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283

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Environmental Stress and Whole-tree Physiology

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5.1 INTRODUCTION

Interactions among bark beetles, pathogens, and conifers constitute a triangle. Another triangle of interactions exists among the invading organisms (bark beetles and pathogens), the trees, and the environment. How important, variable or constant, simple or complex, is the role of trees in these triangles? Understanding the wide range of interactions that take place among trees, bark beetles, and pathogens, and between the organisms and their environments, requires consideration of tree responses to fluctuating environmental conditions and the effect of tree responses on tree-invading organisms (Loomis and Adams, 1983).

In recent years there has been considerable progress in research on interactions among bark beetles, microorganisms, and conifers. This chapter focuses on a few important aspects of tree physiology as it affects tree interactions with bark beetles and pathogens.

5.2 A BASIS FOR UNDERSTANDING STRESS EFFECTS

Biotic and abiotic stresses of various kinds (Chapter 4) are common during the growth and development of conifer forests and virtually all natural systems. Unfortunately, different

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kinds of stress frequently are not distinguished, thus hindering our understanding of effects on tree physiological processes and tree interactions with other organisms (Sharpe *et al.*, 1985). That deficiency and the general perception that stress is inherently bad for trees and good for invading organisms are major obstacles to better understanding and management of bark beetle–pathogen–conifer interactions.

Stress due to water deficit occurs so frequently that, in the long run, it reduces plant growth and crop yield more than all other stresses combined (Kramer, 1983). For this reason, water supply has been the subject of much study concerning interactions among bark beetles, pathogens, and conifers and will be a focus of this chapter.

Our limited knowledge of whole-tree physiology, and particularly stress effects, is imperfectly integrated with the study of bark beetle, pathogen, and conifer interactions. Tree physiology generally has received little attention with regard to solving forestry problems (Kramer, 1986). This state of affairs indicates a need to provide a broad basis upon which to consider the effects of stress on conifers and how stresses, such as water deficits, may affect tree physiology and interactions of trees with other organisms.

Kramer (1986) attributes the limited use of physiology in forestry to a poor understanding of the role of plant physiology. He specifically focuses on the general lack of appreciation of the concept, developed many years ago, that the nature and limitations of physiological processes are controlled genetically, but that the environment determines actual productivity (Fig. 5.1). Clearly, heredity and environment influence plant growth and development through their combined effects on physiological processes. Klebs (1910) provided some of the earliest input to this concept, and his contributions are commonly recognized in both older and recent literature (Krauss and Kraybill, 1918; Loomis, 1932, 1953; Kramer and Kozlowski, 1979; Sachs, 1987). It is interesting and relevant to this chapter that Klebs (1910) worked with both microorganisms and higher plants.

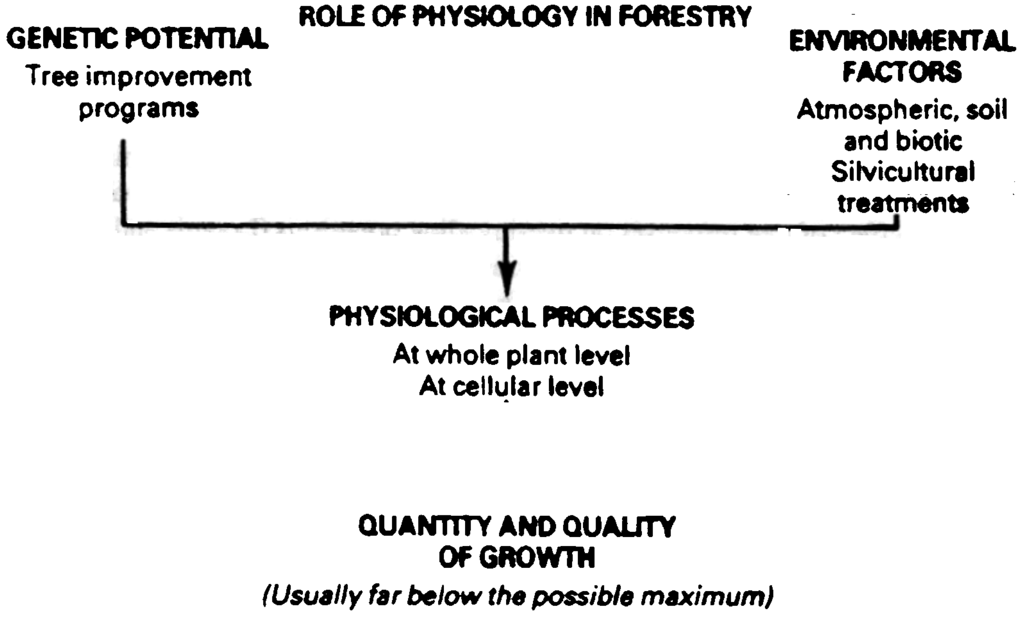

Fig. 5.1. Diagram illustrating the role of physiology in forestry. Genetic potential and environment must operate through physiological processes in determining the quantity and quality of growth. Expression of resistance mechanisms of conifers to invasion by pathogens and bark beetles are likewise governed by these relationships. (From Kramer, 1986.)

5.3 HOST TREE ONTOGENY AND PHENOLOGY

5.3.1 Ontogeny

Tree ontogeny (the development or course of development of an individual) may be considered in various contexts: a tree's life span from seedling to maturity; the development of cells and their differentiation and maturation; the formation of specialized tissues associated with plant development, and the morphological, physiological, and chemical changes that occur through the seasons of the year. Physiological changes normally associated with tree development, apart from severe environmental stresses, may have important effects on tree susceptibility to and suitability for herbivores and pathogens in general. For example, Coleman (1986) proposes that leaves are most subject to herbivore attack at the time of transition from being carbohydrate sinks (recipients) to sources (synthesizers).

Regarding bark beetle, pathogen, and conifer interactions, physiological changes associated with either maturation or aging are important. For example, when trees develop a capacity to flower and fruit (maturity) an additional demand is placed on photosynthates previously partitioned among vegetative growth and differentiation processes. Given limited energy and material resources within trees, the potential production of oleoresin, a primary factor in resistance of *Pinus* species to bark beetle attack (Hodges *et al.*, 1979), is affected by such developmental changes.

Aging eventually leads to slower rates of metabolism, slower wound healing, and reduced resistance to certain insects and fungi (Kozlowski, 1971). Typical hosts for *Dendroctonus frontalis* have reached maturity and have grown to large size. Such trees provide abundant food and habitat for colonizing beetles. Their long boles and large diameters provide large surface areas to accommodate attacking beetles and brood in numbers greatly exceeding that possible in small trees.

