (expected height at 50 years) to be 60 vs 84 feet at Anoka vs.

Colfax. By comparison, site indices calculated for similarly aged red pine stands near Itasca State Park in western MN averaged 58 ft (Ayres et al. 1999).

We have not yet completed analyses of historical growth patterns based on tree rings, but visual inspection of the cores suggests that diameter growth on the Anoka Plains was somewhat lower on average, and much more variable between years, than in the Colfax region. We hypothesize that climatic effects on red pine growth will be weak or absent near Colfax, but strong, and related to droughts as quantified by river discharge, near Anoka.

Objective 2: Site specific patterns in soil moisture profiles, tree-growth, and tree mortality

Tree mortality associated with the 2000 drought on the Anoka Plains ranged from 6 to 122 trees / 1000 (Table 3). There was no obvious association between site-specific tree growth and tree mortality. Anoka sites with the highest tree mortality (4 and 6) had the lowest and highest site indices (Table 3). Neither were there clear associations between mapped soil types and tree growth or tree mortality (Table 3). Soil type 1258 fs included one site with low growth and high mortality and another with high growth and low mortality. Three sites on soil type 158A fs also included a broad range of site indices and tree mortality. Two sites on soil 1256 fs had low site indices and moderate tree mortality. Further tests will be possible after the analysis of growth rings. The original hypothesis predicts that sites with the highest average growth tend to have high interannual variance in growth, and relatively high rates of tree mortality. Ideally, tests for relationships between tree growth, soil, and tree mortality would begin by selecting study sites at random with respect to tree mortality, which was not the case here (because tests for eruptive population dynamics - Objective 3 - were stronger with sites deliberately chosen to span a range of beetle abundance and tree mortality).

Soil moisture profiles showed evidence of perched water in some sites at Anoka but not others (Fig. 15). In 7 of 8 sites at Anoka, soil moisture at most depths, at the time of our sampling was about 5% by mass. In site 2, soil moisture increased from 5% at 60 cm to 12% at 85 cm. In site 5, soil moisture was elevated to near 10% at 18 cm, and to 17% at 78 cm. The fine sandy loam at site 10 had substantially higher water content, averaging about 10%, with higher amounts in the upper 10 cm, and declining amounts below 70 cm (Fig. 15). The sites that showed evidence of perched water (2, 5, and 10) had site indices that were average or below average (56, 61, and 53 ft; Table 3). Soil

moisture profiles varied somewhat within mapped soil types (Fig. 15). Inferences from the soil moisture measurements were constrained because we had no replication within sites or across dates. Thus we cannot judge whether measurements are representative for the stands, even on the day of measurements. However, it appears that more such sampling would be feasible and permit a rigorous test of the hypothesis that red pines growing in banded soils tend to have higher growth on average, but are also more susceptible to drought.

Soil moisture in the two loamy sands at Colfax also tended to be about 5% (Fig. 16). Chamnis North showed evidence of some perched water at about 50 cm and 85 cm. At Dickinson, soil water jumped to > 10% near 62 cm depth. The two loam soils, which lay only 30-60 cm above sandstone, had conspicuously higher soil moisture of ~ 10%. Calculated site indices were very constant among 4 sites (80 - 84 ft) and somewhat higher (89 ft) on one of the sites with PdB loamy sand.

Objective 3a: Abundance, species composition, and pheromone preferences of the bark beetle community

As expected, *I. pini* were more abundant in the Anoka Plains compared to the Colfax region (Table 4). With the same trapping protocol, captures of *I. pini* from late May to late June (the flight time of the overwintering generation) averaged about 8-fold higher in Anoka vs. Colfax (826 / site vs. 111 / site; Table 4). *I. grandicollis* were also more abundant in Anoka, but less so (only about 50% higher). Surprisingly, *I. perroti* were actually less abundant in Anoka than Colfax (Table 4). The two most abundant predators, *Thanasimus dubius* (Coleoptera: Cleridae) and *Platysoma cylindrica* (Coleoptera: Histeridae) were both about 7-fold more abundant in Anoka than Colfax. The abundance of predators relative to prey, (*T. dubius* + *P. cylindrica*) / total *Ips*, was about 2.5x higher in Anoka compared to Colfax. This is consistent with the hypothesis that these specialist predators increase in their abundance after a year or two of high prey abundance. Presumably, this generates some negative feedback (with a delay) on the population growth rates of bark beetles (as has been reported for some other bark beetle systems; Turchin et al. 1999). It is not known whether or not this negative feedback is sufficient to eventually drive bark beetle populations back to an endemic equilibrium, or whether it is merely sufficient to regulate abundance around an epidemic equilibrium (see Fig. 1)

Bark beetle pheromone preferences in both regions

matched those reported in earlier studies conducted near Colfax, WI and Itasca State Park, MN (Table 5): 95 -96% of *I. pini* were captured in traps baited with ipsdienol + Lanierone; and 73 - 94% of *I. grandicollis* were captured in traps baited with ipsenol by itself. The two most abundant predators were captured with all three pheromone signals, but were most attracted to the signal that is produced and preferred by *I. perroti* (ipsenol + ipsdienol). This suggests a hypothesis for why *I. perroti* were relatively rare in the forests where *I. pini* were very abundant.

Objective 3b: Test for eruptive behavior in populations of *Ips pini*

As expected, beetle-attacked trees were common in the Anoka Plains and very rare in the Colfax region: average tree mortality rates during the three years from 2000-2002 were 15.8 vs. 0.5 tree deaths per 1000 trees per year for Anoka and Colfax, respectively (Table 3). Across 8 red pine stands on the Anoka Plains, average tree deaths per 1000 were 6.4 in 2000, 24.7 in 2001, and 6.9 in 2002. In all but one Anoka site, tree deaths peaked in 2001. Tree attacks during 2002 were positively related to abundance of *I. pini* during early summer (Fig. 17, upper). There was a suggestion of a threshold for tree attacks, as predicted by the theoretical model for eruptive population dynamics (Fig. 2, upper). Tree attacks became relatively common when early summer trap captures of *I. pini* exceeded about 500 per two traps per month (Fig. 17, upper).

Colonization densities of logs by *I. pini* were also higher in Anoka than Colfax: mean experienced density \pm SE = 2.5 ± 0.1 vs. 1.1 ± 0.2 ovipositing females / dm², respectively (Table 2). Across all 13 red pine stands that were studied, the density of *I. pini* in logs colonized during August was related to trap captures of overwintering *I. pini* adults during June (Table 2). However, this relationship was nonlinear, with a peak when trap captures were intermediate (Fig. 17, lower). There was strong statistical support for the nonlinearity of this relationships (AIC for 2nd order polynomial vs. linear model = 5.57). The form of this relationship, and the match between a threshold for tree attacks and the peak in colonization density, were as predicted by the theoretical model for eruptive population dynamics (compare Figs. 2 and 17). The support for this model, although based on only a single year of data, is strengthened by the fact that the test involved rather specific predictions about the interrelations among three independent variables (local abundance as measured by trap captures, colonization densities in logs, and the number of live

trees attacked during the summer). Presumably, beetle colonization densities in logs started to decline after trap captures exceeded about 800 because some beetles were participating in successful attacks of live trees, which increased the resource base for ovipositing females, and eased competition for phloem. Results suggest that the escape threshold for *I. pini* (N_{escape} in Fig. 1) is at 600 - 800 captures per two funnel traps per month.

