

APPROACHES TO STUDYING ENVIRONMENTAL EFFECTS ON RESISTANCE OF *PINUS TAEDA* L. TO *DENDROCTONUS FRONTALIS* ZIMMERMANN

PETER L. LORIO, JR.

USDA Forest Service, Southern Forest Experiment Station, 2500 Shreveport Highway, Pineville, Louisiana 71360, USA

INTRODUCTION

Environmental conditions and the genetic potential of loblolly pines, *Pinus taeda* L., affect or determine tree resistance to attack by the southern pine beetle, *Dendroctonus frontalis* Zimmermann, by operating on physiological processes (Fig. 1). Environment and genetic potential must operate through physiological processes to determine the quantity and quality of growth, as well as to express resistance to invasion by pathogens and bark beetles (Kramer 1986). Only in this way can either environment or genetics affect growth and development at the cell or the whole tree level. Here, I would like to focus primarily on one major aspect of the environment that commonly affects the growth and development of loblolly pines and their relative resistance to attack by the southern pine beetle; that is, the water regimes under which they may grow. It is important to consider the effects of environment across a range of time frames, from very short (diurnal or even hourly) to very long (lifetime). For example, trees growing on wet sites and in humid environments may grow rapidly and reach large size over long time frames because of prolonged wet conditions; however, in short time frames of days or weeks they may be subjected to severe water deficits not evident when data are summed over long periods.

ROLE OF PHYSIOLOGY IN FORESTRY

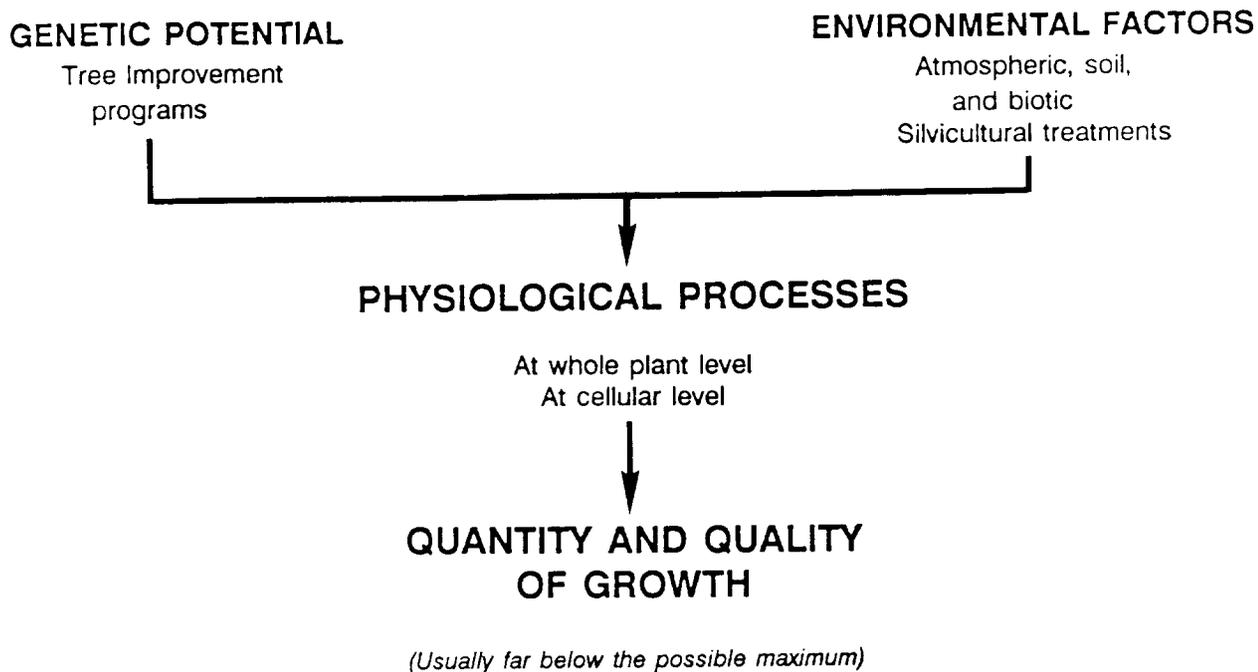


Figure 1.—Diagram illustrating the role of physiology in forestry. Genetic potential and environment operate through physiological processes in determining the quantity and quality of growth. Expression of resistance mechanisms of conifers to invasion by pathogens and bark beetles is likewise governed by these relationships (From Kramer, 1986).