All of the various reproductive and vegetative growth and differentiation processes are energy dependent to some degree, and there are multiple interactions and competitions among them for available substrates. Carbohydrate relations during growth and development of *Pinus* strobili indicate that enlarging cones draw heavily on resources from 1-year-old needles early in the season and from current-year needles late in the season (Kramer and Kozlowski, 1979). Thus, it seems that cones supply little of their own carbohydrate needs for growth and development, that they can suppress both apical and cambial growth, and potentially reduce the synthesis of secondary metabolites (defensive chemicals) such as oleoresins. Some understanding of the relationships between reproductive and vegetative growth and development, and how they may be affected by a variety of environmental conditions over time, is essential to testing effects of environmental stresses. For example, variation in the timing, intensity, and duration of water deficits obviously will affect vegetative and reproductive processes differently (Hsiao *et al.*, 1976b).

5.3.2 Phenology

Tree phenology concerns relationships between climate and periodic biological phenomena, such as flowering, bud burst, foliage production, and leaf fall. Stanley (1958) illustrated the general reproductive growth cycle of the genus *Pinus* (Fig. 5.2), but indicated that exact time of pollination varies with species, latitude, site, and elevation. Environmental factors may cause other phenomena to occur earlier or later in a season, as well as shorten or lengthen their duration. Relationships among flowering, cone growth and development,

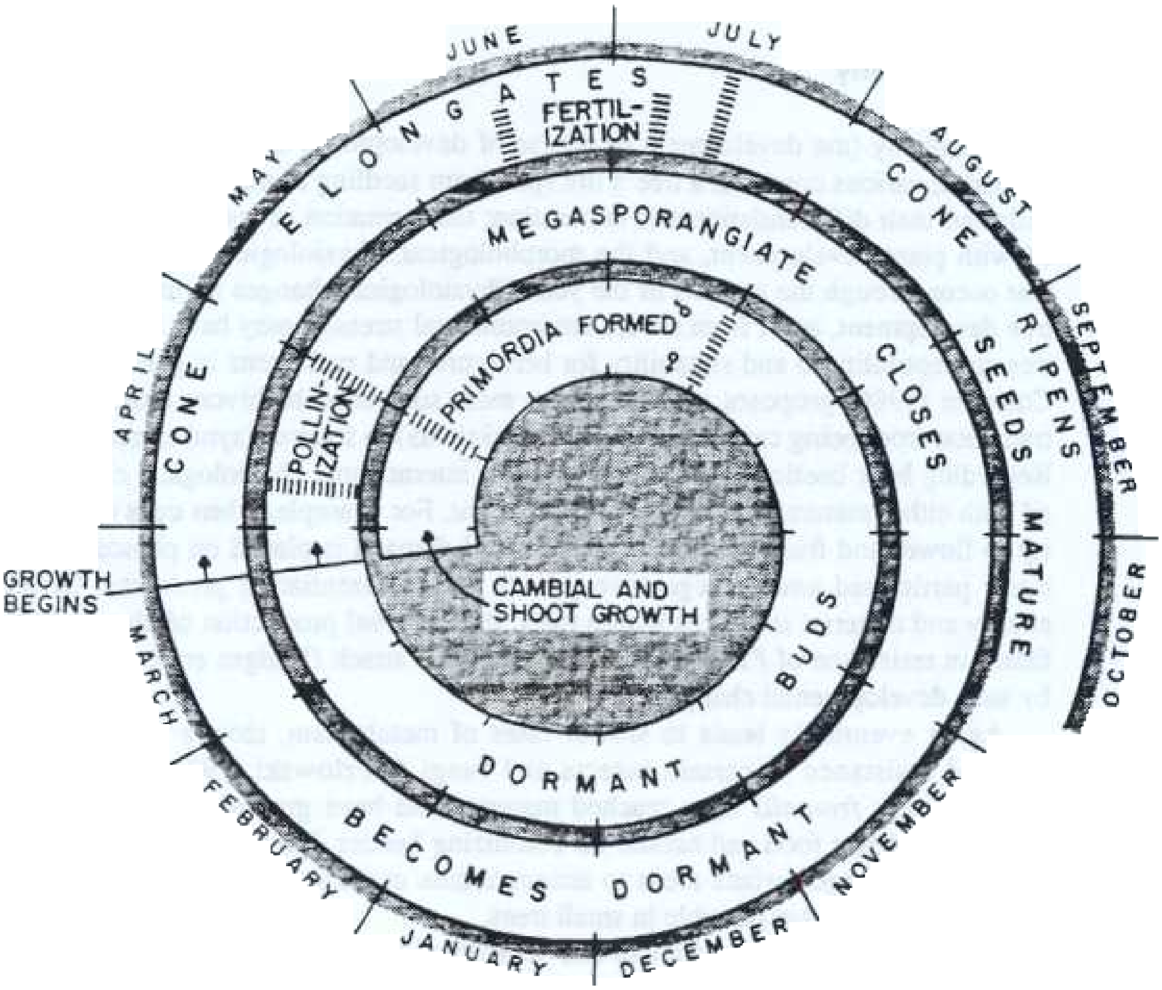

Fig. 5.2. Reproductive cycle of pine. (From Stanley, 1958.)

and other seasonal vegetative growth processes are of interest because competition among such processes for available photosynthates can affect tree resistance to herbivores or pathogens.

The transition from earlywood to latewood in *Pinus* species, the development of the current year's vertical resin ducts, and the seasonal course of resin flow are of particular interest in relation to bark beetle attack (Lorio, 1986). During earlywood formation, partitioning of carbohydrate to oleoresin synthesis is limited by strong demands for reproductive and vegetative growth processes. As rows of earlywood tracheids are produced, the target of beetle attack (the xylem/phloem interface) is displaced progressively from the principal oleoresin reservoir (the vertical resin ducts of the preceding and prior years). With the transition to latewood and the development of the current year's vertical resin ducts, the potential flow of resin at beetle attack sites in the the cambial region increases, as does the inferred resistance to beetle attack. Lorio *et al.* (1990) explored these relationships in testing a conceptual model of seasonal changes in the resistance of *P. taeda* to *D. frontalis* (Figs 5.3 and 5.4). The timing and duration of developmental processes, and associated changes in tree resistance to beetle attack, can be altered considerably during a growing season in response to environmental influences.