Conclusions

Regional differences in tree growth, tree mortality, and beetle outbreaks

Tree mortality rates are clearly much higher on the Anoka Plains than areas within 90 miles that experience similar climates and have similar sandy soils. This was obvious not only from the counts of mortality events during the last 3 years, but also from dramatic differences between the regions in the numbers of downed trees from earlier deaths; such logs were abundant throughout pine stands in the Anoka Plains but were rare or absent in pine stands near Colfax. The differences in tree mortality are difficult to explain based on the modest (6%) difference in average annual precipitation. Apparently there is a strong effect from the Anoka Plains being made up of soils that drain more rapidly than those near Colfax. Still, the direct effects on red pine forests of lower and more variable soil water would probably be modest were it not for the presence of bark beetles that can apparently be triggered by drought episodes to switch from endemic populations that rarely kill trees to epidemic populations that commonly kill trees. Thus the explanation for differences between red pine forests near Anoka and Colfax appear to involve strong interactions between climate, soils, and beetle population dynamics. The regional difference in tree mortality rates is surely enough to influence optimal harvest schedules, and is also surely enough to warrant careful consideration of bark beetle management on the Anoka Plains, even while forest managers near Colfax can generally ignore them without consequence.

With constant annual mortality rates of 0.5 / 1000, such as we observed at Colfax, and other things being equal, a red pine stand would experience 48 deaths / 1000 trees over 100 years. Since 1930, there appear to have been about six significant droughts on the Anoka Plains. We estimated that the 2001 drought resulted in mortality of 15.8 trees / 1000. If there is one drought per 12 years that results in the death of 15.8 trees / 1000, on top of a background annual mortality rate of 0.5 / 1000, a red pine stand would experience

175 deaths / 1000 trees over 100 years. These calculations are very simplistic. In particular, they fail to account for: (1) the risks of catastrophic losses associated with droughts more severe than that of 2001; (2) mortality risks associated with fire, blowdown, fungal pathogens, and ice damage; (3) potential for minimizing risks through selective harvesting. Nonetheless, these calculations suggest that there would be value in developing more sophisticated projections to aid in the development of long term management plans for red pine stands that account for regional differences in tree growth and mortality rates on timber yield and stand structure over 50 - 100 year time frames. Our sense is that it is realistic to manage red pine stands near Colfax for a time frame of >100 years, while reasonable rotation times for red pine stands near Anoka may be substantially less. These calculations also suggest that the expected lifespan for red pine stands near Anoka may be extremely sensitive to consideration of bark beetle risks in site selection and management.

In addition to modifying red pine management strategies on the Anoka plains, it may make sense to consider other tree species for future reforestation. Because tree/bark beetle interactions can be quite species-specific, and because tree species differ in moisture requirements and drought response, planting other conifers instead of red pine, may make sense. Mixed species plantings in some areas have shown promise for managing pest/tree interactions, and offer the additional benefit of providing a more diverse ecosystem. Our work offers no insight as to the suitability of alternate tree species, but could help establish parameters for comparisons.

Application of USGS hydrological discharge data

Analyses of river discharge data suggest that there would be value in monitoring USGS discharge data to recognize potential droughts in the early stages and implement appropriate, cost-effective responses (e.g., minimizing log decks that could permit buildups of bark beetles, and conducting aerial and ground surveys for early signs of tree deaths and beetle activity). This would also facilitate studies of tree water status and resin defenses during the time of presumed maximal water deficits. Such studies are needed to understand how drought influences the defenses of trees that would survive in the absence of beetles. Available data suggest that resin defenses of pines are actually increased by moderate water deficits (Reeve et al. 1995, Ayres et al. 1999, Lombardero et al. 2000), but patterns at Anoka are also consistent with the alternative hypothesis that drought stress compromises

tree defenses. Resolution of these competing hypotheses will aid in understanding how beetle control efforts and stand management can mitigate risks of tree mortality.

USGS river discharge data may have broader applicability for: (1) objectively identifying regions that are generally susceptible to consequential droughts; and (2) monitoring entire states for local or regional droughts. This broader applicability depends upon the unvalidated proposition that patterns identified here based on four rivers in two county-sized regions can be extended to a broader spatial scale. However, it would be cheap and easy to begin evaluating the generality of, for example, the 30% drought threshold suggested here. Among other benefits, results would likely enhance our ability to anticipate the consequences for forests of changes in temperature and precipitation that have already occurred and are likely to accelerate (U.S. Global Change Research Program 2000). We can expect climate changes to continue to alter patterns of soil water availability in Minnesota, and the effects on forests, whether positive or negative, are likely to be the largest and most immediate in regions like the Anoka Plains.

Correlations within a region between local soil types, average tree growth, and stand susceptibility to droughts

We were unable to resolve what, if any, are the patterns between local soil types, tree growth, and stand susceptibility to drought and beetles. However, the question is important and deserves further study. We suggest that a subsequent study include replicate pine stands selected at random from within different mapped soil types. Within these stands, one could measure: (1) soil moisture profiles as in Figs. 15-16, replicated within each stand and across the season; (2) tree mortality via surveys for dead trees and downed logs; (3) historical patterns in height and diameter growth; and (4) depth of roots. Results would aid forest managers and landowners in selecting sites for red pine propagation, and customizing management of red pine stands for site-specific characters (e.g., harvesting schedules, tree selection during harvesting, pest monitoring, and pest control).

Implications for understanding effects of climate on tree mortality and beetle populations

Results indicate that there are potential benefits to monitoring populations and treating those that have exceeded the escape threshold that separates endemic populations from eruptions. Apparently, climate and beetles interact to determine tree mortality rates and forest disturbance regimes. Direct death of trees from

drought may be less important than drought as a factor that triggers state changes of bark beetles from endemic to epidemic. If it were otherwise, the impacts of beetles would be restricted to times when trees are dying, or have compromised defenses, as a result of climatic stress. As it appears to be, beetle mortality may continue for years after a drought abates. Potential control strategies for *Ips* in red pine forests include mass-trapping with pheromone-baited funnel traps, deployment and destruction of trap logs, and aggressive sanitation. In our judgement, it remains to be established that these control strategies can be effective and practical for pine systems in Minnesota, but if *I. pini* populations tend to have endemic and epidemic states (Fig. 1), there is potential value in pest control. The correlation among stands between trap captures in early summer and tree attacks during the summer, suggests that control might be effective at the stand level (not necessarily requiring expensive regional efforts). We recommend that a plan be devised for implementing pest control efforts in some stands that are above the estimated escape threshold (Fig. 17) and leaving other such stands as controls. This would permit the evaluation of different possible control strategies, the continued testing and refinement of models to predict bark beetle population dynamics, careful assessment of possible undesirable side effects (e.g., removal of natural controls by predators) and, hopefully, the mitigation of expensive beetle impacts within treated stands.

