

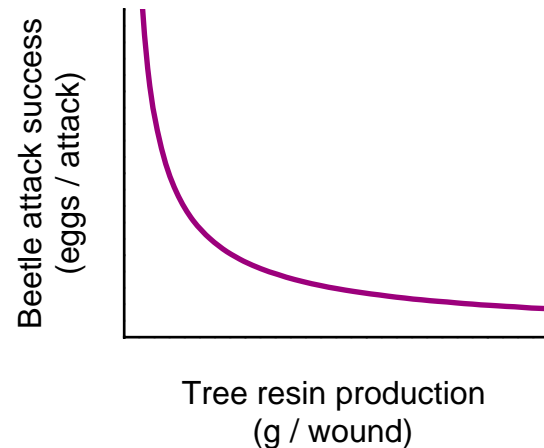
## Chapter 2

### Growth and anti-herbivore defenses of red pine at Itasca State Park

#### 2.1 INTRODUCTION

The susceptibility of pine trees to bark beetles is influenced by the defensive system of the trees and the abundance of bark beetles. Oleoresin, a mixture of terpenes and resin acids, is the primary defense of pine trees against bark beetles. When the bark of a tree is penetrated, as by a bark beetle, resin tends to be exuded from the wound. This resin presents a physical and chemical barrier to beetles. The pool of oleoresin that is preformed and stored within the vertical resin duct system of the trees function as a constitutive defense. In general, higher levels of constitutive resin flow reduce the success of colonizing beetles (Reeve et al. 1995, Fig. 2.1) and tend to protect the trees. Constitutive resin flow, and therefore the susceptibility of pine trees to bark beetles, can be influenced by environmental conditions, tree age, and tree genetics. In this research, we assessed patterns in the constitutive resin flow of red pines at Itasca. Prior to this research, no studies have measured the levels of constitutive resin flow in red pine, and very little was known about the effects of environment or tree age on the susceptibility of red pines to bark beetles. Most pine trees also have a capacity for inducible defenses. For example, wounding by mechanical damage, beetles, fire, or pathogens can potentially lead to increased synthesis of resin within the resin duct system and contribute to increased resistance to subsequent attacks (Cook and Haine 1987, Popp et al. 1991, Tisdale and Nebeker 1992, Nebeker et al. 1993, Ruel et al. 1998). Responses of the resin system to fire are explored in Chapter 6. In some pine trees, there is an additional inducible response to bark beetles and pathogens. In this system, damage to phloem tissue triggers the rapid synthesis of phenols, terpenes, and resin acids within the surrounding cells (Reid et al. 1967, Raffa and Smiley 1988, Klepzig et al. 1996). These cells fill with secondary metabolites, die, and present a physical and chemical barrier that can limit intrusion into the surrounding tissue. Relatively little is known about effects of environment, genotype, or tree age on the efficacy of this necrotic defense system in red pines, and it was beyond the scope of this research to explore it. These studies focused on red pine because this species is of central importance to park management. Chapter 1 includes comparisons of resin flow among the three species of pines that occur at Itasca.

Tree defenses interact with beetle abundance to influence tree susceptibility to attack. In general, we expect trees with higher defenses (e.g., higher levels of constitutive resin flow) to be less susceptible to bark beetles. However, even well defended trees can succumb to high rates of attack by bark beetles because as attack rate increases, the constitutive resin can be depleted and the carbohydrate reserves to support inducible responses can be exhausted (Raffa and Berryman 1983). Therefore, the probability of successful attack is expected to increase with increasing attack rate at any level of constitutive resin flow (Fig. 2.2). One result is that high abundance of bark beetles can beget high reproductive success by the beetles, which begets even higher abundance of bark beetles and creates a positive feedback system that can potentially devastate a forest. This scenario was a primary rationale for bark beetle control efforts and bark beetle research at Itasca following the extensive windstorms in 1995-96.



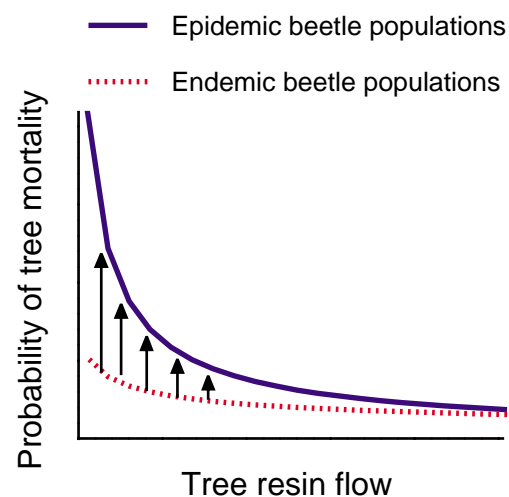
**Figure 2.1: Hypothesized relationship between beetle reproductive success and tree resin flow. Beetle reproductive success in this system is thought to be chiefly restricted to trees with very low resin flow (i.e., low secondary metabolism). This particular function has been parameterized with experimental data for the southern pine beetle (Reeve et al. 1995), which is thought to be more tolerant of resin flow than *Ips*.**

The physiology of pine trees, and their resistance to bark beetle attack, could be influenced by variation in 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. There could be important spatial variation in tree defenses among old-growth stands of red pine at Itasca. If so, identifying attributes of those stands could allow for site-specific management strategies. For example, stands with high susceptibility to bark beetles would merit careful monitoring for beetle infestations, could be given special consideration for beetle control efforts (e.g., rapid removal of trees that fall from windstorms or snowstorm), and could be protected against any avoidable risks of exacerbating mortality from beetles (e.g., by minimizing exposure to prescribed burns, see Chapter 6). We evaluated spatial variation in tree growth and defenses against bark beetles with a standardized sampling scheme that included 20 mature red pines within each of 12 old-growth stands scattered throughout the park. Measurements included an assortment of tree and stand characteristics that might be associated with tree defenses and could allow the easy identification of stands that are more or less resistant to bark beetles.

We also evaluated the effects of tree age on growth and defenses. It could be that the old-growth stands of red pine at Itasca are approaching senescence and, as a consequence, have rapidly 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 very different than if the forest could realistically persist through another century. For example, if the expected lifetime of the forest is only a few decades, it might be sensible to pursue very aggressive regeneration programs, perhaps involving frequent prescribed burns and plantings, even at the expense of some immediate costs in tree mortality (because the expected future lifespan of the trees would be very short in any case). If, instead, the old trees are still physiologically vigorous and relatively well defended, the value of existing trees would be very high (because they are

likely to persist for many decades in the absence of extraordinary disturbance) and management strategies should prioritize survival of the existing trees, even at the expense of some limitations on regeneration rate (because it would not matter very much if regeneration was successful in the next decade rather than this decade). We assessed the effects of age on tree defenses by comparing resin flow in replicated stands of old red pines and young red pines that were growing in comparable environments.

Finally, we compared the anti-herbivore defenses of red pines in Itasca with red pines growing in a region of west-central Wisconsin where precipitation is higher, drought is less severe, and growth rates of red pine are near the maximum for red pines anywhere. Because the forests at Itasca are very near to the western distribution limits of red pine, it could be that Itasca forests are chronically stressed and generally susceptible to insects and pathogens. We tested this hypothesis by comparing the resin flow of replicated stands of similarly aged red pines in Itasca and Dunn County, Wisconsin.