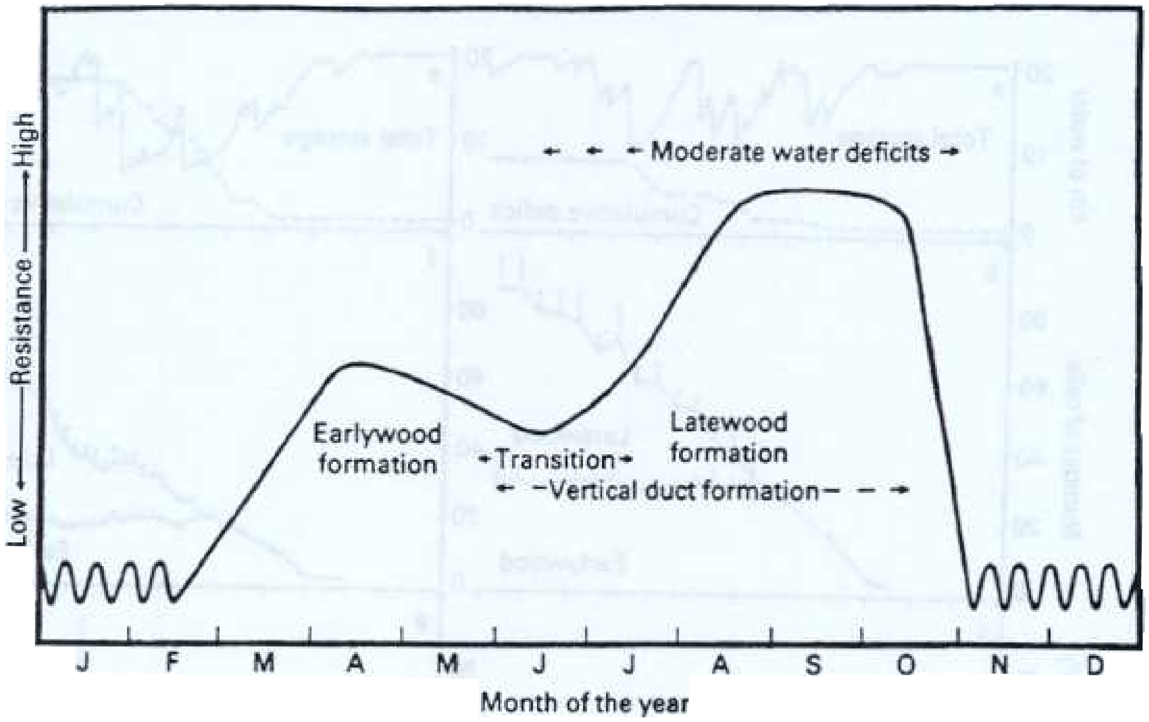

Fig. 5.3. A conceptual model of seasonal changes in pine resistance to southern pine beetle attack for years which have soil water balance patterns similar to that of the long-term average. Resistance to the earliest attacking beetles is considered to be highly dependent on the potential flow of oleoresin at the wound site. (From Lorio *et al.*, 1990.)

5.4 PHYSIOLOGICAL CHANGES ASSOCIATED WITH DEVELOPMENT

Growth response alone may be an unsafe measure of vigor (Kraus and Kraybill, 1918). Tree growth and resistance to bark beetle and fungal invasion are correlated to some degree (Waring, 1983), and resistance may reside in the amount of current and stored photosynthate available for production of defensive compounds (Waring and Pitman, 1985; Christiansen *et al.*, 1987; Dunn *et al.*, 1987). Factors that greatly influence both growth and the production of defensive chemicals include water deficits and excessive crowding of trees. Crowding leads to shortened crowns, reduced photosynthates to support growth and other processes, and thereby to reduced synthesis of defensive compounds. Severe water deficits can reduce cambial growth, but perhaps more importantly they reduce shoot and needle growth, cause premature needle fall, and reduce leaf surface area, with long-lasting effects on photosynthate supply to support growth, maintenance, and production of defensive chemicals. Apart from effects of crowding, water deficits, and other factors, important physiological changes take place in the course of ontogenetic and seasonal growth and development.

5.4.1 Partitioning of assimilate

Seasonal aspects of the competition between growth and the production of defensive chemicals in conifers have not been given much attention. In other systems, however, the integrative control of plant growth and development has been given a great deal of attention (Brouwer, 1983; Chapin *et al.*, 1987; Loomis *et al.*, 1990). Partitioning of carbon during a growing season is partially under genetic control (Fig. 5.1), but phenology and an array of