References cited

- Ayres, B. D., M. P. Ayres, M. D. Abrahamson, and S. A. Teale. 2001. Resource partitioning and overlap in three sympatric species of *Ips* bark beetles (Coleoptera : Scolytidae). *Oecologia* 128:443-453.
- Ayres, M. P., M. J. Lombardero, B. D. Ayres, and A. E. Santoro. 1999. The biology and management of bark beetles in old growth forests of the Itasca State Park. Great Lakes Institute of Pine Ecosystem Research, Colfax, WI.
- Berryman, A. A. 1987. The theory and classification of outbreaks. Pages 3-30 in Barbosa, P. and J. C. Schultz, editors. *Insect outbreaks*. Academic Press, New York.
- Birk, D. A. 1999. Outta the Woods and Onto the Mills: Shifting Timber-Harvest Strategies on Minnesota's Early Lumbering Frontiers. Institute for Minnesota Archeology.
<http://www.fromsitetostory.org/sources/papers/mnlogging/mnlogging.asp>
- Bonnicksen, T. M. 2000. *America's ancient forests*. John Wiley and Sons, New York.
- Curtis, J. T. 1959. *The vegetation of Wisconsin*. University of Wisconsin Press, Madison, Wisconsin.
- Fries, R. F. 1951. *Empire in Pine: The Story of Lumbering in Wisconsin, 1830-1900*. State Historical Society of Wisconsin, Madison, WI. 285 pp.
- 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.
- Kegley, S. J., R. L. Livingston, and K. E. Gibson. 1997. Pine engraver, *Ips pini* (Say) in the western United States. *Forest Insect and Disease Leaflet* 122. USDA Forest Service, Washington, D.C.
- Klepzig, K. D., K. F. Raffa, and E. B. Smalley. 1991. Association of an insect-fungal complex with red pine decline in Wisconsin. *Forest Science*. 37:1119-1139.
- Laberge, G.L. 1994. *Geology of the Lake Superior Region*. Geoscience Press Inc., Phoenix, Arizona. pp 269-273
- Lombardero, M. J., M. P. Ayres, P. L. Lorio, Jr., and J. J. Ruel. 2000. Environmental effects on constitutive and inducible resin defences of *Pinus taeda*. *Ecology Letters* 3:329-339.
- Lundgren, A. L. and Dolid, W. A. 1970. Biological growth functions describe published site index curve for Lake States timber species. - USDA Forest Service North Central Forest Experiment Station Research Paper NC-36: 1-9
- Minnesota Forest Resources Information Cooperative. 2003.
<http://www.cnr.umn.edu/FR/research/centcoop/mfric/data.htm>
- NOAA. 2003. Locate weather observation station record.
<http://wlf.ncdc.noaa.gov/oa/climate/stationlocator.html>
- Paull, R.K. and R.A. Paull. 1977. *Geology of Wisconsin and Upper Michigan*. Kendall/Hunt Publishing Co., Dubuque, Iowa. pp 97-105
- 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 Research Paper INT-RP-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.
- Sartwell, C., R. F. Scmitz, and W. J. Buckhorn. 1971. Pine engraver, *Ips pini* in the western states. Forest Pest Leaflet 122. USDA Forest Service, Washington, D.C.
- Schenk, J. A. and D. M. Benjamin. 1969. Notes on the biology of *Ips pini* in central Wisconsin jack pine forests. *Annals of the Entomological Society of America* 62:480-485.
- Swanholm, M. 1978. Lumbering in the Last of the White-Pine States. Minnesota Historic Sites Pamphlet Series No. 17. Minnesota Historical Society, St. Paul, MN.
- Turchin, P., A. D. Taylor, and J. D. Reeve. 1999. Dynamical role of predators in population cycles of a forest insect: an experimental test. *Science* 285:1068-1071.
- U.S. Global Change Research Program. 2000. Climate change impacts on the United States: the potential consequences of climate variability and change. <http://www.gcrio.org/NationalAssessment/>
- USGS. 2003a. USGS 05275000 Elk River near Big Lake, MN. <http://waterdata.usgs.gov/mn/nwis/uv?05275000>
- USGS. 2003b. USGS 05286000 Rum River near St. Francis, MN. <http://waterdata.usgs.gov/mn/nwis/uv?05286000>
- USGS. 2003c. USGS 05369000 Red Cedar River at Menomonie, WI. <http://waterdata.usgs.gov/wi/nwis/uv?05369000>
- USGS. 2003d. USGS 05368000 Hay River at Wheeler, WI. <http://waterdata.usgs.gov/wi/nwis/uv?05368000>
- Walker, L. C. 1998. The North American forests: geography, ecology, and silviculture. CRC Press, Boca Raton, FL.
- Wisconsin Department of Natural Resources. 1996. <http://www.dnr.state.wi.us/org/land/forestry/Look/highlights1996.htm#All>

Table 1. Comparison of annual precipitation (since 1940) and mean temperatures near Anoka, MN and Colfax, WI

Region	Site	Years	Annual precipitation (inches/yr, Oct-Sept)		Summer temp. (° F, June-Aug)		Winter temp. (° F, Dec- Feb)	
			Average	SD ^a	Average	SD ^a	Average	SD ^a
Anoka, MN	Santiago***	41	30.9	6.6	68.3	1.8	14.5	4.8
Anoka, MN	Elk River***	49	29.1	5.8				
Anoka, MN	Buffalo	40	29.1	6.1	69.8	2.0	15.5	4.2
Anoka, MN	Cambridge	54	28.6	5.6	68.0	2.3	13.7	4.0
Anoka, MN	Cedar	36	31.7	6.7	69.0	1.7	15.7	4.2
Anoka, MN	Collegeville	57	28.4	6.7	69.3	1.8	14.6	4.4
Anoka, MN	Maple Plain	43	29.6	5.3	69.5	2.3	15.1	4.1
Anoka, MN	Milaca	55	29.0	6.7	67.9	2.0	14.0	4.3
Anoka, MN	St. Cloud	53	27.2	5.9	67.8	1.7	13.0	4.2
Anoka, MN	St. Francis	30	31.0	7.1				
		Mean =	29.5	6.3	68.7	2.0	14.5	4.3
		SD ^b =	1.4	0.6	0.8	0.2	0.9	0.2
Colfax, WI	Bloomer***	56	31.3	5.8	68.4	2.1	15.8	4.0
Colfax, WI	Menomonie***	59	30.4	5.4	69.7	1.9	17.9	4.0
Colfax, WI	Amery	61	30.9	5.7	67.9	1.8	14.1	4.2
Colfax, WI	Baldwin	49	31.4	5.5				
Colfax, WI	CedarFalls	51	32.9	5.9				
Colfax, WI	Eau Claire	53	31.0	5.1	68.7	1.7	15.7	4.2
Colfax, WI	Holcombe	60	32.1	5.2	67.3	2.1	15.7	4.5
Colfax, WI	Mondovi	49	32.1	5.9	69.5	1.9	17.9	4.5
Colfax, WI	Rice Lake	49	31.9	5.1	67.3	1.9	14.3	4.1
Colfax, WI	Ridgeland	49	32.5	5.5	67.0	1.8	14.2	4.3
Colfax, WI	Spring Valley	37	31.3	5.6				
Colfax, WI	Weyerhauser	55	32.7	6.0	66.1	1.9	14.9	3.8
		Mean =	31.9	5.5	67.7	1.9	15.3	4.2
		SD ^b =	0.7	0.3	1.2	0.1	1.4	0.2

*** = closest station to study sites

SD^a = standard deviation among yearsSD^b = standard deviation among sites

Table 2. Summary of soil types in red pine stands near Anoka, MN and Colfax, WI (based on soil surveys for Sherburne Co, MN and Dunn Co, WI). One additional soil was represented among the studied pine stands at Anoka (Scandia fine sandy loam at Site 10).