It is seldom feasible to control water regime in the practice of forest management as one can control the density and spacing of trees, or the sites on which trees are grown. They may be planted in various ways, on dry or wet sites, thinned to reduce competition among individuals for light, water, and nutrients, and fertilized or pruned if desired, but in the southeastern United States there is little one can do about the great variation in rainfall through growing seasons and from year to year. Varying water regime can be a major factor in tree growth and development, as well as in tree resistance to southern pine beetle attack.

One may approach the study of tree responses to water regimes in a variety of ways. Commonly, a manipulative approach is chosen to establish a range of conditions that may produce measurable responses considered important to the purpose. Although it is difficult, if not impossible, to modify one aspect of the environment without altering one or more other factors, manipulative studies can be very useful. However, it helps considerably to consider the possible effects of prevailing environmental conditions and the ontogenetic stage of trees on responses to treatment.

Observational studies can be very helpful, if not essential, to the development of the most useful manipulative studies. By conducting such studies, one can develop some understanding that can help in the design of better studies in which treatments are imposed. The two approaches can be complementary. For example, (Chou 1982) emphasized the importance of seasonal predisposition of host trees in planning inoculation trials for any purpose. He found that *Pinus radiata* susceptibility to *Diplodia pinea* varied with season of the year, being high in spring-summer but low in autumn-winter. Knowledge of structural and physiological changes associated with ontogeny can be invaluable to interpretation of results of fungal inoculation studies, as indicated in studies by (Paine 1984) and (Owen *et al.* 1987), as well as with pinewood nematode inoculations (Myers 1986). Similarly, physiological changes that occur during ontogeny of trees may alter their susceptibility to forest pests (Kozlowski 1969).

We have conducted a number of observational studies toward discovering tree and site characteristics correlated with the initiation and recurrence of southern pine beetle infestations (Lorio 1966, 1968; Lorio and Hodges 1968b, 1971; Hodges and Lorio 1971; Lorio *et al.* 1972; Lorio and Bennett 1974). These studies led to practical applications, such as the development of stand risk rating for the southern pine beetle (Lorio 1978, 1980; Lorio and Sommers 1981a, 1981b; Lorio *et al.* 1982; Zarnoch *et al.* 1984; Hedden and Lorio 1985). A compendium on the southern pine beetle was based to a large extent on observational studies (Thatcher *et al.* 1980).

Here, I would like to review some studies that we have conducted with loblolly pine and the southern pine beetle in attempts to determine the effect of water regime on tree resistance to beetle attack. They include both manipulative and observational studies. Contrary to our early assumption that stress in the form of water deficit is bad for trees and good for bark beetles, a more sound assumption is that "it depends." It depends on a number of factors, such as tree size, growth stage or age, the timing of the deficit during the growing season, how severe the deficit becomes, how long it lasts, site conditions, tree root distribution and condition, and perhaps many other factors. It is especially important to remember that any such factors affect trees by operating through physiological processes (Kramer 1986).

METHODS

Early on we conducted both manipulative and observational studies to assess the effects of environmental conditions, principally soil water supply, on loblolly pine physiology and susceptibility to southern pine beetle attack. One of our manipulations was to dig trenches around groups of trees or individuals, and line them with polyethylene sheeting to restrict lateral movement of water and prevent roots of study trees from tapping soil water beyond the trench (Lorio and Hodges 1968b, 1977; Hodges and Lorio 1969). We constructed various types of shelters that limited soil water recharge from rainfall and allowed us access to the trees for measurements. Other methods included continuously flooding tree root systems for long periods of time by maintaining ponded water on the site, and applying collars of solid CO₂ around the lower tree bole to inhibit the movement of water through sapwood to induce acute water deficit (Moeck *et al.* 1981, Stephen *et al.* 1988). In more recent times we have girdled trees (Dunn and Lorio 1992), sheltered root systems without trenching, and irrigated in attempts to provide well-watered conditions to compare with the effects of sheltering (Dunn and Lorio 1993). This and other studies included artificially inducing southern pine beetle attacks (Lorio and Hodges 1977; Dunn and Lorio 1992, 1993), but in some studies, volunteer attack was relied upon (Lorio and Hodges 1968b, Hodges and Lorio 1969).