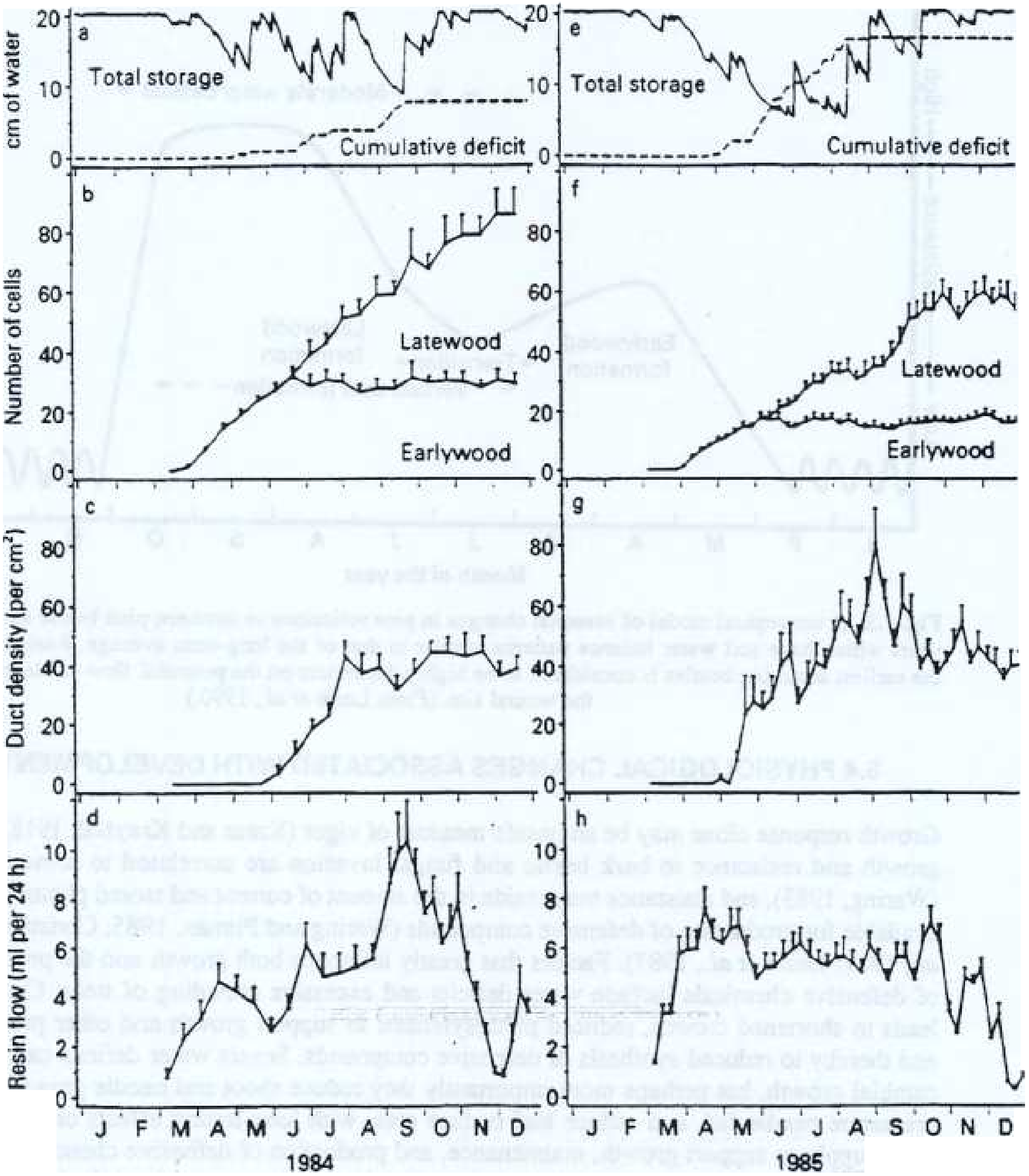

Fig. 5.4. Graphs of water regimes, the course of xylem growth and development, vertical resin duct formation, and resin yield in 1984 (a, b, c, d) and 1985 (e, f, g, h). Daily water storage and cumulative water deficits (a, e). Tree bole cambial growth with total tracheid counts, time of transition to latewood, and amount of earlywood and latewood formed (b, f). Vertical resin duct densities in the current year's growth ring (c, g). Oleoresin yield over 24-hour periods (d, h). Vertical bars are standard errors, $n = 10$ for 1984, $n = 16$ for 1985. Results for 1984 approximate the conceptual model shown in Figure 5.3, but those for 1985, a year abnormally dry in spring and early summer relative to long-term average conditions, do not. (From Lorio *et al.*, 1990.)

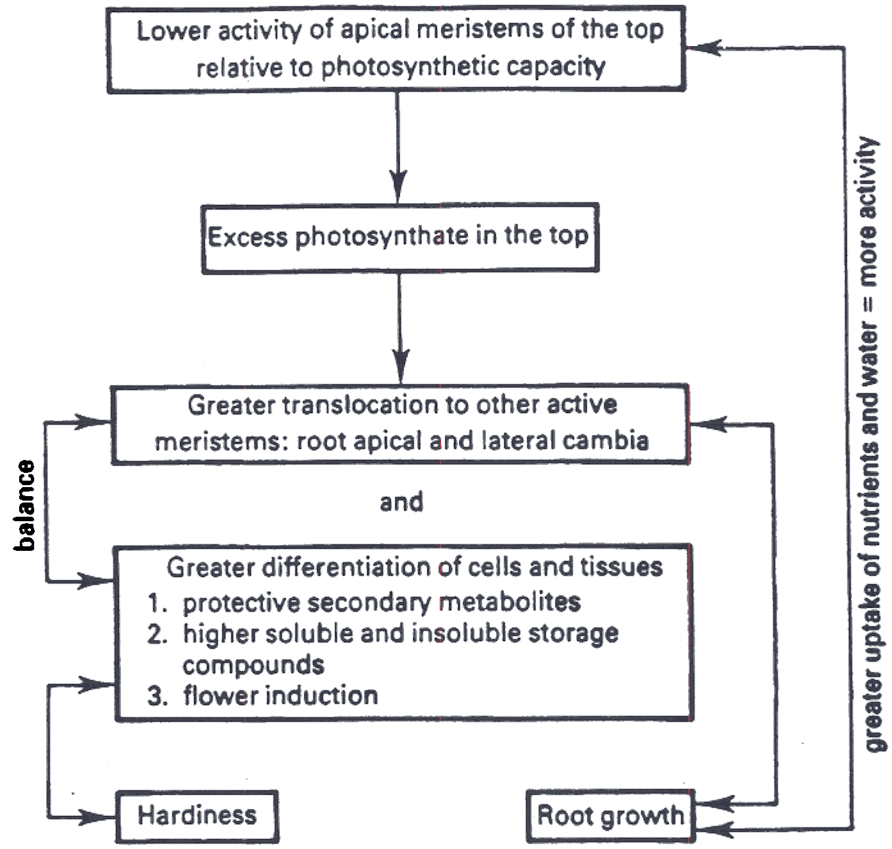

Fig. 5.5. Carbon partitioning among growth and developmental processes in response to greater or lesser nutrient and water supplies, illustrating the competition between growth and differentiation processes as well as among systems within a tree. (After Gordon and Smith, 1987.)

environmental conditions can greatly alter partitioning patterns, especially in the short term. Substrate supply is considered to be a major factor.

Supplies of carbon and nitrogen assimilates are normally limited, and various sinks compete for the limited supplies. Gordon and Smith (1987) illustrate how changes in nutrient and water supply may affect activity of apical meristems relative to photosynthesis and an array of growth and developmental processes (Fig. 5.5). If one process removes a substrate from circulation, another cannot use it. This competition for limited resources results in developmental changes (Trewavas, 1985). Loomis *et al.* (1990) refer to this coordination of plant growth and development as a "nutritional theory" of coordination, that is based on the work of Klebs (1910), Kraus and Kraybill (1918), and Loomis (1932). Loomis (1932) proposed the concept of growth-differentiation balance as a convenient and simplified scheme for predicting or explaining plant behavior.