Soil map symbol	Anoka soils represented in sampling			Colfax soils represented in sampling			
	158	1258	1256	PfA	PbB	EmB	UnB
Soil name	Zimmerman fine sand	Zimmerman fine sand, thick solum	Cantlin loamy fine sand	Plainfield loamy sand	Plainbo Loamy sand	Elk mound loam	Urne-Norden loam
Family or higher taxonomic class	Mixed, frigid Argic Udipsamments	Mixed, frigid Argic Udipsamments	Mixed, frigid Typic Udipsamments	Mixed mesic, Typic Udipsamments	Mixed frigid, Typic Udipsamments	Loamy, mixed, mesic, Lithic Dystrichrepts	Coarse-loamy, mixed, mesic, Dystric Eutrochrepts
Landform	Outwash plains	Outwash plains	Outwash plains	Outwash plains, stream terraces	Base of steep slopes	Sandstone mantle	Upland ridgetops
Parent material	Glacial outwash	Glacial outwash	Glacial outwash	Glacial outwash	Glacial outwash	Sandstone residuum	Sandstone residuum
Cropland considerations	Excessive permeability; limited available water capacity	Excessive permeability; limited available water capacity	Excessive permeability; limited available water capacity; acid soil	Excessive permeability; limited available water capacity, low fertility	Excessive permeability; limited available water capacity, low fertility	Shallow soils subject to erosion and drought, low available water, moderate permeability, medium fertility	Moderate permeability and fertility, medium water capacity
Depth to mottling or banding	banded at 5-6 feet	banded at 6.6 feet +	No bands, mottled at 4 feet				
pH	5.1 - 6.5	5.1 - 6.5	5.0 - 6.0	6.1 - 7.3	6.7 - 7.3	6.1 - 6.5	5.6 - 7.3
Permeability (in / hr)	6 - 20	6 - 20	6 - 20	6.3 - 20	6.3 - 20	0.63 - 2.0	0.63 - 2.0
Available water capacity (in / in)	0.07 - 0.09	0.07 - 0.09	0.10 - 0.12	0.08 - 0.12	0.08 - 0.12	0.18 - 0.22	0.18 - 0.22
Percentage passing sieve #4	95 - 100	95 - 100	100	95 - 100	95 - 100	90 - 100	
Percentage passing sieve #10	95 - 100	95 - 100	100	85 - 95	85 - 95	80 - 90	80 - 90
Percentage passing sieve #40	10 - 20	10 - 20	50 - 75				
Percentage passing sieve #200	15 - 20		50 - 75	20 - 25	20 - 25	55 - 65	55 - 65
Extent of the soil (% acres in county)	58	7	6	8	7.5	1.1	27
Water table depth (ft)*	> 6	>6	3.5 - 6	>5	>5	>5	>5

* "Seasonal high" in Colfax soil survey

Table 3. Stand characteristics, beetle captures in pheromone-baited funnel traps, *Ips* colonization densities in traps logs, and beetle-attacked trees in red pine stands near Anoka, MN and Colfax, WI.

Region	Site	Stand characteristics							Trap captures (per 4-trap array during June 2002)						<i>I. pini</i> in logs ^d	Attacked trees / 1000		
		Soil.ID	Age.2002 ^a	Age.2002 ^b	Height(ft)	Site.Index ^c	DBH(in)	BasalArea	<i>I.pini</i>	<i>I.grand</i>	<i>I.perrot</i>	<i>T.dubius</i>	<i>P.cylind</i>	Ips/Predator	Attacks/dm2	2002	2001	2000
Anoka.MN	1	1256 lfs	49	52	63	61	10.1	107	624	346	33	430	452	1.1	2.11	7	60	0
Anoka.MN	2	1256 lfs	51	53	59	56	10.5	137	1096	206	3	221	95	4.1	2.88	3	10	7
Anoka.MN	4	1258 fs	57	51	52	51	8.7	230	606	252	12	244	217	1.9	3.48	7	84	31
Anoka.MN	5	158A fs	57	55	66	61	10.9	90	866	297	16	363	121	2.4	1.91	15	28	2
Anoka.MN	6	158A fs	48	43	66	75	8.2	180	1657	331	34	1443	304	1.2	1.20	24	52	24
Anoka.MN	8	158A fs	40	45	52	57	9.5	207	261	177	28	1123	143	0.4	2.45	0	10	0
Anoka.MN	9	1258 fs	45	46	64	68	7.7	183	733	269	205	721	216	1.3	2.10	3	3	0
Anoka.MN	10	Sp fsl	35		39	53	8.0	177	762	162	2	153	22	5.3	3.72	10	0	0
		Mean	48	49	58	60	9.2	164	826	255	42	587	196	2.2	2.5	9	31	8
		SE	1.0	0.7	1.2	1.0	0.2	6	51	9	8	59	17	0.2	0.1	1	4	2
Colfax.WI	ChamN	Pdb	39	39	72	89	10.6	183	62	156	56	65	34	2.8	1.44	0	0	0
Colfax.WI	ChamW	EmB	39	39	67	83	11.0	147	169	189	202	130	38	3.3	0.20	2	0	0
Colfax.WI	Dickin	PfA	43	42	72	83	10.2	133	139	145	176	68	25	4.9	2.29	1	5	0
Colfax.WI	ScoreN	PdB	42	41	68	80	10.1	160	69	86	8	45	10	3.0	0.30	0	0	0
Colfax.WI	ScoreS	UnB	42	41	71	84	8.6	230	118	242	224	110	37	4.0	1.52	0	0	0
		Mean	41	40	70	84	10.1	171	111	164	133	84	29	3.6	1.1	1	1	0
		SE	0.4	0.3	0.5	0.6	0.2	8	9	11	19	7	2	0.2	0.2	0	0	0

^a Age based on planting records. Age.2002.b = age at 1 m (from cores) + 5. Site indices calculated from Age.2002.b

Table 4. Average captures per site (in 4 Lindgren funnel traps) of three species of *Ips* bark beetles and two species of bark beetle predators during early summer 2002 in 8 red pine stands on Anoka Plains, MN and 5 pine stands near Colfax, WI.

~Mid-date of collection	<i>Ips pini</i>		<i>Ips grandicollis</i>		<i>Ips perroti</i>		<i>Thanasimus dubius</i>		<i>Playtsoma cylindrica</i>	
	Anoka	Colfax	Anoka	Colfax	Anoka	Colfax	Anoka	Colfax	Anoka	Colfax
27-May		23		136		101		11		4
3-Jun	675	20	229	15	37	20	313	23	98	6
13-Jun	60	10	11	6	4	7	120	14	36	6
20-Jun	91	58	15	6	1	5	155	36	62	13
29-Jun		441*		6		40		30		17

* Presumed to be the 2nd generation.

Table 5. Percent of captures by species and region in Lindgren funnel traps baited with either of three sets of pheromone lures, designed to match the pheromone production of *I. pini* (ipsdienol + Lanierone), *I. grandicollis* (ipsenol), or *I. perroti* (ipsdienol + ipsenol). Bark beetle preferences in both regions matched expectations based on previous studies near Colfax and Itasca (Ayres et al. 1999, 2001). Both of the two most common predators responded to all pheromone signals, but were most attracted to ipsdienol + ipsenol. This, plus the generally high abundance of predators near Anoka, might explain the relative rarity of *I. perroti* near Anoka (Table 4).

Pheromone lure(s)	<i>Ips pini</i>		<i>Ips grandicollis</i>		<i>Ips perroti</i>		<i>Thanasimus dubius</i>		<i>Playtsoma cylindrica</i>	
	Anoka	Colfax	Anoka	Colfax	Anoka	Colfax	Anoka	Colfax	Anoka	Colfax
Ipsdienol + L*	95	96	3	0	4	2	35	29	34	38
Ipsenol	2	0	73	94	0	0	24	23	19	12
Ipsdien. + Ipsenol	3	4	23	6	95	98	41	48	47	50

* Lanierone, = pheromone synergist of ipsdienol for *Ips pini*

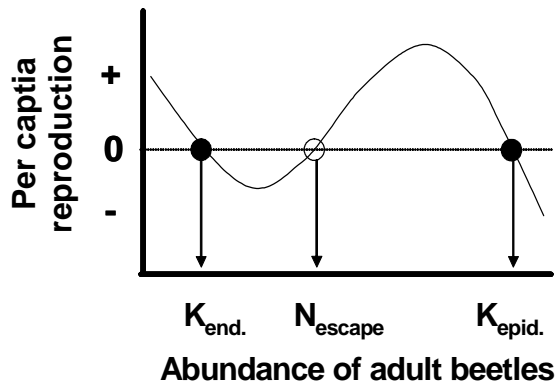


Fig. 1. Theoretical model of an eruptive forest insect. Per capita population growth rate is a complex function of abundance. When abundance is less than N_{escape} , populations tend to be regulated around an endemic equilibrium (K_{endemic}). However, if exogenous forces permit the population to exceed an unstable equilibrium or escape threshold (N_{escape}), populations will tend to grow to a much higher epidemic equilibrium (K_{epidemic}). We tested whether this model applies to the pine engraver beetle, *Ips pini*, by testing some predictions derived from this model (Fig. 2)