Observational studies included examining site and stand conditions associated with southern-pine beetle infested stands compared with noninfested stands (Lorio 1968), measuring soil water regimes, depth to free water in perforated tubing, and tree diameter growth (Lorio and Hodges 1971); determining tree rooting characteristics and distribution, and oleoresin exudation pressures in relation to microrelief (Lorio and Hodges 1968a, Lorio *et al.* 1972); and comparing methods of measuring field techniques for assessing the water status of trees (Hodges and Lorio 1971). One study, conducted over several years, included calculation of soil water balance (Zahner and Stage 1966), measurement of cambial growth by periodically extracting xylem plugs from tree boles and counting the number of tracheids produced in the current annual ring, counting vertical resin ducts in the current annual ring and calculating their density, and periodically sampling resin flow from wounds through the years (Lorio *et al.* 1990).

RESULTS

Manipulative studies to establish levels of water deficit that would severely weaken trees relative to nontreated controls (Lorio and Hodges 1968b, 1977; Hodges and Lorio 1969, 1975) demonstrated that severe water deficits, aside from reducing growth, caused physical and chemical changes apparently associated with reduced tree resistance to beetle attack. However, it was not demonstrated that the southern pine beetle preferentially attacked trees subjected to severe water deficit, or that they required such weakened hosts for successful attack. On the contrary, it was clear that vigorously growing hosts could be overcome readily by this bark beetle species, and that such hosts could produce abundant brood.

An observational study of relationships among xylem water potential of twigs (Scholander *et al.* 1965), relative water content of needles (Weatherley 1950), oleoresin exudation pressure in the lower main bole (Vité 1961), and short-term flow of resin (Mason 1969, 1971) showed good relationships between resin pressure and the conventional measures of water status, but no relationship between resin pressure and flow (Hodges and Lorio 1971). The question of a direct relationship, or lack thereof, between oleoresin exudation pressure and oleoresin flow from bark wounds is discussed elsewhere (Lorio *in press*).

Recent attempts to evaluate the effects of environmental conditions on loblolly pine resistance to the southern pine beetle provide some insight about the importance of environment to tree resistance. Results from over a 2-year period (1984-1985) of an observational study (Lorio *et al.* 1990) indicated substantial differences between years in calculated soil water storage, cumulative soil water deficits, cambial growth, density of resin ducts in the current year's annual ring, and the patterns of resin yields through the growing seasons. The results for 1986 and 1987 are reported here (Fig. 2). Clearly different water regimes prevailed from one year to the next, as did the apparent effects on cambial growth, resin duct densities, and resin yields. No treatments were applied and beetle attacks were not induced, and the apparent responses are correlative. However, the pattern of resin yields in 1987 closely mimics a conceptual model of seasonal changes in pine resistance to beetle attack in years having soil water balance patterns similar to the long-term average (Fig. 3). Resin flow from small bark wounds is considered indicative of the relative resistance of southern pines to southern pine beetle attack (Hodges *et al.* 1979).

A manipulative study carried out within the same stand in the spring of 1986 and the late summer of 1987 indicated a strong environmental effect preceding and during the study (Stephen *et al.* 1988). Another manuscript that focuses on important differences in environmental conditions, growth and development of the host trees, and southern pine beetle population levels is pending.

Girdling of bark to the face of the xylem prior to the development of latewood, and under well-watered conditions, produced considerably different responses to fungal inoculations or induced southern pine beetle attacks at 2 weeks compared to 8 weeks after girdling (Dunn and Lorio 1992). Two weeks after girdling, carbohydrate status, cambial growth, resin flow, phloem moisture content, lesion formation, and beetle colonization differed little above or below girdles. After 8 weeks the carbohydrate status below girdles was greatly reduced, as was cambial growth (no latewood formed). Although not statistically significant, resin flow was reduced almost 50% below compared to above girdles. Phloem moisture was significantly higher below than above girdles, and beetles oviposited three times as many eggs and constructed three times as much egg gallery below than above girdles. These results were obtained during a period of almost continually declining soil moisture and steadily accumulating calculated soil water deficits (Fig. 4).