5.4.2 Relevance to bark beetle–pathogen–tree interactions

Several studies illustrate the great seasonal variation in physiological responses to inoculation with fungi vectored by bark beetles (Reid and Shrimpton, 1971; Paine, 1984; Stephen and Paine, 1985; Cook *et al.*, 1986; Owen *et al.*, 1987; Raffa and Smalley, 1988). Much of the variation may be associated with differences in carbohydrate partitioning due to ontogeny and environment. For the study of interactions among bark beetles, fungi, and trees, it is especially important to recognize that significant chemical changes occur seasonally in conifer phloem and cambial tissue. For example, starch contents increased dramatically, but lipids decreased, from winter to spring in *Abies balsamea* (Little, 1970). Similar changes took place in *Pinus strobus*, and both starch and lipids declined during rapid cambial growth prior to mid-June (Parkerson and Whitmore, 1972). The work of Chung and Barnes (1980a,b) illustrates other dynamic changes in the seasonal production, consumption, and balance of photosynthates in *P. taeda*. Their results agree with those of Gordon and Larson (1968) who found close correlation between time of maturation of the current year's needles and the initiation of latewood formation in 4-year old *P. resinosa*. Using Mooney and Chu's (1974) assignments of biochemical constituents to different functional categories (i.e. metabolism, storage, structure, and protection), Chung and Barnes (1980a) found that seasonal pattern of photosynthate partitioning into protection components (phenolics) in shoots and needles was the inverse of that for structural components. Termination of shoot and needle elongation seemed to be correlated with a rapid increase in photosynthate partitioned to defensive constituents, similar to the findings of Mooney and Chu (1974) with *Heteromeles arbutifolia*.

Other studies, such as Bernard-Dagan's (1988) assessment of the seasonal variation of energy sources in organs and tissues of *Pinus pinaster* are relevant to research on tree interactions with invading organisms. She clearly illustrated the dramatic change from lipids to starch that takes place in secretory (epithelial) cells in needles and buds from winter to early spring. Monoterpene and diterpene compounds, major components of oleoresin, are formed during a very short time (a few days) when the epithelial cells are active. As tissues age the activity of the secretory cells decreases and eventually stops. Presumably, this same phenomenon would occur in epithelial cells associated with bole cambial growth and xylem formation. However, vertical resin ducts are usually absent in earlywood, except in juvenile xylem formed in or near the crown (Figs 5.3 and 5.4). Vertical resin ducts generally appear during and after the transition to latewood.

Many changes occur in the production and distribution of photosynthates in *Pinus* through the year. Bernard-Dagan's (1988) description of the seasonal pattern for *P. pinaster* may not differ greatly from what occurs in North American conifers. These basic physiological changes may vary somewhat with latitude and among species, but knowledge of the general patterns is extremely important for understanding bark beetle, pathogen, and tree interactions (Cheniclet *et al.*, 1988).

Until recently, bark beetle researchers have paid little attention to Kozlowski's (1969) advice concerning study of tree physiological changes associated with ontogeny. Physiological ecologists, however, have made considerable effort to study resource partitioning patterns in plants with respect to growth, reproduction, and defense against herbivores (Bazzaz *et al.*, 1987).

The seasonal ontogeny of southern *Pinus* species, in terms of vegetative and reproductive growth (Fig. 5.2), has great potential significance regarding the resistance of even the healthiest trees to bark beetle attack. For example, high priority demands by apical and cambial growth, and even higher demands by reproductive growth, limit the potential partitioning of photosynthates to secondary metabolic processes and the production of defensive compounds at the same time (Veihmeyer and Hendrickson, 1961; Mooney and Chu, 1974; Chung and Barnes, 1980a; Lorio and Sommers, 1986). However, environmental factors, such as moderate water deficits during the spring and early summer growth flush can alter relationships among ontogenetic processes and result in proportionately less of the currently available energy being used in growth and more in oleoresin synthesis (Lorio *et al.*, 1990).

The ontogeny and phenology of trees are associated with physiological changes of great significance to bark beetle, pathogen, and tree interactions. Further, one should recognize the importance of seasonal changes apart from environmental stress such as water deficits, as well as the need to evaluate the effects of water deficits in terms of their timing, severity, and duration.

5.5 WATER DEFICITS, TREE DEVELOPMENT AND PHYSIOLOGY

Because of its seemingly overall importance to tree growth and yield (Zahner, 1968), water deficit, rather than the variety of other biotic and abiotic stresses (Chapter 4), is the focus of this chapter. Tree responses to water deficits, as to other stresses, are related to the tree's stage of development.

5.5.1 Plant factors affecting responses

A plant's response to water stress depends on its metabolic activity, morphology, stage of growth, and yield potential (Gardner *et al.*, 1985). Water deficits during vegetative growth phases have effects entirely unlike effects during flowering and fruiting, and fruit and seed development and maturation (Hsiao *et al.*, 1976b). While cell growth is most sensitive to water deficit, xylem conductance reduction may not be affected until water potential is below -0.7 to -3.0 MPa (7 to 30 bars) (Hsiao *et al.*, 1976a; Tyree and Dixon, 1986; Jones, 1989). However, assessing the effects of water deficits on plants is not a simple problem.

Bradford and Hsiao (1982) provided a thorough discussion of inherent difficulties in understanding the direct effects of water deficits on physiological processes within plants, and on the long-term behavior of plants. They point out that because of feedback loops among various metabolic processes, it is difficult to distinguish between cause and effect following the onset of a perturbation. Further, in nature, water stress usually develops gradually, over days to weeks, providing ample time for coordinated responses of internal processes, and resulting in adaptation and enhancement of survival under stress.

5.5.2 General patterns of response

Some patterns of gross plant responses to water stress are generally applicable to a large number of plant species (Bradford and Hsiao, 1982). It appears that overall changes in response to stress almost always lead to adjustments in water use and supply that increase the probability of survival and propagation of the species. Bradford and Hsiao (1982) reviewed a number of gross responses and adaptations that occur with many species: reduced foliage growth during early water deficit, resulting in reduced transpiration and a rationing of water supply to meet the demands of a longer ontogenetic span; increases in roots relative to shoots; osmotic adjustment throughout the plant, resulting in maintained turgor and physiological functions at reduced water potential; changes in leaf shape and orientation, leaf abscission, and closing of stomates, resulting in reduced light interception, reduced transpiration, and conserved water. Studies by Linder *et al.* (1987) with *Pinus radiata*, and by Cregg *et al.* (1988) and Hennessey *et al.* (1992) with *P. taeda*, illustrate these important relationships.