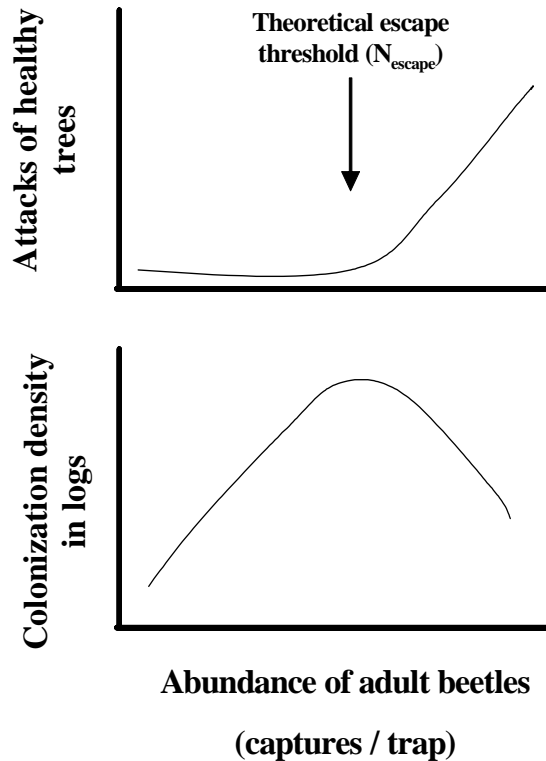


Fig. 2. Predictions derived from Fig. 1 for *Ips pini*. As local population abundance increases, the colonization density in logs (ovipositing females / dm^2) is predicted to increase (generating the initially negative relationship in Fig. 1 between adult density and per capita reproduction), until populations reach a threshold where they begin to attack live trees, at which point competition for food resources is theoretically alleviated and colonization density is predicted to decline.

The maps shown in Figures 3-6 are not reproduced here, but can be viewed online at: <http://www.dartmouth.edu/~mpayres/pubs/Anoka/>

Fig. 3. Location of study sites on Anoka Plains, MN, and Colfax lobe Central Plains in WI.

Fig. 4. Location of seven red pine stands studied within Sand Dunes State Forest, MN. Site 10 (not shown) was 11.3 miles due east of site 3.

Fig. 5. Location of climate stations (highlighted waypoints) used for analysis of precipitation patterns on Anoka Plains, MN. Eight red pine study sites (1-10) are near center. Elk Weir and Rum Weir are USGS gaging stations used for analysis of hydrologic discharge patterns

Fig. 6. Location of climate stations used for analysis of precipitation patterns near Colfax, WI. Five red pine study sites are near center. Hay Weir and Red Weir are USGS gaging stations used for analysis of hydrologic discharge patterns.

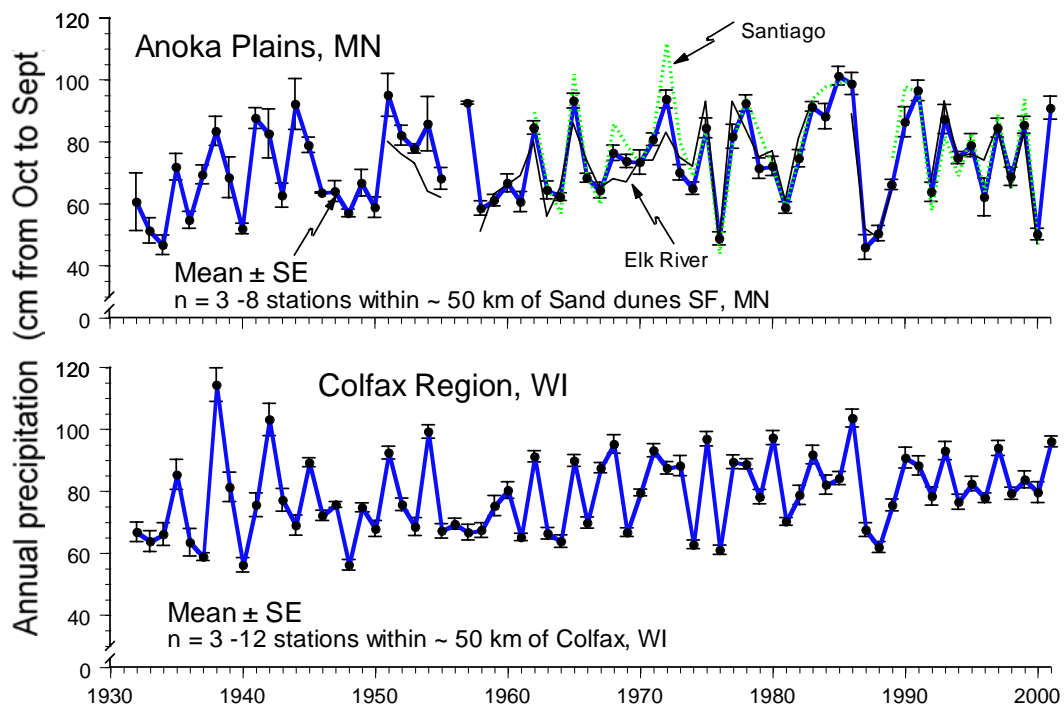


Fig. 7. Annual precipitation on the Anoka Plains and Colfax Plains since 1932. There was only minor variation among climate stations within the region (note small SEs and close tracking of data from Santiago and Elk River with regional data). See Figs. 5-6 for location of climate stations.

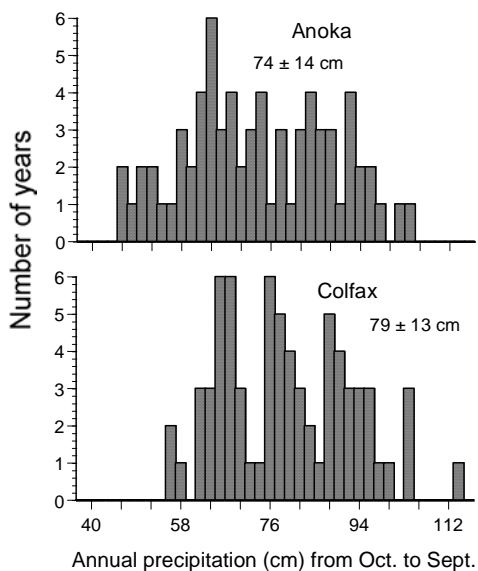


Fig. 8. Frequency distribution of annual precipitation since 1932 near Anoka, MN and Colfax, WI. Average precipitation was 5 cm / year lower near Anoka vs. Colfax (6%), but interannual variance was similar.

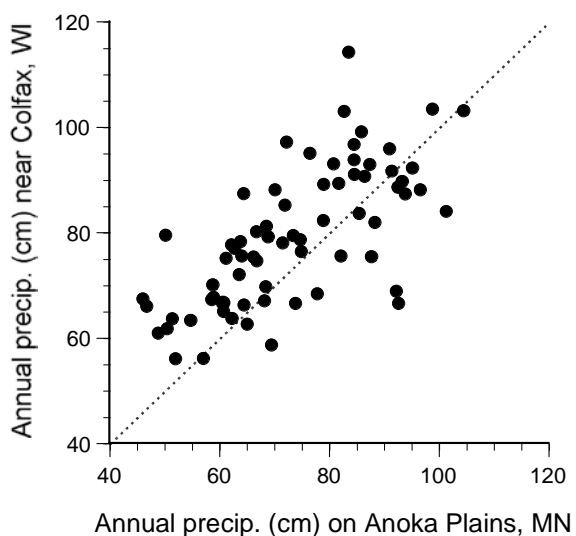


Fig. 9. Annual precipitation near Colfax, WI and Anoka, MN are well correlated (same data as in Figs. 7-8). In 50 of 69 years, annual precipitation was greater near Colfax vs. Anoka. The average difference was 5.9 cm / year.