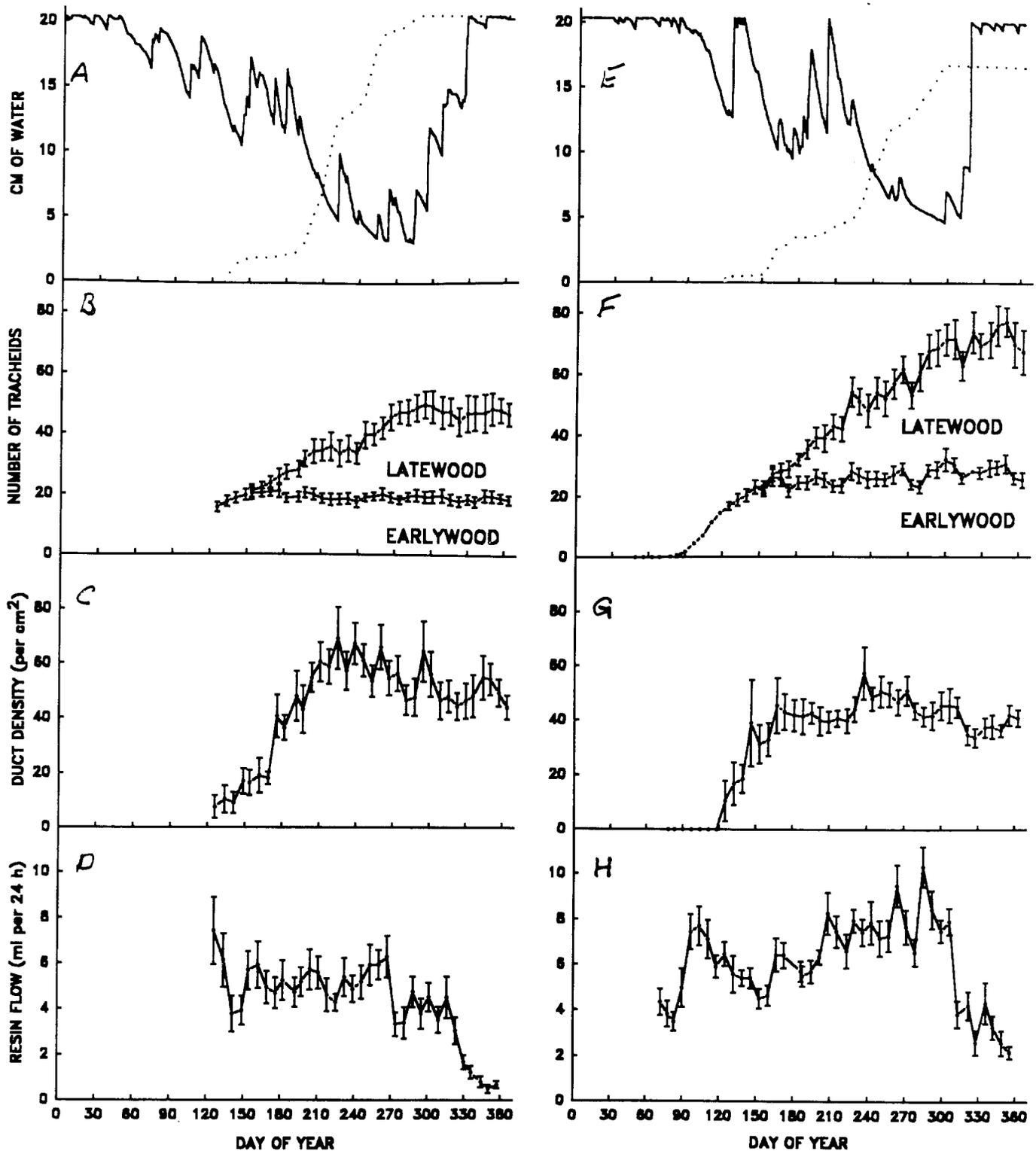


Figure 2.—Graphs of water regimes, the course of xylem growth and development, vertical resin duct density in the current annual ring, and resin yield from standard bark wounds in 1986 (A, B, C, D) and 1987 (E, F, G, H). Daily soil water storage (solid line) and cumulative daily water deficits (dotted line), (A, E). Tree bole cambial growth and development expressed as the number of tracheids formed, time of transition from earlywood to latewood, and the total amount of earlywood and latewood formed (B, F). Vertical resin duct densities in the current annual ring (C, G). Oleoresin yield over 24-hour periods (D, H). Vertical bars are standard errors, $n=11$ for 1986, $n=13$ for 1987. Water regimes, growth and development, and resin yields differ dramatically between years. Resin yields for 1987 closely approximate the seasonal changes in resistance suggested in the conceptual model shown in Figure 3 for resistance to southern pine beetle attack in years that have soil water regimes similar to that of the long-term average. Severely dry conditions in the summer of 1986 apparently not only limited carbon partitioning not only to growth, but also to secondary metabolism; e.g., oleoresin synthesis.