Bradford and Hsiao (1982) concluded that insufficient attention has been given to plant responses to water stress that precede stomatal closure and changes in photosynthesis. In

Pinus, responses to such deficits no doubt include greater partitioning of photosynthates to oleoresin synthesis, an important response relative to resistance to bark beetle attack (Lorio and Sommers, 1986; Lorio *et al.*, 1990).

5.5.3 Flowering and reproduction

The process of flower initiation in plants is complex and only partially understood, but Sachs (1987) notes that moisture and osmotic stress and reduced nitrogen nutrition can reduce growth, accelerate flowering, and result in increased carbohydrate concentration in shoots. In *Pinus*, which initiate strobili primordia in mid- to late-summer in the southern US, research has demonstrated important relationships between rainfall and flower initiation and cone production (Wenger, 1957; Bengtson, 1969; Shoulders, 1967, 1968, 1973; Dewers and Moehring, 1970; Grano, 1973).

Wenger (1957) found that *P. taeda* seed crops varied directly with May-to-July rainfall of the second preceding year, and suggested that irrigation in seed orchards might be beneficial. Early results of irrigation trials with *P. elliottii* var. *elliottii* were ambiguous (Bengtson, 1969). However, Dewers and Moehring (1970) found that irrigation of *P. taeda* in a 13-year-old seed orchard April through June, followed by drought treatment July through September, resulted in significantly higher conelet production than any other treatment. Results indicated that a period of soil water deficit in *P. taeda* stands during or just prior to initiation of ovulate primordia is conducive to cell differentiation into reproductive tissues. Late season irrigation may suppress conelet production. These results support Wenger's (1957) findings for natural stands of *P. taeda*, and Shoulder's (1967) findings for *P. palustris* and illustrate that timing of water deficit greatly influences the nature of tree responses.

Later studies by Shoulders (1973) with *P. elliottii* var. *elliottii* in Louisiana, and Grano (1973) with *P. taeda* in southern Arkansas, showed that flowering and seed yields were enhanced by plentiful spring rain followed by moderate water deficits during the summer. These results are consistent with results expected from consideration of plant growth and differentiation balance principles (Loomis, 1932, 1953), and clearly indicate the need for a broad approach to the study of conifer responses to stresses such as water deficits, and the potential effects of environmental stresses on carbon partitioning to growth, reproduction, and defensive compounds.

5.6 MECHANISMS OF TREE DEFENSE

5.6.1 Theories

There is an extensive literature dealing with theories of defensive mechanisms and relationships to energy supply in plants: apparency (Rhoades and Cates, 1976; Feeny, 1976), defensive chemistry (Rhoades, 1979; Schultz and Baldwin, 1982), carbon/nutrient balance (Bryant *et al.*, 1983), resource availability (Coley *et al.*, 1985; Bazzaz *et al.*, 1987), multiple modes (Mattson *et al.*, 1988; Berryman, 1988), to name a few. Other literature more specific to bark beetles includes Wood (1972), Cates and Alexander (1982), Raffa and Berryman (1983), Hodges *et al.* (1985), Matson and Hain (1985), Hain *et al.* (1985), Sharpe and Wu (1985), Sharpe *et al.* (1985), Lorio and Hodges (1985) and Lorio (1986).

The defensive mechanisms that function in conifers in response to invasions by bark beetles and associated pathogens seem to center on some aspects of their oleoresin systems.

In those conifers that possess a primary resin system, such as Pinus species, the potential rate and duration of flow from wounds is considered an important defensive mechanism (Chapter 8). However, induced responses to wounding by bark beetles or pathogens also may be important in Pinus and in other conifers not possessing preformed resin systems (Berryman, 1972; Chapter 8).

5.6.2 Oleoresin in conifers

Stark (1965) extensively reviewed the subject of oleoresin as a resistance mechanism to attack by forest insects. He considered the subject fundamentally important and of immediate practical applicability. The resin problem has been researched considerably since Stark's review, with much progress. See Chapter 8 for a discussion of the oleoresin system in *Pinus* species in relation to colonization by bark beetles. This section focuses on some aspects of host tree water status and the potential for resin to flow from bark wounds.

Oleoresin exudation pressure (OEP), measured with glass capillary manometers (Bourdeau and Schopmeyer, 1958), Bourdon gauges (Vité, 1961), or other devices such as potentiometer-type pressure transducers (Helseth and Brown, 1970), generally is perceived to be directly related to resin flow. However, little experimental evidence is available to support this idea.

Schopmeyer *et al.* (1954) reasoned that flow through radial resin ducts could be expressed by a modification of Poiseuille's equation for the flow of liquid through capillaries:

$$Y = [KN(ab)^2P]/\eta$$

where Y is the yield of resin over a fixed time, K is a constant, N is the number of radial resin ducts per unit area of wound surface, $(ab)^2$ is the average of squared products of the major and minor semiaxes (a and b) of the duct cross section, P is the exudation pressure at the point of discharge, and η is resin viscosity.

Bourdeau and Schopmeyer (1958) found a statistically significant relationship between resin yield per inch of wound width over two 2-week periods of commercially tapped *Pinus elliottii* var. *elliottii* and the function

$$[N(ab)^2P]/\eta$$

for variables as defined above. When P was removed, the relationship was not significant. They concluded that number and size of resin ducts, pressure, and viscosity were related to resin yield from wounds in *P. elliottii* var. *elliottii* stems and that pressure, viscosity, and pressure:viscosity ratios might be useful variables in progeny testing because they are under strong genetic control.

Since the work of Schopmeyer *et al.* (1954) and Bourdeau and Schopmeyer (1958), few studies have been conducted in which both OEP and resin flow were measured along with other variables. In contrast to the results of Bourdeau and Schopmeyer (1958), Barrett and Bengtson (1964) found no correlation between OEP and resin yield from seven seed sources of *P. elliottii* var. *elliottii*. They did find that the ratio of OEP to viscosity was related to flow, as did Bourdeau and Schopmeyer (1958), but viscosity alone was more closely related to flow than was the OEP:viscosity ratio. Hodges and Lorio (1971) found OEP of *P. taeda* to be positively correlated with the xylem water potential of twigs and the relative water content of needles (relative turgidity of Weatherley, 1950), but not correlated ($r = 0.03$) with oleoresin flow measured as described by Mason (1969). Subsequently, Hodges *et al.* (1981) reported no correlation between resin flow and the size or number of resin ducts for any of four *Pinus* species studied.