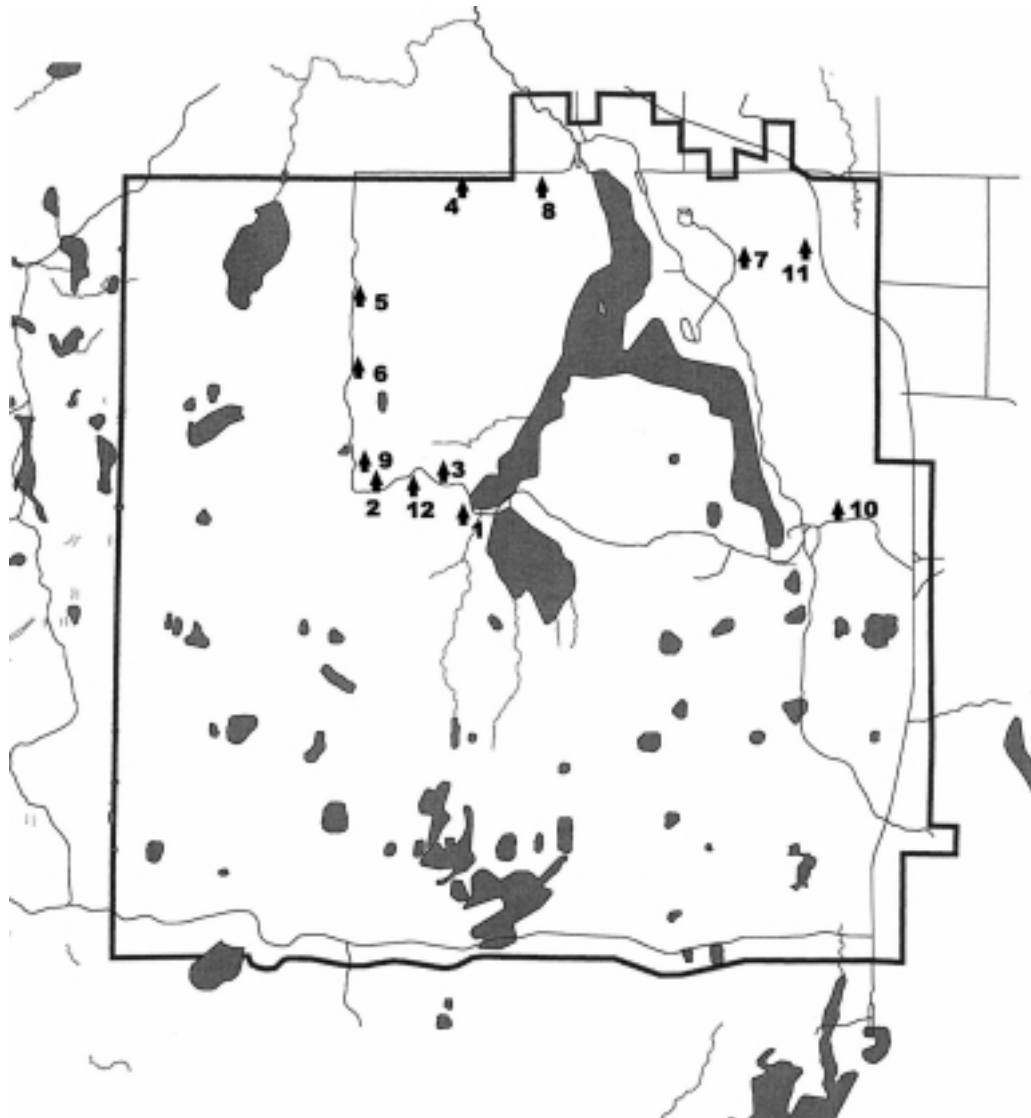


**Figure 2.2: The probability of tree mortality from bark beetles is hypothesized to be a function of tree resin flow and bark beetle population size. Upward arrows indicate the potential effects of high population size in bark beetles (epidemic populations) on tree mortality.**

## 2.2 METHODS

We measured variation in resin flow and phloem chemistry within and among 12 stands of old growth red pine in Itasca Park (Fig. 2.3). Resin flow was evaluated by measuring the resin with standardized wounds as described in Chapter 1. Phloem disks were simultaneously collected, dried, and weighed to provide a measure of phloem thickness, which indicates carbohydrate reserves in the tree and is

positively related to nutritional suitability for bark beetles in the absence of tree defenses (as in a blowdown). We measured height, diameter, and percent live crown for each tree, and measured the local density of trees around each study tree with an English BAF 10 prism. Two fascicles (dropped the previous year) were collected from the base of each tree to compare needle morphology among sites.



**Fig. 2.3.** Location of 12 study sites where we measured growth and constitutive resin flow in old growth stands of red pine at Itasca State Park.

We measured the gap light index (GLI) at each site with digital analysis of eight photographic samples collected from each site with a fisheye lens (Fig. 2.4; Canham 1988). Gap light index is inversely related to canopy closure, so provides a measure of competition among tree crowns. Two soil cores (22 mm diameter) were extracted from each stand on 25 August 1997 to measure depth of organic layer and percent water. During 1998, we also compared relative soil moisture at each site using a neutron probe. The elevation of each site was measured with an altimeter calibrated before and after each measuring bout at a site of known elevation (Mississippi headwaters).

One core was extracted from each tree at 1.5 m and subsequently analyzed as described in Chapter 5 to reconstruct the growth histories of the trees. Half of the trees were cored in 1997 using a 6" corer, and the other half of the trees were cored in 1998 with a 10" corer. The 10" corer reached the center of the trees so provided tree age as well as annual growth. For those cores that included the central ring, we estimated the year in which a tree germinated as five years before the age of the core (to allow for growth of the seedling to 1.5 m. For each tree, we extracted six different growth parameters from the ring data to test for physiological correlations between tree defenses (resin flow), age, and growth. *Grow62* = average radial growth for 62 years from 1935 – 1996. *Grow10* = average radial growth for the most recent 10 years. *CVGrow* = the coefficient of variation in annual growth (a measure of physiological stability in the tree; = standard deviation in annual growth over 62 years divided by the average annual growth). *Slope* = the slope from a linear regression of annual growth vs. year over the 62 year time series (negative slope indicates declining growth and positive slope indicates increasing growth). *DroughtGrow* = the magnitude of growth decreases during a drought that occurred from 1988-90, defined as annual growth in 1990 (the nadir of the drought) minus the annual growth in 1986 (the zenith of growth prior to the drought). *%Latewood* = the percentage of annual radial growth that was made of latewood rather than earlywood, which is potentially relevant to resin flow in that the majority of vertical resin ducts are formed within the latewood, so trees with relatively more latewood could have relatively more resin ducts.

## 2.3 RESULTS AND DISCUSSION

**Age and growth of mature red pines.** We obtained the age of 71 mature red pines (4-9 trees at each of the 12 sites). Overall, the median year of establishment was 1850 (SD = 36 years). The oldest tree in the sample reached 1.5 m in height in 1770. There was at least one tree dating to the late 1700s at sites 2, 10, and 11. The youngest tree in the sample dated to 1922 and came from site 11, the same site as one of the oldest trees. Among sites, the oldest median age of establishment was in 1819 (site 7) and the youngest median age of establishment as 1902 (site 10). Sites 3, 4, 6, 7, and 8 were even-aged (standard deviation in age of establishment of 3-9 years). Sites 1, 2, 9 and 12 contained trees of mixed ages (SD in age of establishment of 15-25 years). Sites 10 and 11 were of very uneven ages (SD in age of establishment of 46 and 59 years). The fact that half of the sites were of mixed age indicates that stand-clearing fires have not always been required for the regeneration of red pine at Itasca. At these sites, we found adjacent trees that differed in age by as much as 50 - 140 years. The even ages at sites 3, 6, and 7, suggest stand-clearing fires at those sites in approximately 1830, 1826, and 1811 respectively. Sites 4 and 8, which are near each other in the north end of the park, were both established in about 1888-89, presumably as a result of the same stand-clearing fire.

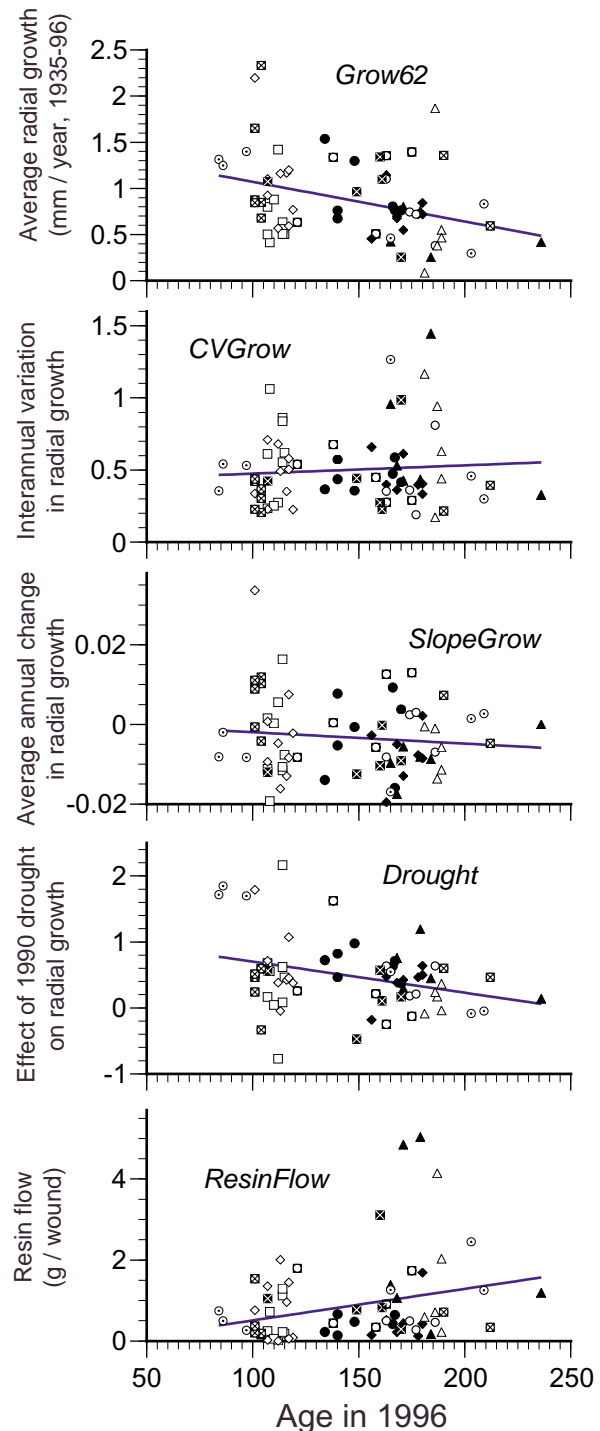
Our estimates of stand ages at Itasca must be qualified because the sample of trees that we were able to age may be biased towards younger trees. In 1998, we used a 10" corer to extract cores from 110 trees (those with ID numbers from 1001 - 1120 in Appendix 2, excepting site 5). These 110 trees were a representative sample of the tree population, but the core missed the center of the tree (and therefore did not provide the age) in 39 cases. The trees for which we lack ages tended to be of larger diameter than the trees we were able to age (least square means  $\pm$  SE = 49.1  $\pm$  1.7 cm vs. 39.1  $\pm$  1.1 cm) and so may have tended to be older. This probably did not affect our estimates of age within the five stands that were clearly even-aged, but we may have underestimated the median age in stands 1, 2, 9, and 12 where we were unable to age 17 of 40 trees. In retrospect, this potential bias was unfortunate but does not affect any of the central conclusions in this report.