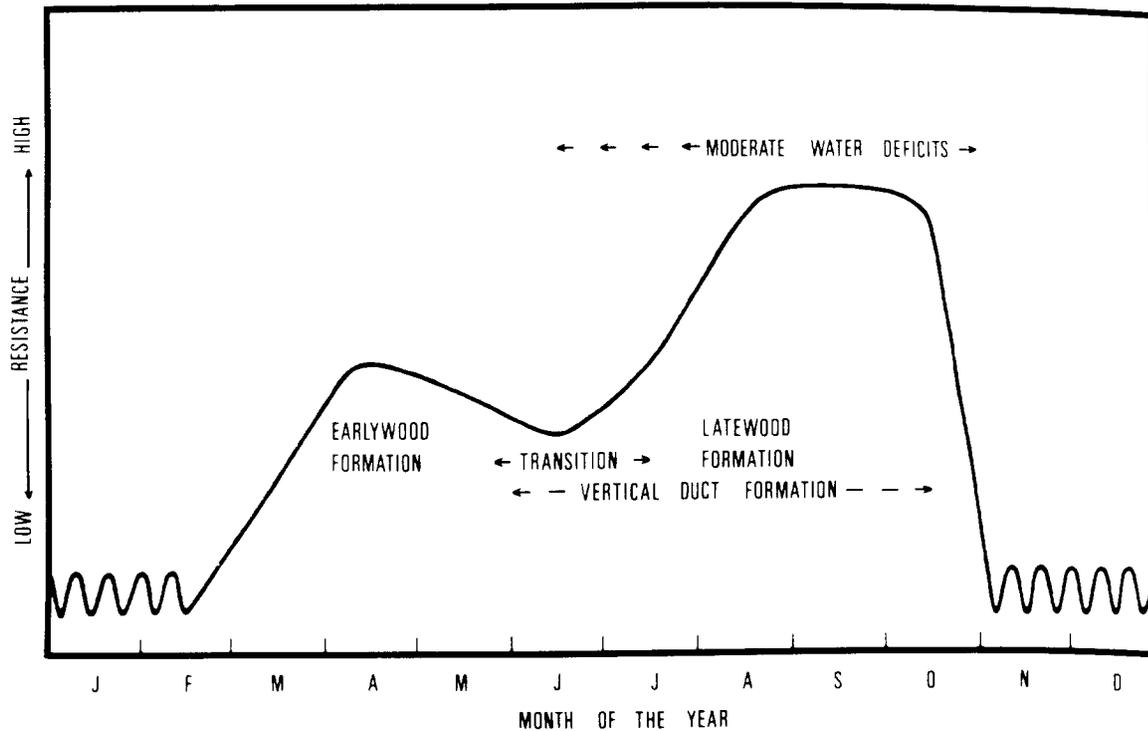


Figure 3.—A conceptual model of seasonal changes in pine resistance to southern pine beetle attack for years that have soil water balance patterns similar to that of the long-term average. Resistance to the earliest attacking beetles is considered to be highly dependent on the potential flow of oleoresin at the wound site. (From Lorio *et al.* 1990).