Vité (1961) used the work of Bourdeau and Schopmeyer (1958) as a basis for development of a technique for measuring OEP in *Pinus ponderosa* in an intensive study of relationships among OEP, water supply, phloem moisture, and severity of bark beetle attack. Vité did not measure oleoresin flow, but he considered OEP to be an expression of the water balance of a tree (and its oleoresin flow) and a dependable indicator of *P. ponderosa* resistance or susceptibility to bark beetle infestation. Vité and Wood (1961) found that a high percentage of successfully attacked trees had low OEP and suggested that OEP be used for risk rating individual trees and stands of second growth *P. ponderosa*. However, Wood (1962) reported that *Ips confusus* failed to colonize *P. ponderosa* with extremely low OEP (less than 1 bar) over a span of 26 days or longer. Stark (1965), Raffa and Berryman (1982), Matson and Hain (1985), and others have concluded that OEP is an unreliable predictor of tree susceptibility to bark beetles, as discussed below.

Lorio and Hodges (1968b) showed that OEP of *P. taeda* was very responsive to changes in atmospheric evaporative demand and soil water status, as did Vité (1961) for *P. ponderosa* and Bourdeau and Schopmeyer (1958) for *P. elliottii* var. *elliottii*, but they also did not measure resin flow. Cobb *et al.* (1968) measured both OEP and resin flow in *P. ponderosa* affected by photochemical air pollution and reported that OEP was reduced gradually as disease severity increased. However, resin flow rate remained relatively constant through intermediate stages of disease development. Total resin flow apparently followed the same pattern, but the limited capacity of the collection vials may have contributed to the similar yields for healthy and moderately diseased trees. Although OEP seems to be well related to tree water status, neither OEP nor tree water status appear to be directly related to resin flow. Several studies indicate a more complex or subtle relationship may exist (Harper and Wyman, 1936; Ostrom *et al.*, 1958; Mason, 1971).

Harper and Wyman (1936) studied the daily pattern of resin yield from *P. elliottii* var. *elliottii* and observed a decided decline in rate of resin yield whenever tree boles expanded between 6 a.m. and 4 p.m. A small increase in flow occurred when stems contracted. Further, they showed that resin yield peaked between 8 a.m. and 10 a.m. during the second day after wounding, when temperature was increasing at its fastest rate during the day, and rate of stem shrinkage was greatest. The time of their observed maximum resin yield for the day coincides with the time that OEP typically is dropping at a fast rate (Bourdeau and Schopmeyer, 1958; Vité, 1961; Lorio and Hodges, 1968a,b; Helseth and Brown, 1970; Hodges and Lorio, 1971).

Ostrom *et al.* (1958) found that acid applied to wounds made to the face of the xylem of *P. taeda*, *P. elliottii* var. *elliottii*, and *P. palustris* destroyed the cambium to about 2 cm above a wound, enlarged openings of ducts near the cambium by collapsing or destroying epithelial cells and ray parenchyma, and served chiefly to facilitate outflow of resin from ducts (essentially reducing OEP to zero in the affected area). Mason (1971) found that resin flow in *P. taeda* was affected more by overstocking in an unthinned stand than by temporary soil moisture stress. Induced drought alone did not affect the mean OEF for the season. He concluded that resin flow must be controlled mostly by factors only indirectly influenced by tree water status.

Perhaps the resin duct systems in conifers are not sufficiently similar to hydraulic systems with rigid-walled capillaries for a modification of Poiseuille's equation to predict flow adequately. It appears that resin flow from wounds made to the face of the xylem is enhanced by a reduction in turgor of the epithelial cells (Harper and Wyman, 1936; Ostrom *et al.*, 1958). With full turgor, as resin flow begins near the wound site, resin ducts may be rapidly closed as epithelial cells distend in response to reduced back pressure from the resin column. With less than full turgor, which commonly occurs in mid-morning, epithelial cells may distend less rapidly, perhaps incompletely closing the ducts, thus allowing faster and more prolonged resin flow than with full turgor.

Measurement of OEP may at times be useful to estimate the relative water status of trees. However, caution should be used in inferring any relationship with resin flow. It seems clear that considerably more detailed and elaborate studies will be required to describe adequately the diurnal and seasonal relationship between OEP and resin flow.

5.7 FACTORS AFFECTING EXPRESSION OF RESISTANCE

As suggested by Raffa and Berryman (1983), trees vary in their quantitative resistance to invading organisms due to genetic, environmental, and seasonal factors. This section focuses on some aspects of the growth and development of trees that could affect the potential expression of defense against bark beetles and pathogens. If the resin systems, primary or secondary, are important to defense, it seems likely that the partitioning of photosynthates would be very important to the expression of resistance to invasion. Accordingly, trees with large and efficient crowns that produce sufficient photosynthates to meet the demands for both vegetative and reproductive growth, as well as synthesis of differentiation products, such as allelochemicals, will likely be more resistant to invasion than trees with small, inefficient crowns. Several factors, including forest or stand structure, carbohydrate status of trees, and seasonal environmental factors, influence expression of resistance. The effects of these factors may vary with the developmental stage of the tree.

5.7.1 Forest and stand conditions

Site quality, species composition, stand density, tree ages and sizes, disease incidence, and other insect activity are among the many factors that can affect tree growth and development, and interactions with bark beetles (Waring and Schlesinger, 1985). Growth, especially bole radial growth, often has been viewed as indicative of tree susceptibility or resistance to beetle attack (Miller and Keen, 1960; Hicks, 1980; Waring, 1983). Relationships among growth, environment, and invading organisms are complex and confounded, but there is little doubt that crowded stand conditions result in reduced light absorption, leaf area, photosynthesis, growth, and potential production of allelochemicals, compared to uncrowded stands (Waring, 1983; Christiansen *et al.*, 1987; Lorio, 1980). Furthermore, merely the close proximity of neighboring trees in such stands greatly facilitates the movement of bark beetles from tree to tree (Gara and Coster, 1968). Close spacing may play a more important role in facilitating *D. frontalis* infestation growth during endemic periods than during epidemics (Johnson and Coster, 1978). Further, in stands with closed canopies, beetle aggregation to sources of pheromones may be more effective than in open stands where high insolation and convection disrupt pheromone plumes (Fares *et al.*, 1980).