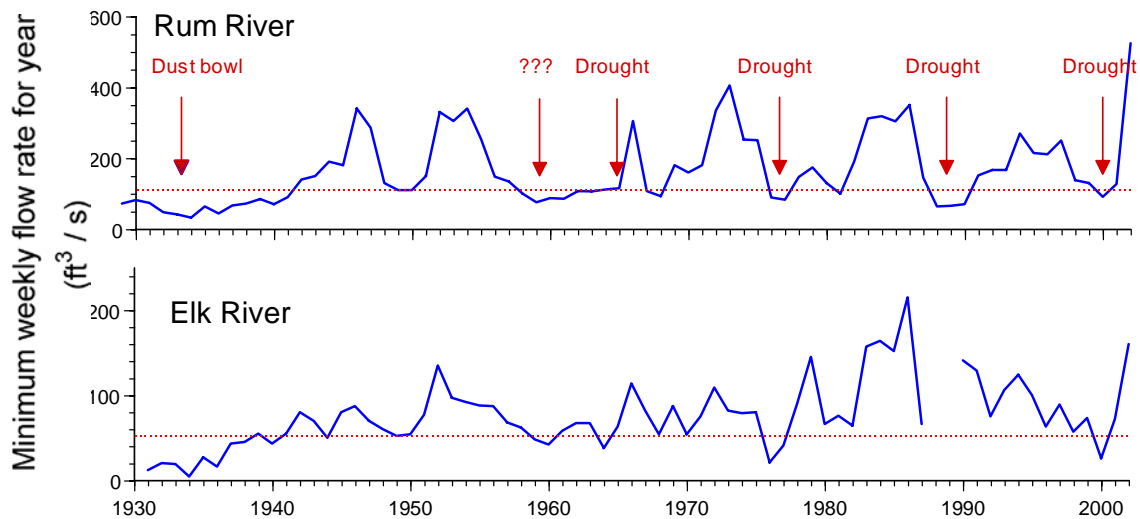


Fig. 10. Annual minimum of weekly discharge rates from two gaged rivers draining the Anoka Plains. Historical droughts at Sand Dunes State Forest (as reconstructed without reference to the discharge data) are indicated with arrows labelled “Drought”. Based upon these data, we hypothesize that there was another drought in 1959-60. The dotted lines indicate an empirical drought threshold calculated as 30% of the longterm average in median weekly discharge rates (Fig. 13): 113 and 53 ft³ / s for Rum and Elk Rivers, respectively. Note that the historic droughts are more evident in the discharge data than the precipitation data (Fig. 7), and that the discharge data are available online in real-time through the USGS. See Fig. 14 for close-ups of weekly discharge rates during droughts.

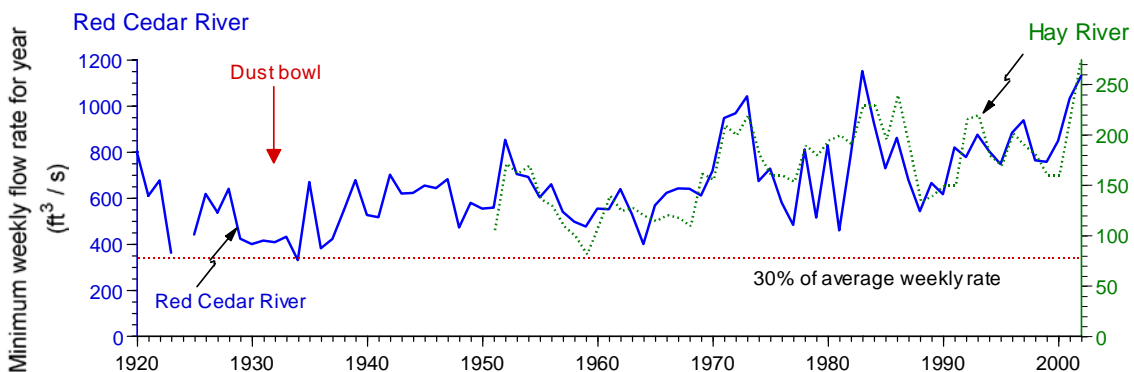


Fig. 11. Annual minimum of weekly discharge rates from two gaged rivers draining the Colfax lobe of the Central Plains in Wisconsin (see maps in Figs. 4 and 6). Unlike the Anoka Plains, river discharge rates near Colfax rarely drop below a putative drought threshold of 30% of the long term average. This is consistent with tree mortality from drought being common in Anoka and rare near Colfax. The lowest recorded discharge rates in the Colfax area were in 1934 during the Dust Bowl. Low precipitation during 1988-89 (Fig. 7) produced a noticeable dip in discharge rates, but did not approach the 30% threshold, and did not produce significant mortality in red pines. Based on these data, we hypothesize that low soil water in 1959 and 1964 had notable impacts on agricultural yields in the area.

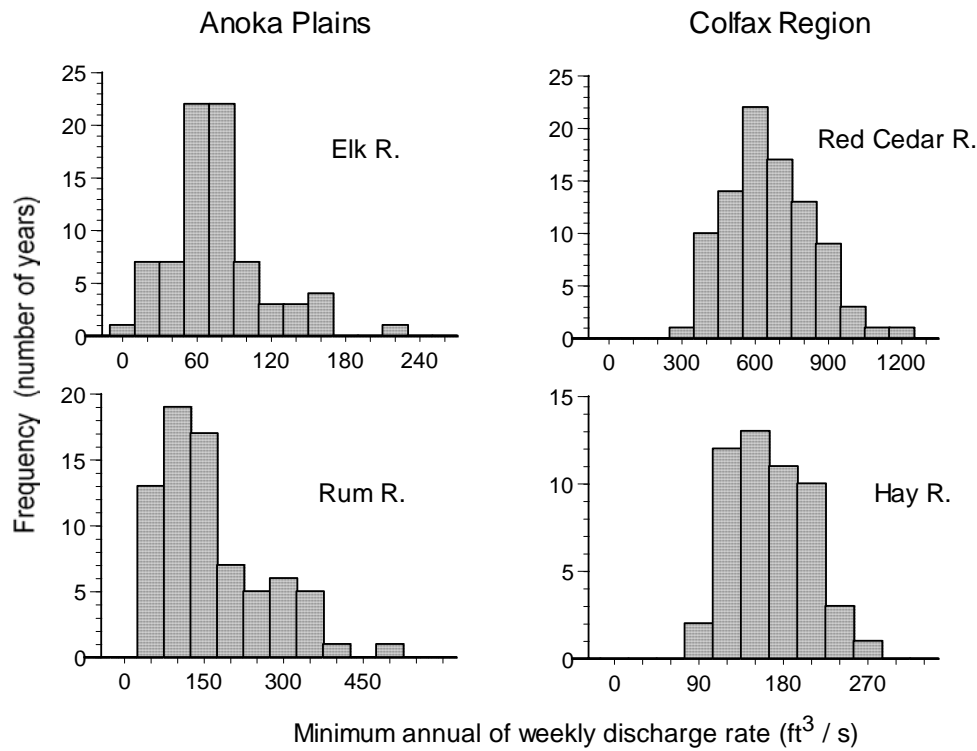


Fig. 12. Frequency distributions of annual minima in weekly discharge rates in two rivers draining the Anoka Plains (left) and the Colfax region (right). Note that there are relatively more years with low discharge in the Anoka Plains.