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

**Fig. 2.4. Representative canopy photographs used to compare the extent of canopy closure within and among stands of mature red pine at Itasca. Images were collected with an 8 mm fish-eye lens and digitally analyzed (Canham 1988). Upper image, taken near tree 68 at site 7, yielded a gap light index of 54%. Lower image, taken near tree 52 at site 6, yielded a gap light index of 32%.**

Appendix 1 shows the pattern of annual growth from 1935 to 1996 for each of 20 individual trees at 12 sites. Radial growth per year ranged from highs near 4 mm to lows of less than 0.3 mm. Trees with intermediate crown classes tended to grow slower than trees with codominant crown classes. This relationship can potentially reflect both cause and effect in that slow-growing trees are less likely to attain codominant crown stature and trees that do not share the upper forest crown are less likely to attain high radial growth. There was considerable variation among trees in the temporal patterns of growth. For example, tree 1077 in site 8, has increased its annual growth from less than 0.4 mm in the late 1940s to  $> 2$  mm per year since 1972. Presumably, this reflects the death of one or more nearby trees. In contrast, tree 82 in site 9 has declined from near 2 mm / year in the late 1930s to near 0.6 mm / year in the last two decades. Trees 1073 and 1075 in site 8 have been sustaining high growth rates near 2 mm / year throughout the last 60 years, while other trees, such as tree 1102 in site 11, have been barely growing through the entire time series (average = 0.33 mm / year).

Overall, there was only a weak tendency for declining growth rates during this century in the population of mature red pines at Itasca (Fig. 2.5, upper). Average radial growth rates held near 1 mm / year for most of the time series, with distinct peaks in 1942 and 1952, and conspicuous troughs from about 1978-82 and from 1989-91. The latter trough corresponds to a sequence of drought years (minimum Palmer drought severity index = -6, -4, and -5). Other patterns in the time series are not easily explained by the Palmer drought severity index, but climatic conditions, perhaps related to temperatures or length of the growing season, are the most likely mechanism for synchronous effects on forest growth. When the aged trees were pooled across sites, there was some tendency for older trees to have lower growth rates (*Grow62* in Fig. 2.6), but there were no effects of age on physiological stability as measured by interannual variation in growth rate (*CVGrow* in Fig. 2.6), nor were old trees any more likely to be in growth decline than young trees (*SlopeGrow* in Fig. 2.6). Furthermore, older

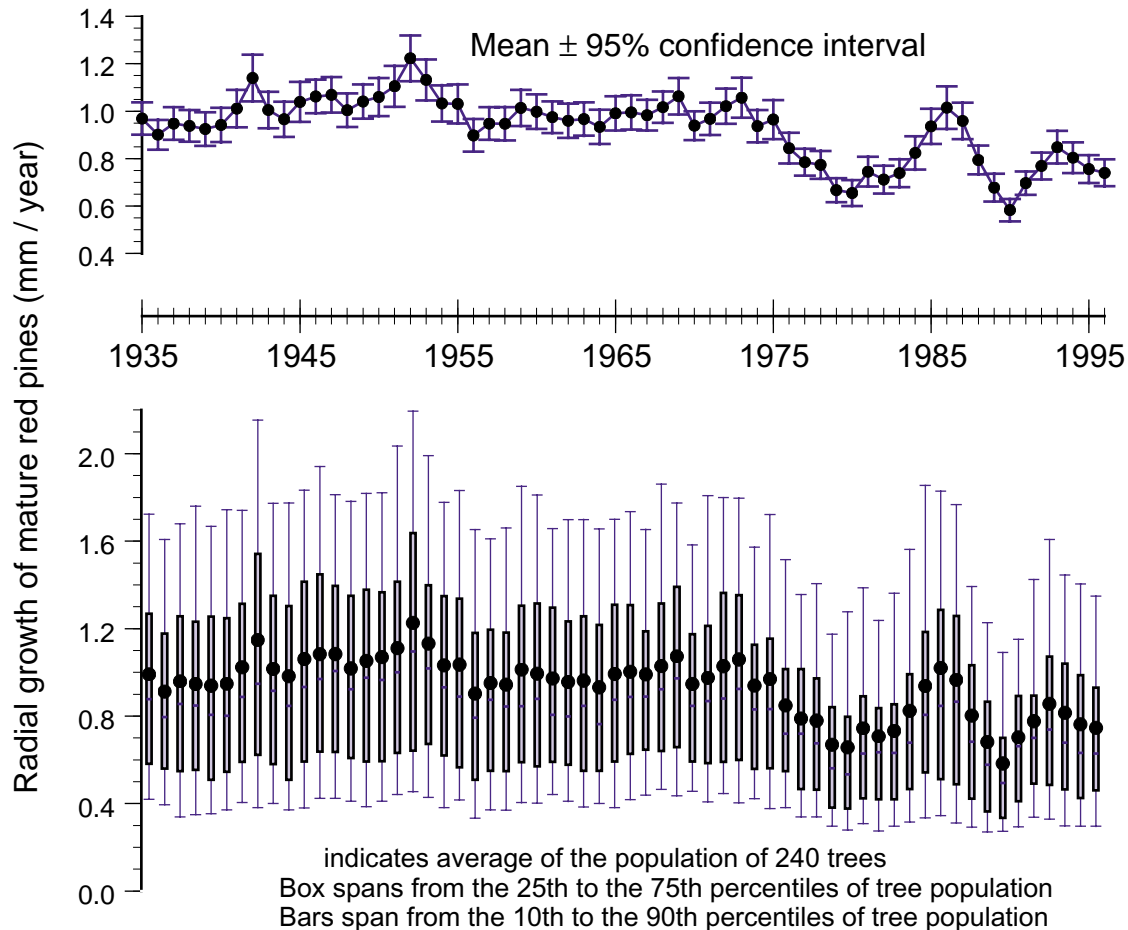


**Fig. 2.6.** Correlations of tree age with four different measures of tree growth and with constitutive defense against bark beetles (resin flow). Different symbols represent different sites.

trees actually tended to suffer less impacts from the most recent drought (*DroughtGrow* in Fig. 2.6), and tended to have significantly higher constitutive resin flow than younger trees (*ResinFlow* in Fig. 2.6). These data indicate generally high vigor and high defense in even the oldest red pines at Itasca. There is no suggestion of physiological senescence or growth declines in trees up to almost 250 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 argues for placing a high priority on minimizing any manageable risks of tree mortality from disturbance. Given the long potential

lifespan of these trees, even very small increases in mortality risk can have a meaningful effect on tree survivorship and the lifetime of the forest (see Figs. 5.7 and 6.9 in Chapters 5 and 6)

**Variation in growth and defenses among old growth red pine.** There was highly significant variation among old growth stands of red pine in constitutive resin flow and all measurements of tree growth, tree morphology, and stand attributes (Figs. 2.7 - 2.9;  $F_{11,201} = 12.39$ ,  $P < 0.0001$  for site effect for resin flow). Measurements of resin flow were quite consistent between measurements in August 1997, July 1998, and August 1998 (Fig. 2.12; highly



**Fig. 2.5. Annual growth of mature red pine at Itasca during 1935 - 1996. Upper figure shows population mean with confidence interval. Lower figure summarizes the frequency distribution of the population (20 trees at each of 12 sites). Trough in growth rates from 1988 - 1990 correspond to a significant drought in the region.**

significant effects of tree:  $F_{201, 198} = 4.41$ ,  $P < 0.0001$ ; no effects of data:  $F_{1, 198} = 0.01$ ,  $P = 0.93$  for comparisons of 240 trees across two dates in 1998, and  $F_{2, 166} = 2.00$ ,  $P = 0.10$  for comparisons of 120 trees that were measured on all three dates). Patterns of resin flow across sites remained very constant across the 3 sampling dates ( $r = 0.78$  to  $0.89$  for correlations of sites means across dates). Patterns of phloem thickness were equally similar across sampling dates. Thus the old growth forest at Itasca is comprised of a mosaic of red pine stands that differ in their constitutive defenses against bark beetles and many other attributes as well.