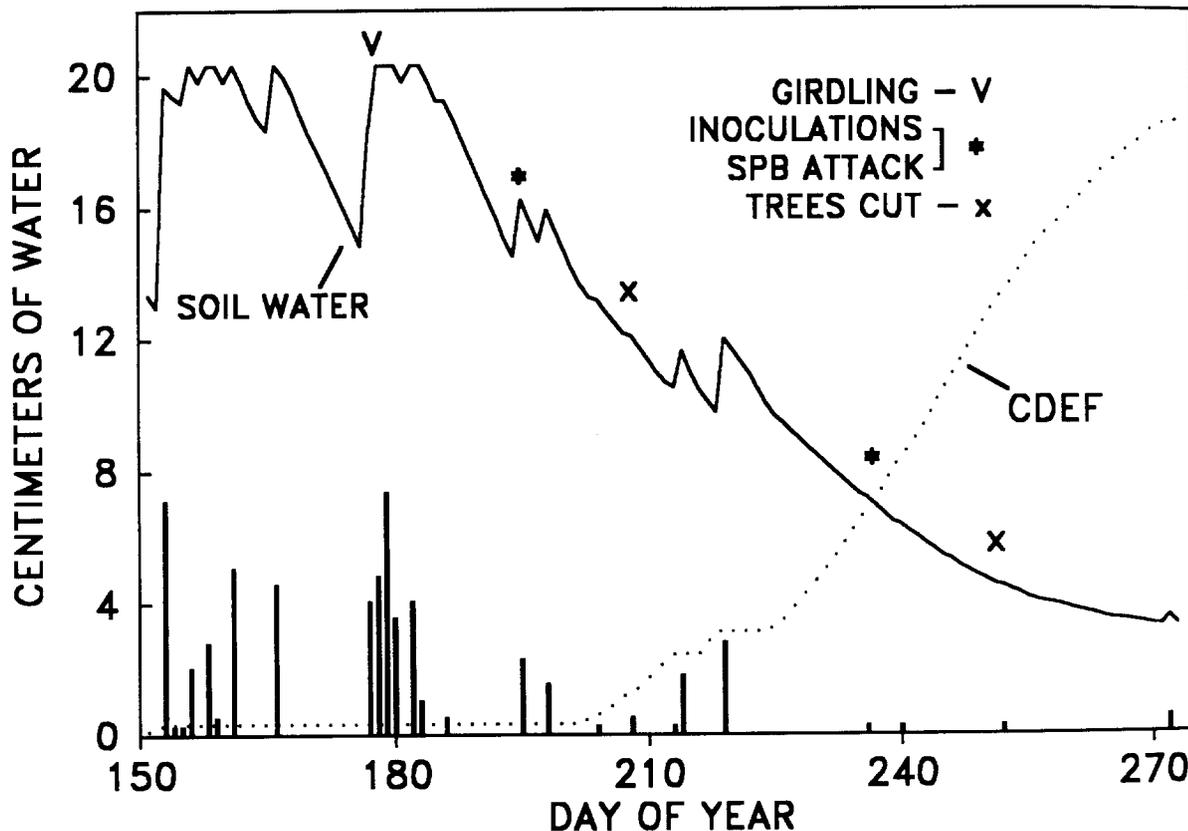


Figure 4.—Daily precipitation (vertical bars), calculated daily soil water storage and cumulative daily water deficits (CDEF) for June-September, 1989, near Alexandria, LA. The two-level soil water storage program of Zahner and Stage (1966) was used, assuming as sandy clay loam soil holding 20.32 cm of available water in the tree rooting zone. Dates of girdling, inoculations, and induced southern pine beetle attack are indicated. (Modified from Dunn and Lorio 1992).

Only recently have we conducted studies with juvenile pines (trees not yet into reproductive growth). One such study involved sheltering root systems to limit water supply and irrigating to supplement rainfall (Dunn and Lorio 1993). Environmental conditions were such that no treatment effects could be established early in the growing season because of high rainfall through the month of May. Subsequently, with very high evaporative demand and low rainfall from June through early August, it was not possible to irrigate sufficiently to recharge soils to field capacity (soil water content after excess water has drained away). Two tests were conducted in which southern pine beetle attack was induced in early August in one case and in late October in another. Compared with irrigated trees, sheltered trees exhibited lower xylem water potentials, and reduced cambial growth, photosynthesis, and resin flow. However, sheltered trees demonstrated a capacity for internal adjustments that maintained twig water potentials at relatively high levels (> -0.8 MPa at predawn) even when photosynthesis was reduced 30-60% compared to irrigated trees. In the early test, about half as many beetles attacked sheltered trees as irrigated trees, but beetle success was low in general, with only 4.3 eggs per attacking pair of beetles for sheltered trees and 2.9 for irrigated. Over 70% of egg gallery length excavated over 13 days from initial attack was resin filled. In the late test, attacks were allowed to progress for 25 days, and egg galleries of both groups of trees were much less affected by resin soaking, but eggs per attacking beetle pair was still low for both sheltered and irrigated trees (7.9 versus 3.8). Dramatic increases occurred in resin flow during beetle attack in both tests. Although resin flow often decreases rapidly following mass attack by the southern pine beetle (Hodges *et al.* 1979), attack densities in this study were relatively low and may not have been sufficient to rapidly deplete the preformed resin supply and resin synthesized in response to invading beetles or associated microorganisms.

DISCUSSION

In our research we have taken both manipulative and observational approaches to study relationships between characteristics of the environment and loblolly pine resistance to the southern pine beetle. Although this bark beetle's behavior differs considerably from other important species within its range, such as *Ips* species and the black turpentine beetle, *Dendroctonus terebrans* (Olivier), general relationships should apply to those species as well, if modified appropriately. Typically, the *Ips* species cannot withstand resin flow as well as the southern pine beetle, but they can withstand higher temperatures and drier inner bark conditions. The black turpentine beetle apparently can withstand abundant resin flow, even when attacking in very low numbers. It appears that death of the tree is an unavoidable result only with the southern pine beetle.