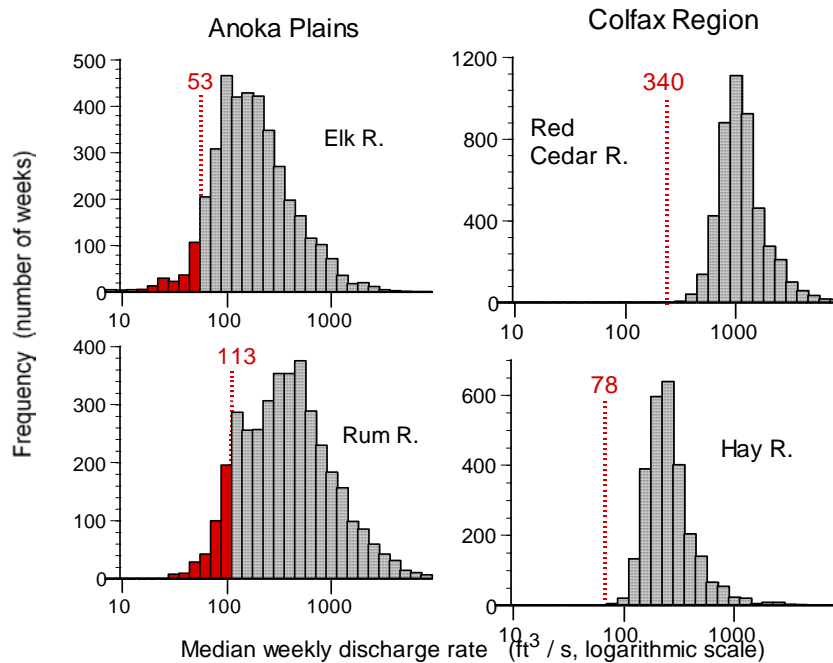


Fig. 13. Frequency distributions of weekly discharge rates in two rivers draining the Anoka Plains and Colfax region. Note markedly higher variance in rivers draining the Anoka Plains. Values of 53, 113, 340, and 78 indicate putative drought thresholds defined as 30% of the average (same as indicated in Figs. 10, 11, and 14).

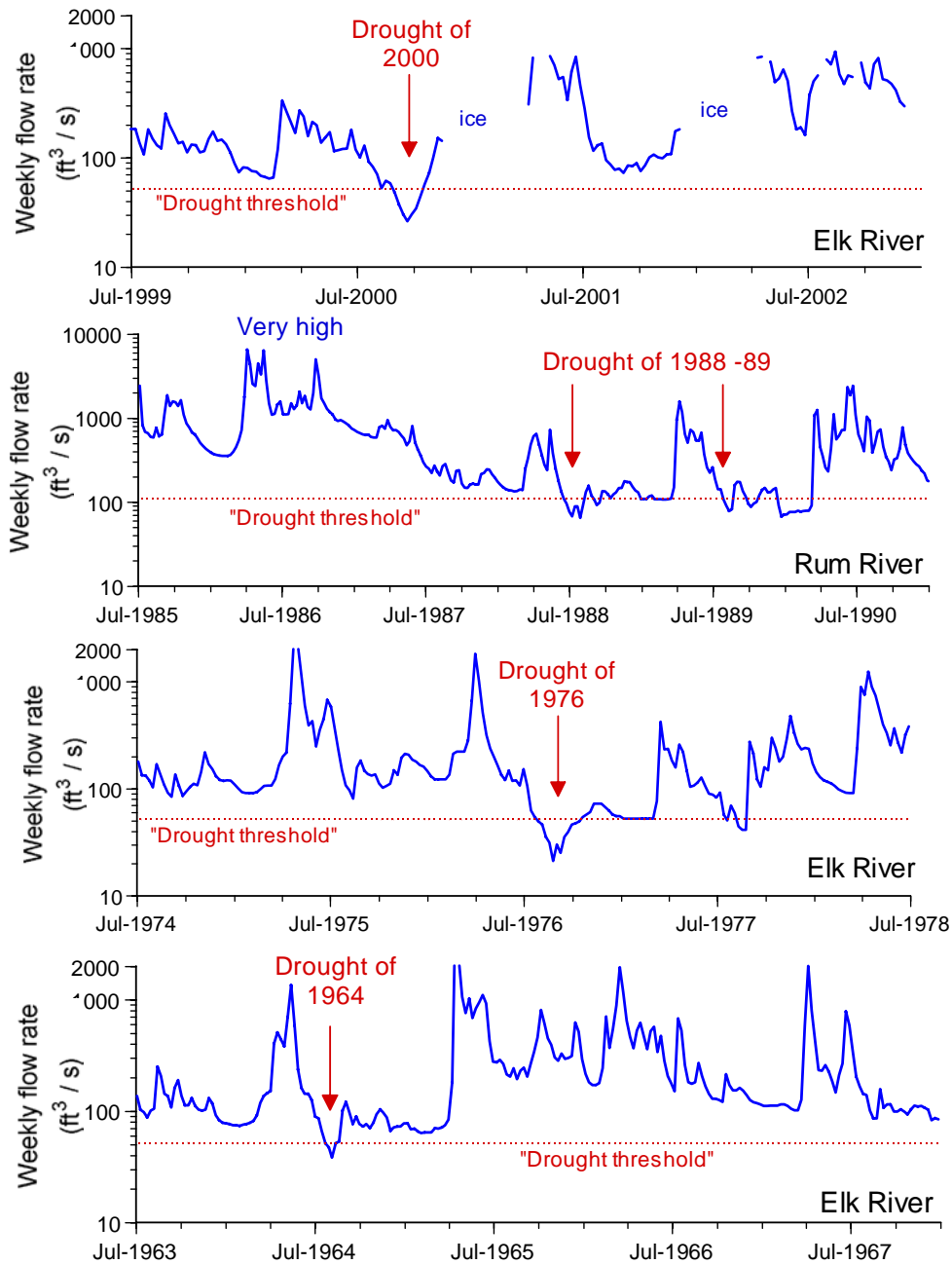


Fig. 14. Weekly discharge rates from the Anoka Plains before, during, and after droughts (in 2000, 1988-89, 1976, and 1964) that were recognized based on tree mortality, beetle outbreaks, and peat fires. Note that a “drought threshold” defined as 30% of the long term weekly discharge rates seems to provide an objective and reasonably accurate metric for recognizing consequential droughts. This metric has particular value because discharge data are available on-line, in real time, which could permit the recognition of future droughts as they occur, before tree mortality, beetle outbreaks, and peat fires.