We explored correlations among site-specific characteristics (Tables 2.1 - 2.2; Fig. 2.10) and used stepwise regression to identify the simplest combinations of parameters that could predict spatial patterns in constitutive resin flow. Tree diameter had a strong positive relationship with average resin flow at a site (Fig. 2.10). Equation 2.1 explained 63% of the variation among sites in resin flow ( $P = 0.0019$  for the statistical effect of diameter,  $DBH$ ). There appeared to be some additional contribution of basal area once the effects of diameter had been accounted for. A model that also included basal area (Eq. 2.2) explained 74% of the variation among sites in resin flow ( $P = 0.0021$  and  $P = 0.082$  for effects of  $DBH$  and  $BA$ , respectively). The coefficients for diameter were positive, indicating that sites with bigger trees tended to have higher resin flow. The coefficient for basal area was negative, indicating that if average tree diameter is comparable, sites with high basal area tended to have lower resin flow than sites with high basal area. Differences among sites in average tree diameter appear to be largely influenced by stand age ( $r = 0.65$  for correlation between stand age and  $DBH$ ), so equations 2.1 - 2.2 reflect the same pattern as indicated in Fig. 2.6 lower. Comparisons of resin flow in mature red pine vs those 30 - 80 years old further reinforce the conclusion that the constitutive resin flow of red pines tends to increase markedly with age (see next section). Presumably, the negative effect of basal area on resin flow is because increased competition among trees for canopy space within a stand tends to limit the carbon resources that are available for the synthesis of oleoresin.

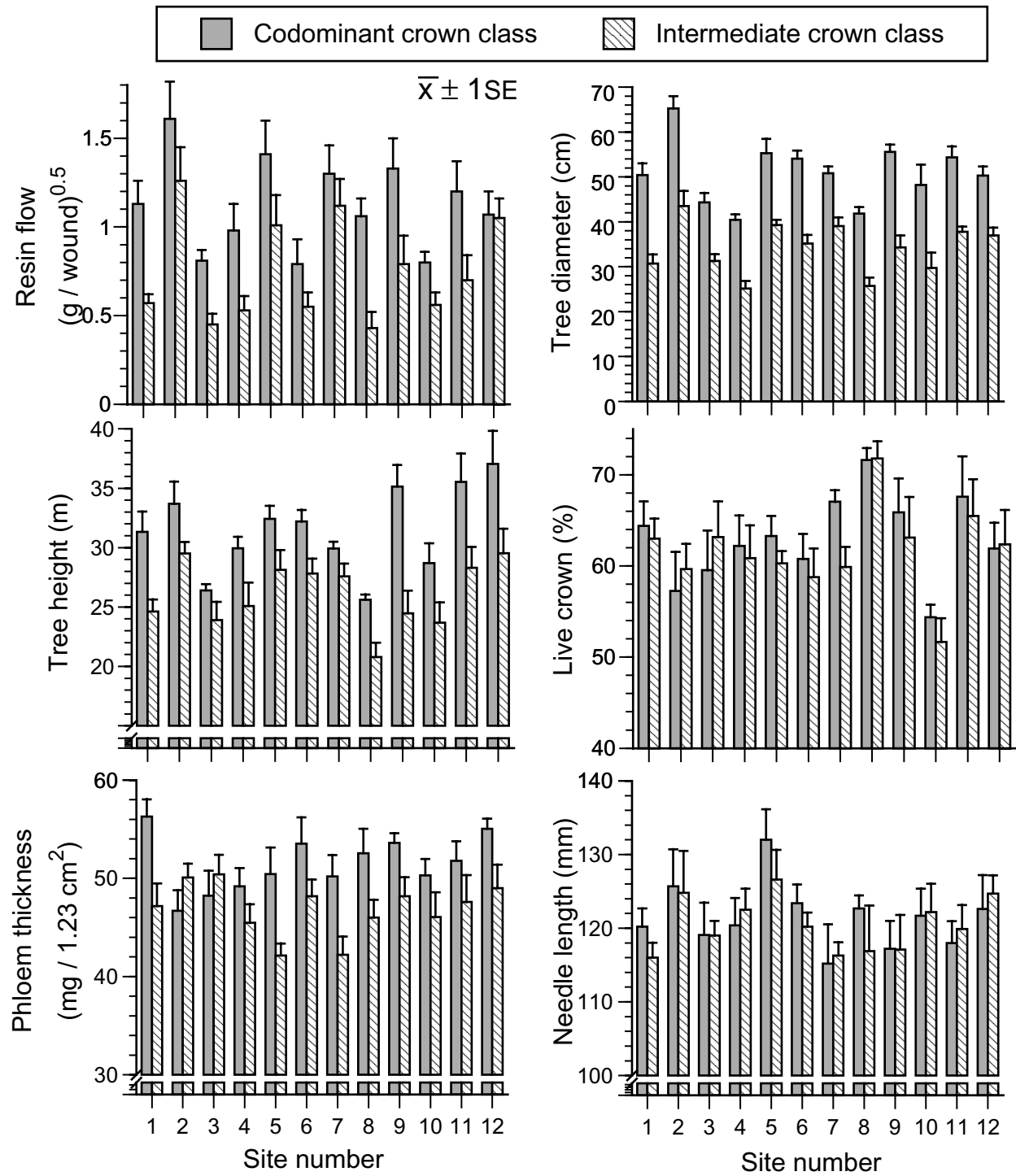
$$Resin = -0.51 + 0.034 \cdot DBH \quad \text{Eq. 2.1}$$

$$Resin = 0.00 + 0.031 \cdot DBH - 0.013 \cdot BA \quad \text{Eq. 2.2}$$

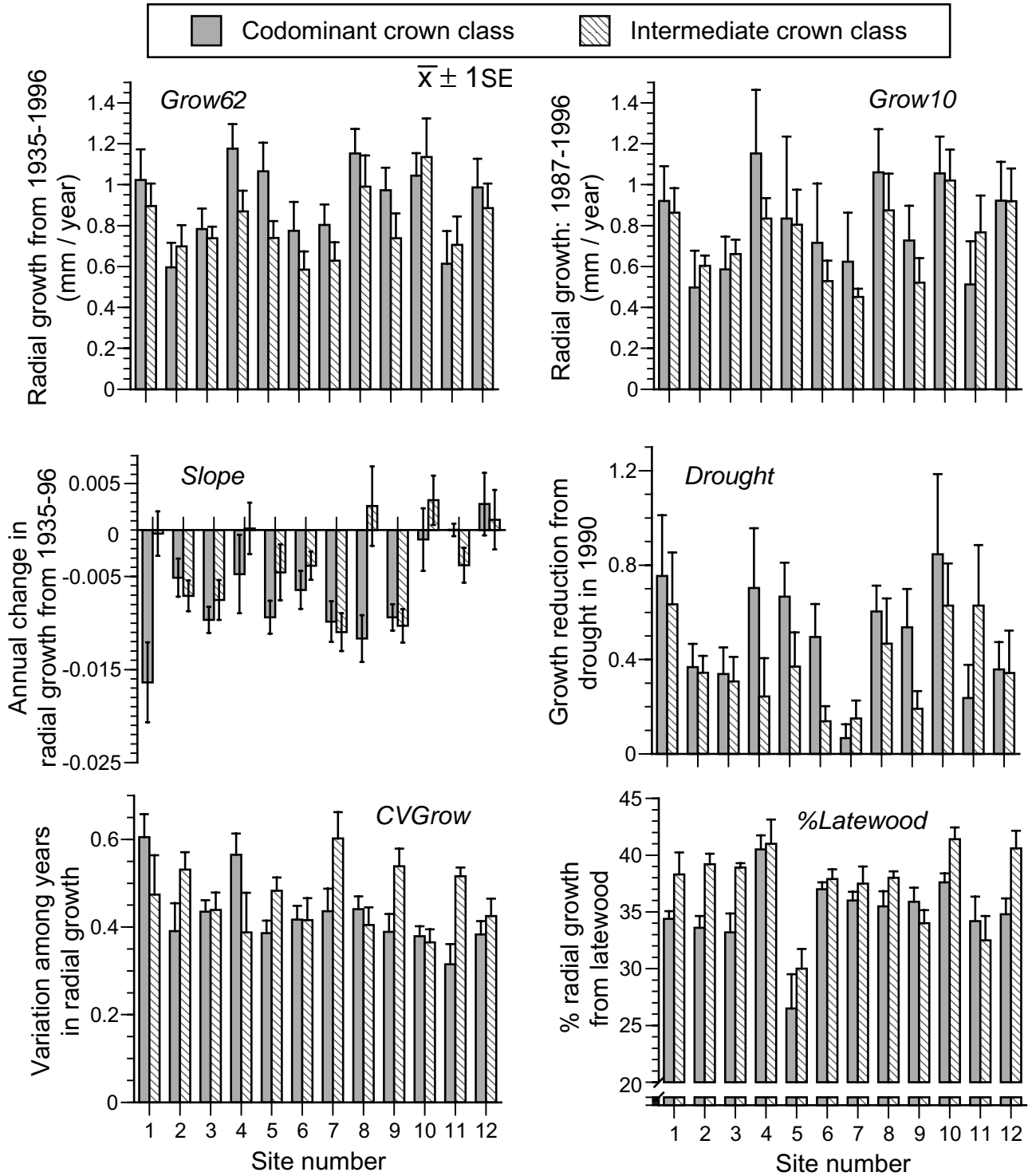
There were numerous other correlations among stand attributes (Table 2.2, Fig. 2.10). Most of these are obvious. For example, tree height was positively correlated with diameter and stands with low basal area tended to have open canopies (high gap light index). Other relationships would have been less easy to predict. The extent of canopy closure changed systematically over an elevation gradient of only 50 m, with higher sites tending to have more open canopies (higher gap light index); the tallest trees tended to occur on the sites where the water content of the organic soil was highest (in September 1997); the greatest effects of a recent drought (1988-1990) were most evident in sites where the water content of the mineral soil was lowest (in September 1997); and sites where trees had the lowest interannual variation in radial growth ( $CVGrow$ ) were the sites most likely to have declining growth rates (Fig. 2.10).