Earlier studies lacked guidance of a broad conceptual framework within which to frame hypotheses and test them. Basically, we considered that stress of various kinds was *bad* for trees and *good* for bark beetles, but we had little understanding of how factors such as water deficit affected trees and reduced their resistance to beetle attack. Observational studies indicated that stand characteristics such as high density and slow growth were frequently associated with infestation incidence. However, it was not clear what mechanism of resistance was affected by the conditions. It was generally believed that the oleoresin system was an important aspect of tree resistance, and for some time it was thought that oleoresin exudation pressure could be a useful surrogate measure of resin flow and tree resistance. In time, it became evident that oleoresin exudation pressure was a reasonably good indicator of tree water status, but that it did not necessarily correlate closely with resin flow or tree resistance to beetle attack.

Work was started in 1984 to conduct research that would lead to better understanding of loblolly pine resistance to southern pine beetle attack. The concept of plant growth-differentiation balance (Loomis 1932, 1953) provided a framework for hypothesis formation and gave us a rationale for interpreting our results (Lorio 1986, Lorio and Hodges 1985). Application of Loomis's concept provided us with a sound foundation for interpreting results of previous studies, both manipulative and observational. In a sense, the concept provided a physiological basis for our research that meshed well with Kramer's (1986) thesis of how both genetics and environment influence tree growth and development by operating through physiological processes (Fig. 1).

Gordon and Smith (1987) provide a useful diagram of carbon partitioning among various meristems and aboveground and belowground tissues as it is affected by greater or lesser nutrient and water supplies (Fig. 5). It effectively incorporates concepts of both Kramer (1986) and Loomis (1932). Supplies of carbon and nitrogen assimilates are normally limited in trees, and various sinks compete for the limited supplies. If one process removes a substrate from circulation, another cannot use it. This competition results in coordinated developmental changes (Trewavas 1985). Loomis *et al.* (1990) refer to this as a "nutritional theory" of coordination, which can be traced back at least to the work of Klebs (1903, 1910).