Thinning often is recommended to reverse the growth reduction and susceptibility to bark beetle attack observed at high stand densities (Chapter 11). Few direct tests of thinning effects on stand susceptibility to bark beetles have been reported, but Brown *et al.* (1987) reported increased resistance of *P. taeda* to attack by *D. frontalis* following thinning of stands to 23 m^2ha^{-1} or less. Nebeker *et al.* (1985) and Wood *et al.* (1985) reviewed thinning practices for southern and western *Pinus* species and made recommendations for pest management, including consideration of activities that could aggravate pathogen problems. Amman and Schmitz (1988) and Amman *et al.* (1988) discussed several management strategies, including the use of partial cuts, to minimize losses of *P. contorta* var. *latifolia* to *D. ponderosae*. Several studies conducted in the western US demonstrated that thinning reduced tree mortality to bark beetles (Sartwell and Stevens, 1975; Mitchell *et al.*, 1983; McGregor *et al.*, 1987). As with the southern *Pinus* species, consideration must be given to potential problems resulting from stand disturbance (root diseases, windthrow, dwarf mistletoe, etc.) (Witcosky *et al.*, 1986).

Although the greatest potential benefit would seem to come from well-planned, early, and scheduled thinnings over the life of a stand, thinnings of mature stands can result in improved physiological condition of the remaining trees (more photosynthate production, leading to more allelochemics production). In some instances beetle attack is reduced so quickly after thinning that drastic changes in the microclimate may be the primary factor inhibiting beetle activity (Amman *et al.*, 1988; Bartos and Amman, 1989)

5.7.2 Carbohydrate status of host trees

The carbohydrate status of host trees determines tree ability to produce or mobilize compounds critical for defense against bark beetle attack (Christiansen *et al.*, 1987) or defense against infections by pathogenic fungi (Shigo, 1985). The little-explored literature on the formation of lightwood (oleoresin-saturated woody tissue) seems particularly relevant to this issue (Schwarz, 1983; Stubbs *et al.*, 1984; Chapter 8).

Pinus responses to paraquat, a bipyridilium herbicide, applied in appropriate concentrations to living stem tissue beneath the outer bark, results in extensive resin soaking of the xylem. Years of intensive research on this process in *Pinus* species demonstrated clearly that the current and stored photosynthate status of trees at the time of treatment is important to the response obtained (Brown *et al.*, 1976, 1979; Wolter and Zinkel, 1984). In general, spring applications (when carbohydrate status normally would be high) produces the best average oleoresin yields (Stubbs *et al.*, 1984). Physiological responses to paraquat application include ethylene synthesis and heightened respiration, both of which are associated with cell-wounding response and stress (Wolter and Zinkel, 1984). Fungal colonization of phloem and xylem in association with bark beetle attacks appear to elicit similar responses (Berryman, 1972; Raffa and Smalley, 1988; Chapter 8). The nature and extent of response probably is mediated by the same factors that influence response to paraquat applications.

5.7.3 Environment and tree development

Drought may play an important role in the development of insect outbreaks (White, 1974; Mattson and Haack, 1987; Chapter 4). Martinat (1987), however, questions the role of "climatic release" as a mechanism to explain widespread periodic outbreaks, partially because of methodological problems. Further, Connor (1988) and McQuate and Connor (1990a,b) report results of studies with *Corythucha arcuata* on *Quercus alba*, and *Epilachna varivestis* on *Glycine max* that are inconsistent with, and contrary to, White's (1974) hypothesis that water deficit leads to improved insect performance and abundance. Recently, Turchin *et al.* (1991) concluded that outbreaks of *Dendroctonus frontalis* are not driven by stochastic fluctuations of weather, but by some unknown population process acting in a delayed density-dependent manner. While severe water deficits may greatly reduce tree resistance to bark beetle attack (Vité, 1961; Lorio and Hodges, 1968a, 1977), it does not follow that bark beetle outbreaks will necessarily occur. Further, it is important to realize that general relationships vary among species of insects, pathogens, and trees.

In the south and southeast, severe droughts usually are associated with high temperatures during the mid- to late-summer, conditions that are typically unfavorable for adult beetle survival and brood development (Gagne *et al.*, 1980). Moreover, drought seldom, if ever, develops so rapidly that plants do not have an opportunity to respond physiologically in a manner that will enhance their survival and reproduction. A developing drought should limit growth before it limits photosynthesis, resulting in more carbohydrate for processes other than growth. However, carbohydrate use for respiration may increase temporarily (Brix, 1962). Perhaps, if drought severely depletes carbohydrate levels by reducing effective leaf area, the response of photosynthesis to improved water conditions may be lower than necessary to meet needs for growth and development as drought is alleviated.

Inoculation studies with pathogens or fungal associates of bark beetles could benefit from consideration of environmental and developmental factors that can affect results. For example, Chou (1982), working with *P. radiata* and *Diplodia pinea*, a fungus that causes shoot dieback, found that susceptibility fluctuates with season, being high in spring–summer but low in autumn–winter. He concluded that seasonal predisposition is important in planning inoculation trials for any purpose. Studies with a variety of organisms and tree species support Chou's conclusion. Paine (1984) found significantly different rates and lengths of lesions formed in response to inoculation of the mycangial fungi of *Dendroctonus brevicomis* in *P. ponderosa* from spring through autumn. Owen *et al.* (1987) found *P. ponderosa* seedlings to be more susceptible to a number of fungi isolated from *Dendroctonus* spp. during shoot elongation than after bud set. Myers (1986), working with several *Pinus* species and *Bursaphelenchus xylophilus*, found greater mortality from spring inoculations, when cambial activity was greater, than from late summer and autumn inoculations.

5.8 CONCLUSIONS

The greatest challenge in the study of interactions among bark beetles, pathogens, and host conifers is to integrate the roles of all three elements effectively. The physiology of host trees has been the least effectively integrated element in past research, partially because of a generally poor understanding of the role of plant physiology in forestry (Kramer, 1986). Excessive emphasis has been placed on presumed effects of stresses, such as water deficits, without consideration of host-tree ontogeny and phenology, and the importance of timing, intensity, and duration of stresses. Greater attention must be paid to the role of tree physiology, phenology and ontogeny in the triangle of interactions among invading organisms, trees, and environment.

Ultimately, adequate knowledge of tree, bark beetle, and pathogen interactions is needed to permit mechanistic modeling of "what if?" situations, an extremely difficult problem considering the myriad of organisms and conditions involved, and the complexities of forest systems. Progress could be enhanced greatly with more effective cooperation and development of integrated studies, as in approaches recommended by Landsberg (1986) and by framing hypotheses in explanatory, rather than statistical, models, an approach strongly endorsed by Loomis and Adams (1983).

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