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, and phloem mass 11% higher in codominant vs intermediate trees;  $F_{1, 201} = 80.39$  and  $30.11$ , respectively;  $P < 0.0001$  in both cases). Trees of intermediate crown class were significantly shorter, of smaller diameter, and their wood tended to be comprised of a higher percentage of latewood (Figs. 2.7 - 2.8;  $P < .01$  for all parameters; the result that intermediate trees had relatively more latewood but lower resin flow was opposite the prediction based on density of vertical resin ducts.) However, trees of intermediate crown class did not have relatively less live crown ( $\%LiveCrown$ ), did not have conspicuously lower rates of radial growth ( $Grow62$  and  $Grow10$ ), were no more likely to have declining growth rates ( $Slope$ ), and were no more susceptible to growth reductions from drought ( $Drought$ ) or other climatic factors that influence year-to-year variation in growth rates ( $CVGrow$ ) (Figs. 2.7 - 2.8).

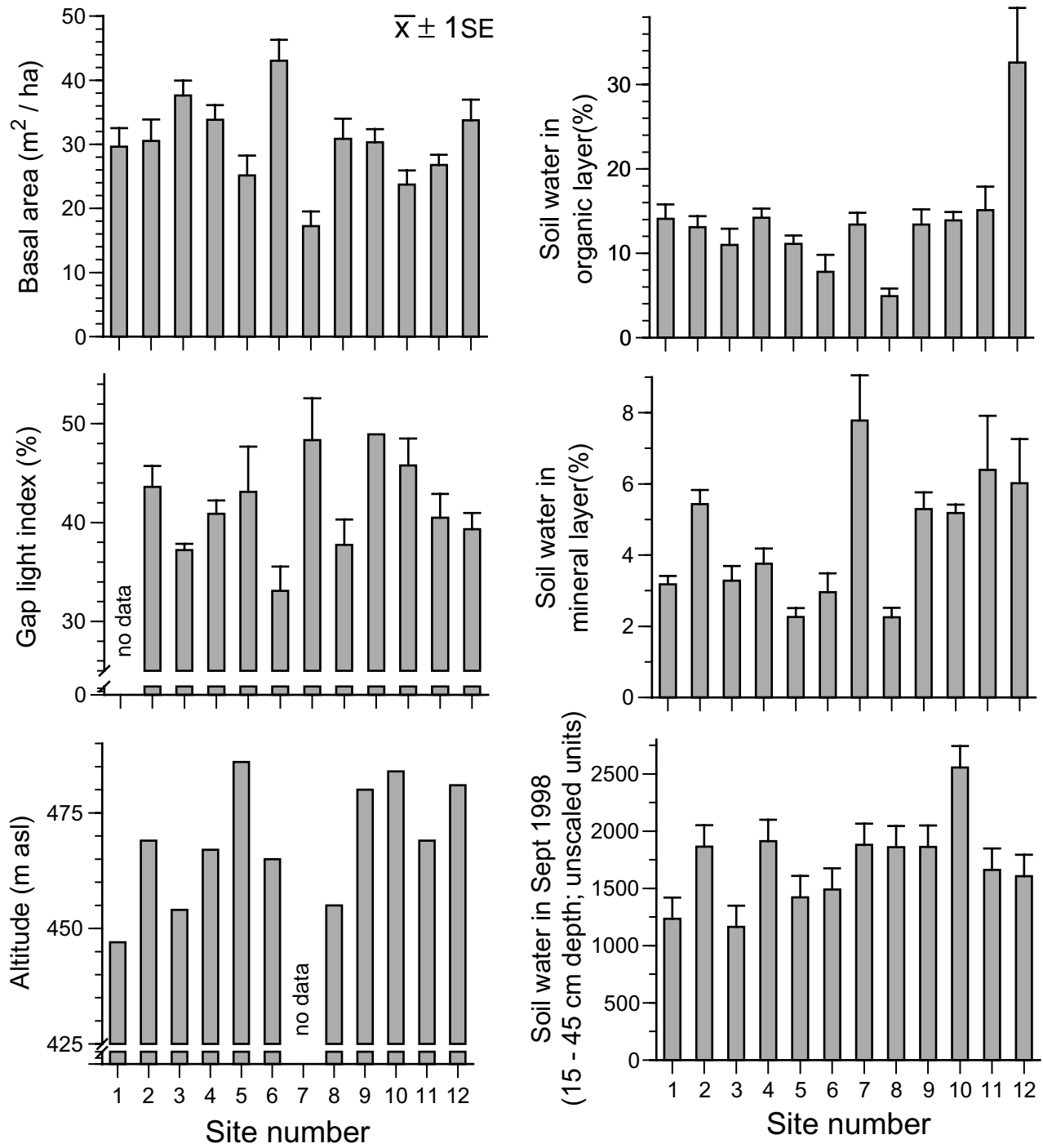
The full set of measurements summarized in this section are provided in Appendix 2. Neutron probe measurements of soil water, which were collected in September 1998, are provided in Appendix 3.