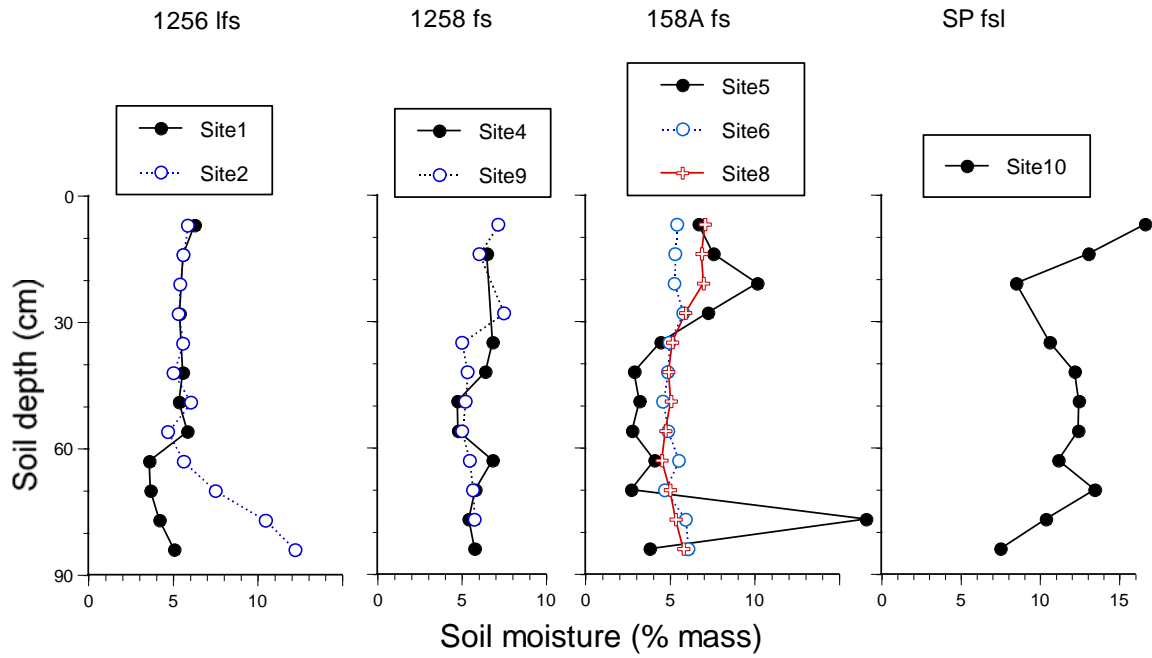


Fig. 15. Soil moisture vs. depth on 23-24 August 2002 in 8 red pine stands on four soil types near Anoka, MN.

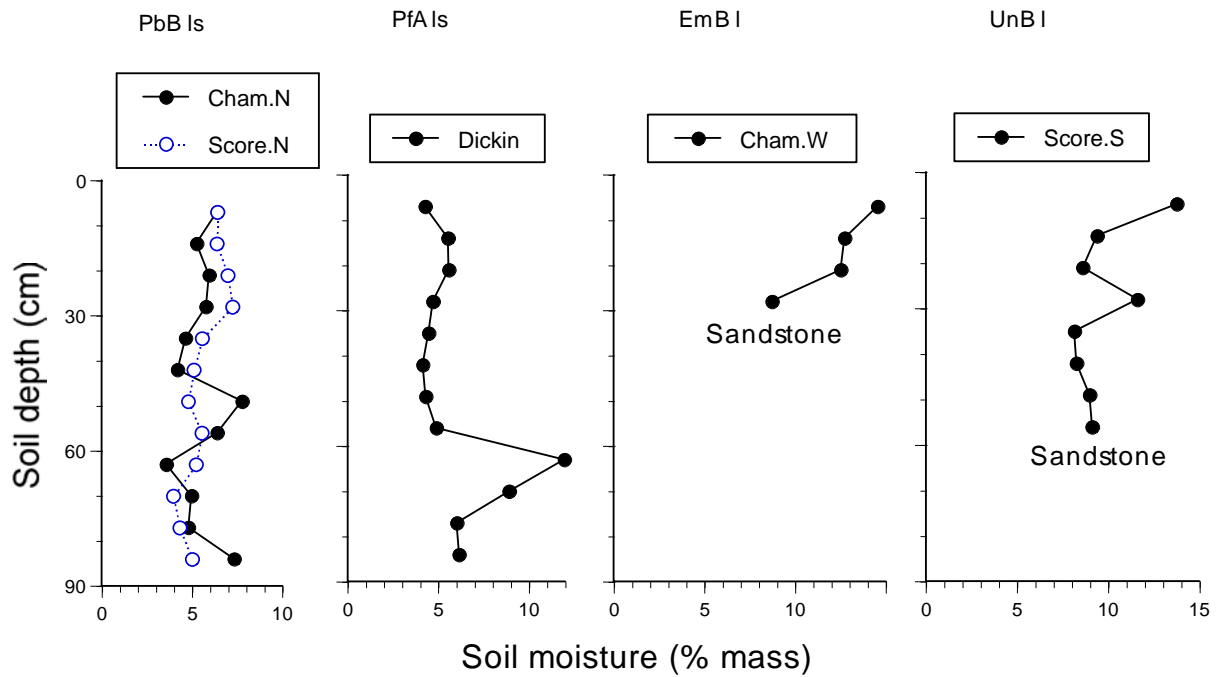


Fig. 16. Soil moisture vs. depth on 26-27 August 2002 in 5 red pine stands on four soil types near Colfax, WI.

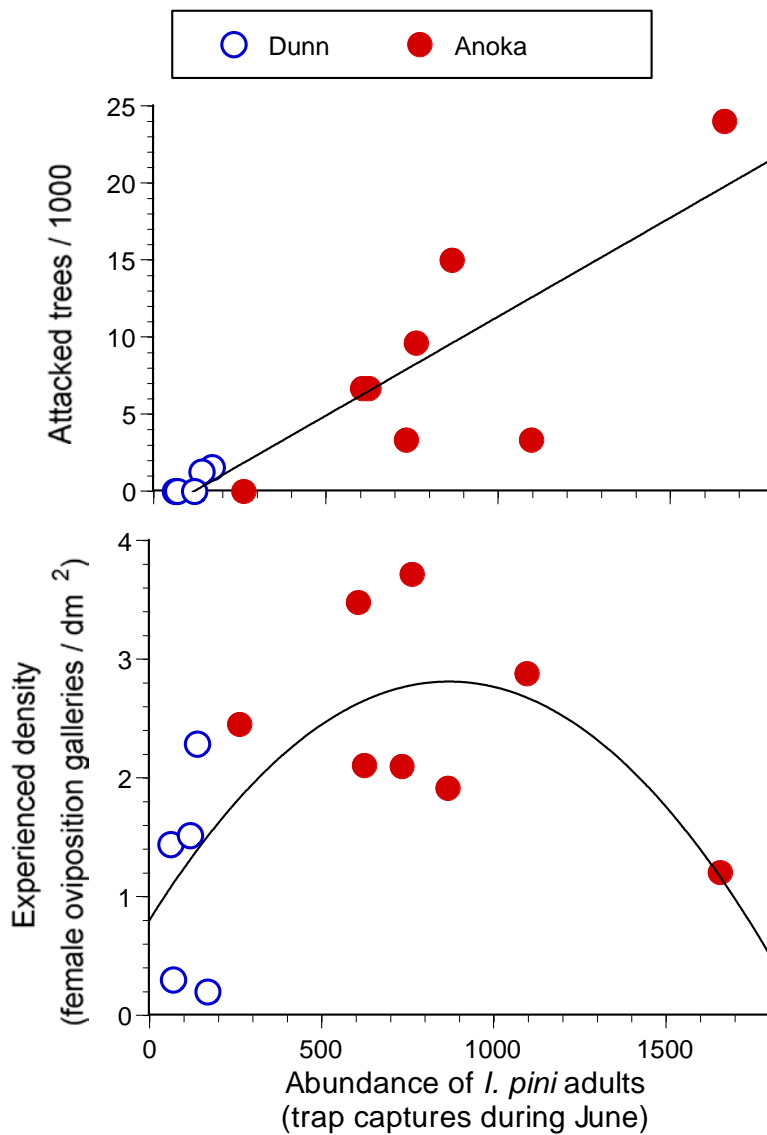


Fig. 17. Trees attacked by *Ips pini* during summer 2002 as a function of *I. pini* trap captures during early summer (upper) and *I. pini* colonization density in logs as a function of trap captures (lower). Best fit function for upper: $Y = -1.5 + 0.013 \cdot X$ ($P = 0.0002$). Best fit function for lower: $Y = 0.79 + 4.63E-3 \cdot X - 2.66E-6 \cdot X^2$ ($P = 0.035$ for full model, $P < 0.02$ for both coefficients). Compare these empirical data to theoretical predictions in Fig. 2 for an eruptive population (Fig. 1).