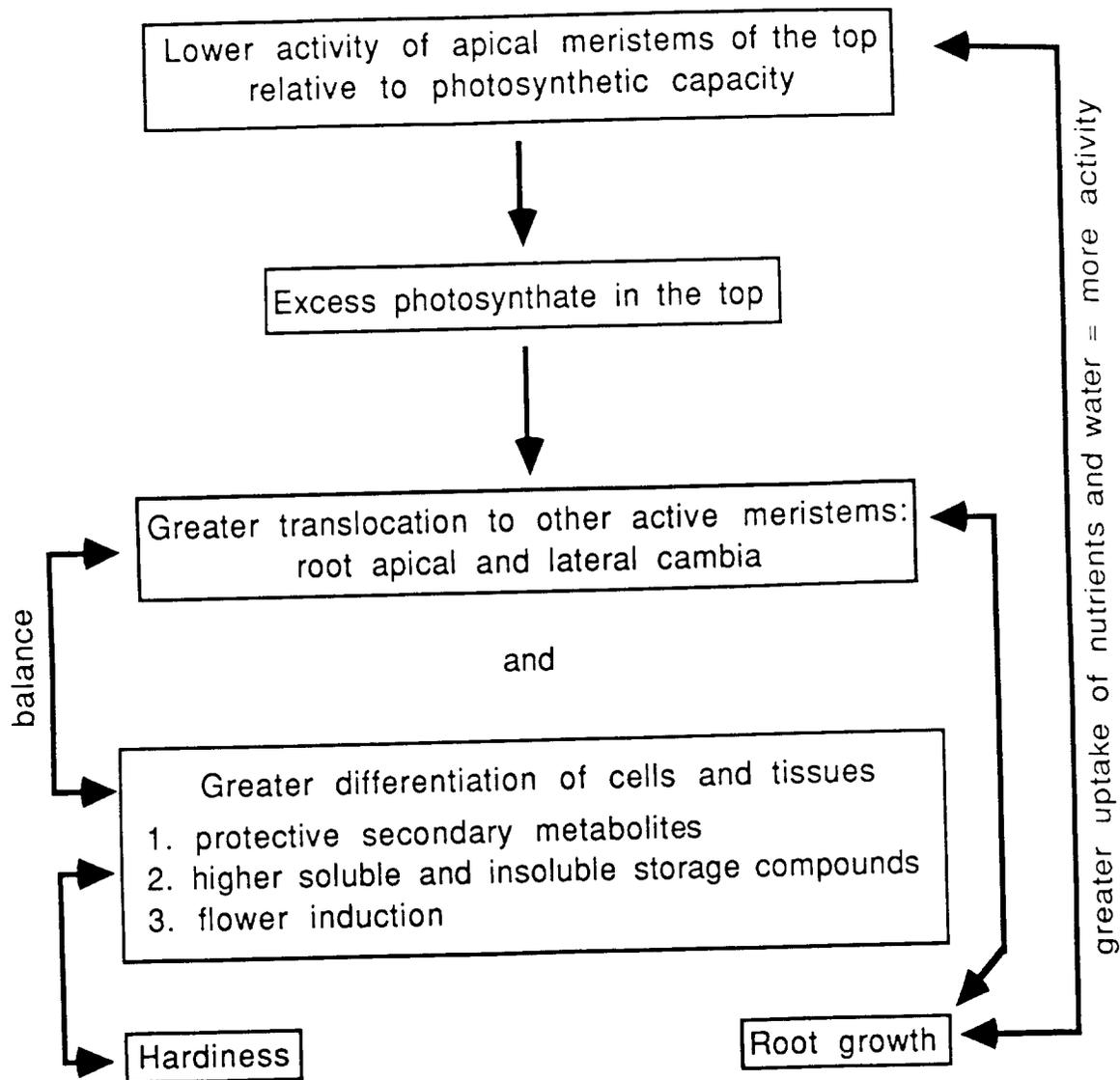


Figure 5.—Carbon partitioning among growth and developmental processes in response to changing nutrient and water supplies influence the competition and fluctuating balances between growth and differentiation processes, e.g., the various cambial meristems versus protective secondary metabolites; as well as among aboveground and belowground systems within a tree. (After Gordon and Smith 1987).

Voluminous literature in the area of physiological ecology and plant/herbivore interactions in general appears to be related closely to the growth-differentiation balance concept (Mooney and Chu 1974, Mooney *et al.* 1983, Bryant *et al.* 1983, Coley *et al.* 1985, Chapin *et al.* 1987, and others). Although the paths of research in those areas did not include consideration of Loomis's (1932) concept, I find that it provides considerable support for developments in those fields. For example, it seems to me to be essentially in agreement with the carbon-nutrient balance hypothesis (Bryant *et al.* 1983, Tuomi *et al.* 1988), but provides a broader framework, primarily by providing explicit consideration for water. Several papers include consideration of the plant growth-differentiation balance concept in forming theories of evolutionary development of plant defenses against insects (Tuomi *et al.* 1990, Herms and Mattson 1992, Tuomi 1992).

Here, I have indicated some of the research results from both early and recent studies. The more recent studies were carried out with consideration of plant growth-differentiation balance relationships in mind, and with considerable stimulation from advances in physiological ecology and studies of plant/herbivore interactions in general. We are continuing research in the same vein. The study with juvenile pines (Dunn and Lorio 1993) has been extended to an older stand, with some improvements in techniques, and with results indicating strongly that water deficits have nonlinear effects on tree

resistance to beetle attack. Another study is in progress, once again with juvenile pines, in a plantation subjected to thinning and fertilization. We will be continuing work in that direction. At this time preliminary results indicate that the short-term effects of thinning and fertilization are to enhance carbon partitioning to growth and to reduce carbon committed to secondary metabolism: e.g., resin synthesis.

SUMMARY

There are a number of ways to approach the problem of assessing the effects of environmental conditions, such as water regime, on tree physiological responses and resistance to bark beetle attack. It helps to keep in mind that environmental factors operate through physiological processes (Fig. 1, and Kramer 1986), and that there are concepts, such as plant growth-differentiation balance (Loomis 1932) and carbon-nutrient balance (Bryant *et al.* 1983; Tuomi 1992; Tuomi *et al.* 1988, 1990), that can provide bases for forming testable hypotheses. It is especially important to know as much as possible about the host tree and the specific bark beetle of interest. Observational studies are particularly important because they can provide a baseline for interpreting the results of manipulative studies. Whenever feasible, it is especially helpful in manipulative studies to characterize environmental conditions before and during a study. Because physiological changes that occur during ontogeny of trees can alter their susceptibility to herbivores, knowledge of tree stage of growth and development can be especially helpful.

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