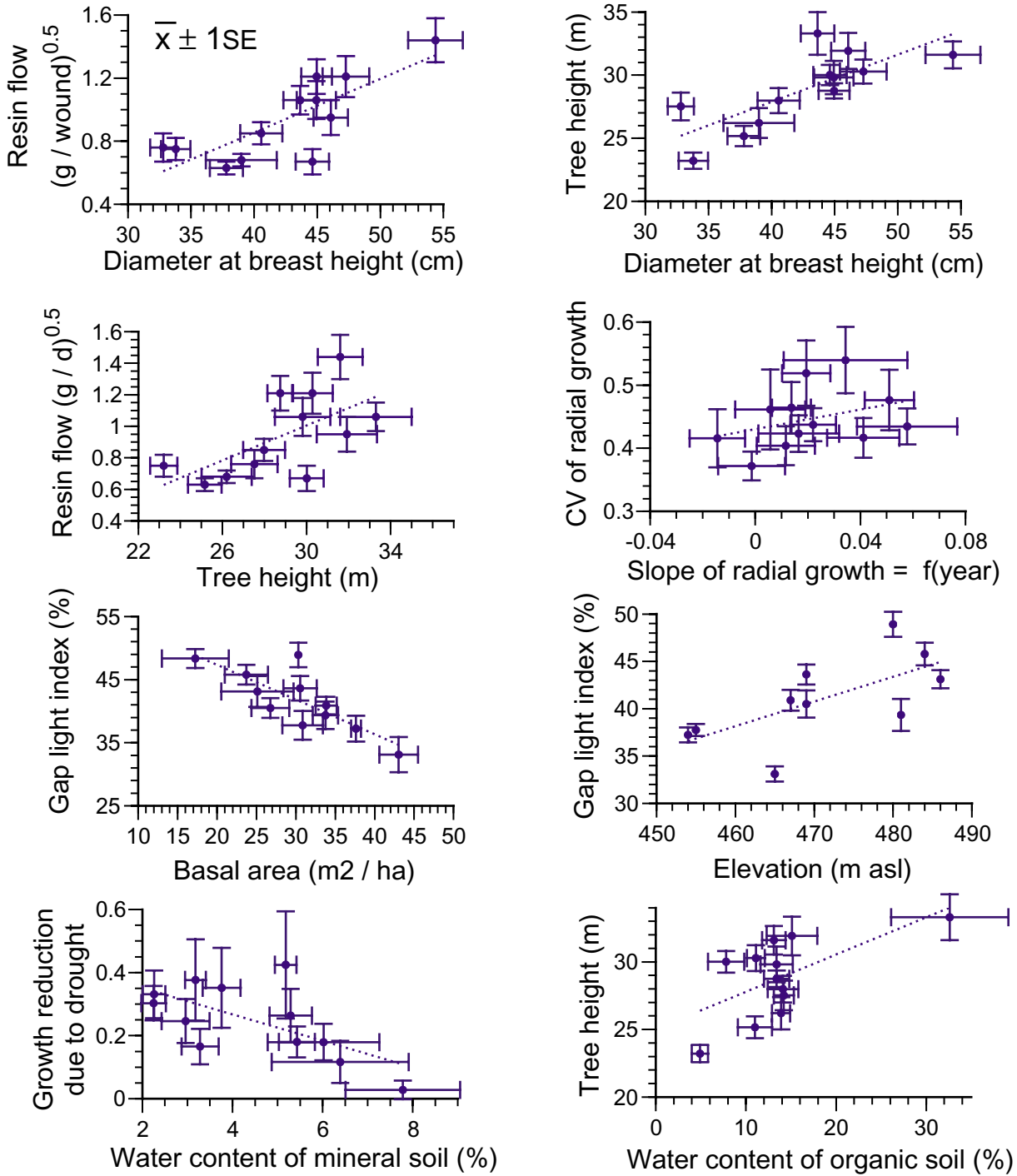
**Fig. 2.7.** Average characteristics of mature red pines at each of 12 different sites in Itasca Park.  $N = 10$  codominant trees and 10 intermediate trees at each site. Analysis of variance indicated significant variation among sites for all parameters.



**Fig. 2.8.** Average characteristics from analysis of tree cores of mature red pines at each of 12 different sites in Itasca Park.  $N = 10$  codominant trees and 10 intermediate trees at each site. Analysis of variance indicated significant variation among sites for all parameters.



**Fig. 2.9. Average site characteristics in each of 12 stands of mature red pine in Itasca Park. Analysis of variance indicated significant variation among sites for all parameters.**



**Fig. 2.10.** Some of the significant correlations among sites in the attributes of mature red pine stands. See Tables 2.1 - 2.2 for site specific means and correlation matrix.

**Table 2.1. Mean attributes of 12 old growth red pine sites in Lake Itasca Park (20 trees / site; see Appendix 2 for measurements of individual trees).**

| Site | Age | Elev. | GLI  | DepthOrg | WaterOrg | WaterMin | WaterN | DBH  | BA   | Ht   | %LC  | Resin | Phloem | Fasc  | Grow62 | Grow10 | CVGrow | Slope   | Drought | Latewood |
|------|-----|-------|------|----------|----------|----------|--------|------|------|------|------|-------|--------|-------|--------|--------|--------|---------|---------|----------|
| 1    | 148 | 447   |      | 29.7     | 14.1     | 3.2      | 1234   | 40.6 | 29.6 | 28.0 | 63.7 | 0.85  | 51.7   | 118.1 | 0.96   | 0.89   | 0.54   | -0.0084 | 0.38    | 36.4     |
| 2    | 175 | 469   | 43.6 | 30.7     | 13.1     | 5.4      | 1866   | 54.4 | 30.5 | 31.6 | 58.5 | 1.44  | 48.4   | 125.2 | 0.65   | 0.55   | 0.46   | -0.0061 | 0.18    | 36.4     |
| 3    | 171 | 454   | 37.2 | 25.6     | 11.0     | 3.3      | 1163   | 37.8 | 37.6 | 25.2 | 61.4 | 0.63  | 49.3   | 119.1 | 0.76   | 0.62   | 0.44   | -0.0086 | 0.17    | 36.0     |
| 4    | 112 | 467   | 40.9 | 28.7     | 14.2     | 3.8      | 1913   | 32.8 | 33.8 | 27.5 | 61.5 | 0.76  | 47.3   | 121.5 | 1.02   | 0.99   | 0.48   | -0.0023 | 0.35    | 40.8     |
| 5    |     | 486   | 43.1 | 27.7     | 11.1     | 2.3      | 1423   | 47.3 | 25.1 | 30.3 | 61.8 | 1.21  | 46.3   | 129.3 | 0.90   | 0.82   | 0.43   | -0.0070 | 0.33    | 28.3     |
| 6    | 176 | 465   | 33.1 | 26.4     | 7.8      | 3.0      | 1490   | 44.6 | 43.0 | 30.0 | 59.8 | 0.67  | 50.9   | 121.8 | 0.68   | 0.62   | 0.42   | -0.0051 | 0.25    | 37.5     |
| 7    | 187 |       | 48.3 | 26.4     | 13.4     | 7.8      | 1880   | 45.0 | 17.2 | 28.8 | 63.5 | 1.21  | 46.2   | 115.8 | 0.72   | 0.54   | 0.52   | -0.0104 | 0.03    | 36.8     |
| 8    | 113 | 455   | 37.7 | 26.4     | 4.9      | 2.3      | 1860   | 33.8 | 30.9 | 23.2 | 71.7 | 0.75  | 49.3   | 119.8 | 1.07   | 0.97   | 0.42   | -0.0045 | 0.30    | 36.8     |
| 9    | 161 | 480   | 48.9 | 31.2     | 13.4     | 5.3      | 1863   | 44.9 | 30.3 | 29.8 | 64.5 | 1.06  | 50.9   | 117.2 | 0.86   | 0.62   | 0.46   | -0.0098 | 0.26    | 34.9     |
| 10   | 104 | 484   | 45.8 | 31.2     | 13.9     | 5.2      | 2557   | 39.0 | 23.7 | 26.2 | 53.0 | 0.68  | 48.2   | 122.0 | 1.09   | 1.04   | 0.37   | 0.0011  | 0.42    | 39.5     |
| 11   | 131 | 469   | 40.5 | 29.1     | 15.1     | 6.4      | 1662   | 46.1 | 26.8 | 31.9 | 66.5 | 0.95  | 49.7   | 119.0 | 0.66   | 0.64   | 0.42   | -0.0019 | 0.12    | 33.4     |
| 12   | 158 | 481   | 39.3 | 27.3     | 32.6     | 6.0      | 1608   | 43.6 | 33.7 | 33.3 | 62.1 | 1.06  | 52.0   | 123.7 | 0.94   | 0.92   | 0.40   | 0.0020  | 0.18    | 37.7     |

**Table 2.2. Correlation matrix of site-specific attributes. Significant correlations are in bold.**

|          | Age          | Elev.       | GLI          | DepthOrg | WaterOrg    | WaterMin     | WaterN | DBH          | BA    | Ht          | %LC   | Resin | Phloem | Fasc  | Mean60      | Mean10      | CVGrow       | Slope | Drought | Latewood |  |
|----------|--------------|-------------|--------------|----------|-------------|--------------|--------|--------------|-------|-------------|-------|-------|--------|-------|-------------|-------------|--------------|-------|---------|----------|--|
| Age      | 1.00         |             |              |          |             |              |        |              |       |             |       |       |        |       |             |             |              |       |         |          |  |
| Elev.    | -0.10        | 1.00        |              |          |             |              |        |              |       |             |       |       |        |       |             |             |              |       |         |          |  |
| GLI      | 0.03         | <b>0.66</b> | 1.00         |          |             |              |        |              |       |             |       |       |        |       |             |             |              |       |         |          |  |
| DepthOrg | -0.31        | 0.36        | <b>0.60</b>  | 1.00     |             |              |        |              |       |             |       |       |        |       |             |             |              |       |         |          |  |
| WaterOrg | 0.09         | 0.38        | 0.12         | 0.13     | 1.00        |              |        |              |       |             |       |       |        |       |             |             |              |       |         |          |  |
| WaterMin | 0.30         | 0.42        | 0.58         | 0.25     | 0.51        | 1.00         |        |              |       |             |       |       |        |       |             |             |              |       |         |          |  |
| WaterN   | -0.50        | 0.50        | 0.55         | 0.51     | 0.00        | 0.40         | 1.00   |              |       |             |       |       |        |       |             |             |              |       |         |          |  |
| DBH      | <b>0.65</b>  | 0.39        | 0.28         | 0.28     | 0.17        | 0.41         | -0.09  | 1.00         |       |             |       |       |        |       |             |             |              |       |         |          |  |
| BA       | 0.13         | -0.41       | <b>-0.80</b> | -0.28    | -0.05       | -0.52        | -0.44  | -0.19        | 1.00  |             |       |       |        |       |             |             |              |       |         |          |  |
| Ht       | 0.43         | 0.49        | 0.12         | 0.24     | <b>0.62</b> | 0.48         | -0.13  | <b>0.77</b>  | -0.01 | 1.00        |       |       |        |       |             |             |              |       |         |          |  |
| %LC      | -0.06        | -0.43       | -0.16        | -0.36    | -0.19       | -0.14        | -0.34  | -0.23        | -0.02 | -0.17       | 1.00  |       |        |       |             |             |              |       |         |          |  |
| Resin    | 0.50         | 0.42        | 0.55         | 0.26     | 0.27        | 0.47         | 0.03   | <b>0.80</b>  | -0.48 | <b>0.64</b> | 0.01  | 1.00  |        |       |             |             |              |       |         |          |  |
| Phloem   | 0.11         | -0.31       | -0.42        | 0.11     | 0.36        | -0.08        | -0.34  | -0.02        | 0.56  | 0.21        | 0.18  | -0.27 | 1.00   |       |             |             |              |       |         |          |  |
| Fasc     | -0.13        | 0.55        | -0.20        | 0.05     | 0.13        | -0.36        | -0.02  | 0.33         | 0.13  | 0.33        | -0.37 | 0.31  | -0.25  | 1.00  |             |             |              |       |         |          |  |
| Grow62   | <b>-0.76</b> | 0.07        | 0.08         | 0.16     | 0.07        | -0.38        | 0.36   | <b>-0.71</b> | -0.11 | -0.52       | 0.02  | -0.40 | 0.00   | 0.09  | 1.00        |             |              |       |         |          |  |
| Grow10   | <b>-0.83</b> | 0.07        | -0.12        | 0.14     | 0.18        | -0.38        | 0.31   | <b>-0.67</b> | -0.01 | -0.37       | -0.05 | -0.44 | 0.05   | 0.24  | <b>0.94</b> | 1.00        |              |       |         |          |  |
| CVGrow   | 0.38         | -0.55       | 0.42         | 0.02     | -0.12       | 0.09         | -0.34  | 0.05         | -0.24 | -0.03       | 0.26  | 0.30  | -0.09  | -0.42 | -0.15       | -0.27       | 1.00         |       |         |          |  |
| Slope    | <b>-0.61</b> | 0.39        | -0.29        | 0.15     | 0.51        | 0.11         | 0.43   | -0.21        | 0.12  | 0.18        | -0.27 | -0.25 | 0.17   | 0.36  | 0.39        | <b>0.62</b> | <b>-0.70</b> | 1.00  |         |          |  |
| Drought  | <b>-0.68</b> | 0.07        | -0.04        | 0.41     | -0.20       | <b>-0.64</b> | 0.22   | -0.44        | 0.14  | -0.39       | -0.26 | -0.42 | 0.07   | 0.31  | <b>0.77</b> | <b>0.77</b> | -0.15        | 0.26  | 1.00    |          |  |
| Latewood | -0.39        | -0.25       | -0.12        | 0.07     | 0.15        | 0.19         | 0.44   | -0.49        | 0.25  | -0.29       | -0.27 | -0.44 | 0.18   | -0.37 | 0.29        | 0.32        | 0.00         | 0.37  | 0.14    | 1.00     |  |

Age = median age in 1996. Elev. = m above sea level. GLI = gap light index (% light transmission through canopy). DepthOrg = depth of organic layer (cm).

WaterOrg = water content of organic layer in September 1997 (% mass). WaterMin = water content of upper mineral layer in September 1997 (% mass).

WaterN = soil water content in August 1998 as measured by neutron probe (unscaled units). DBH = diameter at breast height (cm). BA = basal area (m<sup>2</sup> / ha).

Ht = tree height (m). %LC = percent live crown (% of total height). Resin = resin flow / wound (square root transformed). Phloem = phloem thickness (mg dry mass / 1.23 cm<sup>2</sup>).

Fasc = fascicle length (mm). Grow62 = average radial growth for 62 years from 1935 to 1996 (mm / year). Grow10 = average radial growth for 10 years from 1987 to 1996.

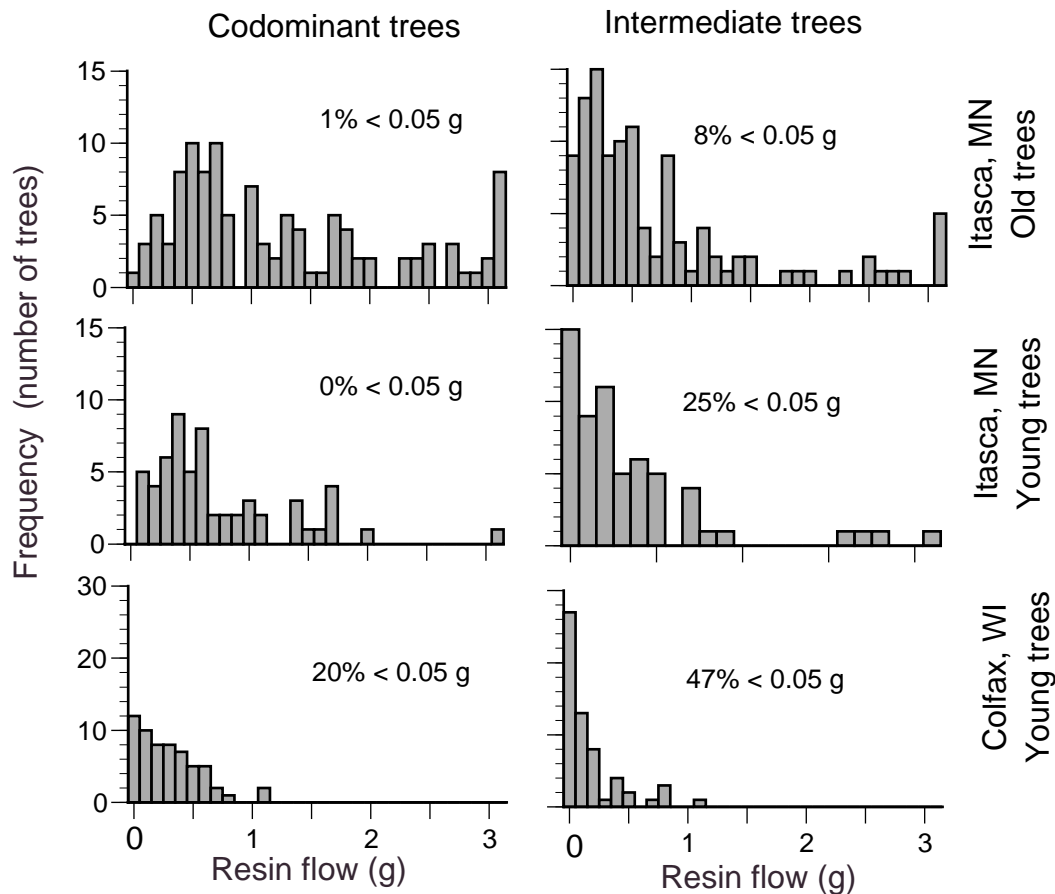
CVGrow = coefficient of interannual variation in annual radial growth (SD / mean). Slope = slope from linear regression of annual radial growth vs year from 1935 to 1996.

Drought = reduction in annual radial growth due to drought: growth in 1986 (predrought) - growth in 1990 (drought).

Latewood = percent of radial growth comprised of latewood xylem vs earlywood xylem.

**Constitutive defenses of mature red pine vs. young red pine.** Mature red pines at Itasca had dramatically higher resin flow (about two-fold) compared to red pines in the same area that were 35 - 60 years old (Fig. 2.11 - 2.12). It could be that old trees have higher resin flow as a result of physiological changes associated with maturation, such as an increase in the size and integration of the resin duct system. It could also be the result of tree responses to wounds that tend to be accumulated during the lifespan of a long-lived tree (i.e., if wounds from insects, fires, pathogens, and mechanical damage induce incremental, sustained, increases in resin flow). It is also possible, but perhaps less likely, that old growth forests represent a subset of the original tree population that has been

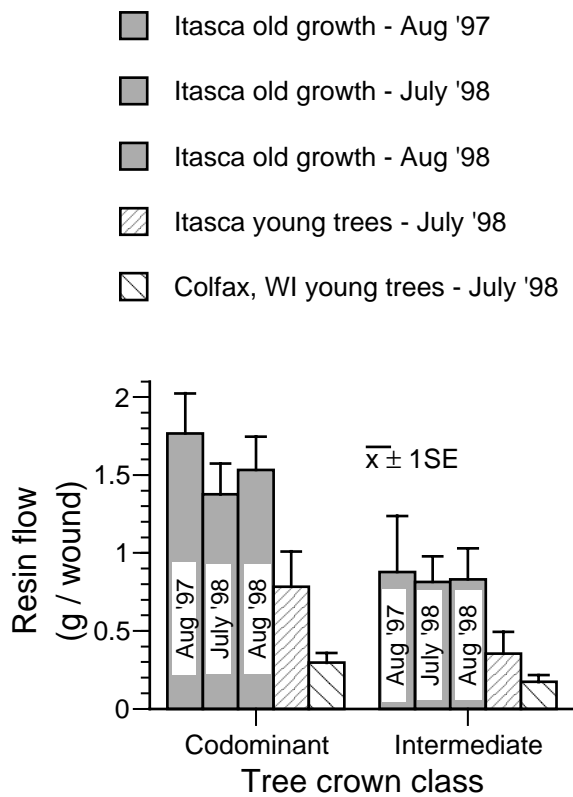
selected for those individuals that are best defended against bark beetles. In any case, these results strongly reinforce the conclusions from growth analyses that mature red pines at Itasca are not senescing and are not poorly defended against bark beetles. This conclusion is consistent with our observations in charred trees that came under beetle attack of strong resinous barriers around the site of the attack that limited the extent of permanent damage to the cambium. In fact, our results indicate that they should be generally more resistant to bark beetles, and suggest that mortality from bark beetles (Chapter 5) is the product of long exposure to low risks rather than an indication of a forest that is in rapid decline.



**Fig. 2.11.** Frequency distribution of resin flow, a measure of tree defenses against bark beetles, for mature red pines at Itasca ( $\approx 100 - 250$  years old), younger red pines at Itasca (30 - 78 years old), and young red pines near Colfax, Wisconsin (31 - 40 years old). Average resin flow differed between the populations, as did the proportion of trees that lacked constitutive resin defenses against bark beetles. In old trees at Itasca, < 10% of the trees lacked resin flow, compared to up to 25% of the young trees at Itasca, and up to 47% of the young trees in west central Wisconsin.

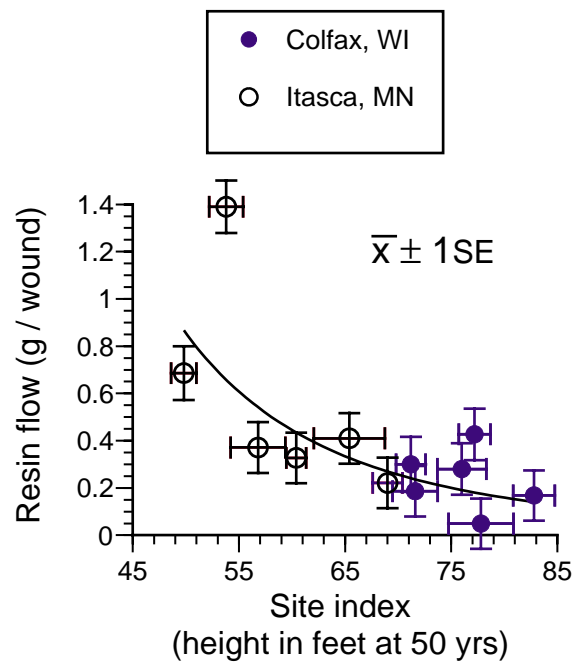
**Constitutive defenses of red pine at Itasca compared to more favorable sites in Wisconsin.**

For comparably aged red pines, resin flow averaged nearly twice as high in Itasca compared to WI (Figure 2.11 - 2.12). In Itasca, none of the young codominant trees, and only 25% of the young intermediate trees had zero resin flow, compared to 20% of the young codominant trees and 47% of the young intermediate trees in WI (compare middle and bottom pairs of histograms in Fig. 2.11). These results are exactly contrary to the hypothesis that trees growing on marginal sites, such as Itasca, will tend to be less well defended against bark beetles, than trees growing on high quality sites. The site index for young stands at Itasca ranged from 50 to 69 feet (site index = expected height at 50 years), substantially lower than the site indexes of 71 to 83 feet at sites in west central Wisconsin. Across sites there was a significant negative correlation between resin flow and site index (Fig. 2.13).



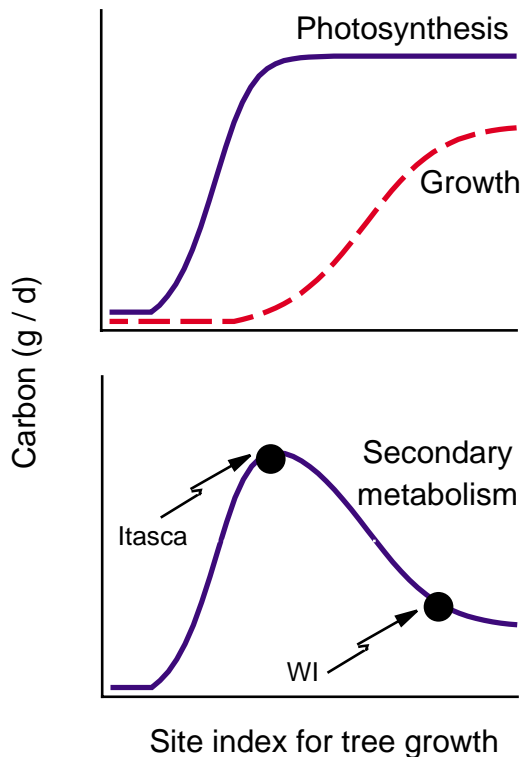
**Fig. 2.12. Average resin flow in mature red pines at Itasca, young red pines at Itasca, and young red pines in west central Wisconsin. Differences among tree populations was highly significant.**

This result seems counter-intuitive if it is assumed that trees under all environmental conditions invest an equal proportion of their carbon resources into resin production. However, it is completely consistent with an alternative physiological model (Lorio 1986, Reeve et al. 1985, Wilkens et al. 1997), which recognizes that the carbon available for secondary metabolism (e.g., resin synthesis) often depends upon the carbon resources that are left after investments to growth. Tree growth is frequently limited by water and nutrient availability more than it is limited by carbon. Site indexes for red pine are largely a function of water and nutrient availability. Growth potential of red pine at Itasca is low in large part



**Fig. 2.13. Relationship between resin flow and site index for 30-80 year old red pines at Itasca and in west central Wisconsin. Red pines grow relatively slowly near Itasca (expected height at 50 years of only 49 - 69 feet), but they have higher levels of constitutive defenses against bark beetles. This pattern matches a physiological model that predicts secondary metabolism (resin flow) based upon the carbon resources that are left after trees have grown to the limits set by availability of water and nutrients (Fig. 2.14).**

because of water limitations. Moderate water deficits tend to constrain growth more than photosynthesis (Fig. 2.14). Under these conditions, relatively more carbon is left after growth has been maximized to the limits of water availability. If a constant proportion of this carbon remainder goes into secondary metabolism, then resin flow will tend to be highest on sites with moderate water deficiencies and relatively low growth (Fig. 2.14). The comparisons of resin flow in red pines in Wisconsin and Itasca are consistent with this model.



**Figure 2.14: Hypothesized relationship between site index for tree growth, which is primarily a function of water and nutrient availability, and patterns of carbon acquisition, growth and secondary metabolism in pine trees (after Lorio 1986, Reeve et al. 1995). At moderate water deficiencies, resin flow and resistance to bark beetles is predicted to be high because tree growth is limited relative to photosynthesis, so there is a larger surplus of carbon for secondary metabolism after growth has been maximized. This model is consistent with the high resin flow of trees at Itasca compared to similarly aged forests in west central Wisconsin, where growth conditions for pine are better (see Fig. 2.13).**

In any case, these data strongly falsify the hypothesis that red pines at Itasca are more susceptible to bark beetles because low growth rates are associated with chronic stress and low defenses.

One additional consequence of the interpretation represented in Fig. 2.14 is that drought, which is predicted to increase secondary metabolism and resin flow (i.e., shift trees to the left in Fig. 5), will have opposite effects on resin flow in Itasca and WI, tending to reduce resin flow in Itasca and increase resin flow in WI. This would be consistent with the observations of foresters and forest entomologists which associate drought with pine tree mortality in western MN but not in WI. Our study did not include a period of significant drought, so we can only guess at the magnitude of drought that would be required to compromise tree defenses at Itasca and significantly increase the risk of bark beetle infestations: it might require drought such as only occurs once a century or it might be facilitated by more moderate droughts that occur many times a century. However, the available data clearly indicate that (1) red pine in Itasca are not chronically susceptible to bark beetles compared to red pine in WI and (2) old red pine stands in Itasca are not chronically susceptible to bark beetles because of reduced resin flow associated with senescence and a collapse of the resin duct system. The low growth of red pines at Itasca appears to reduce risks from bark beetles, and therefore increase the potential longevity of the forest.

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