Forest Ecology and Management, 14 (1986) 259—273
Elsevier Science Publishers B.V., Amsterdam — Printed in The Netherlands

GROWTH—DIFFERENTIATION BALANCE: A BASIS FOR UNDERSTANDING SOUTHERN PINE BEETLE—TREE INTERACTIONS

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(Accepted 31 October 1985)

ABSTRACT

Lorio, P.L., Jr., 1986. Growth—differentiation balance: a basis for understanding southern pine beetle—tree interactions. *For. Ecol. Manage.*, 14: 259—273.

Interrelationships between the southern pine beetle (SPB), *Dendroctonus frontalis* Zimm.) and its host pines are explained in terms of the growth—differentiation balance concept. A general hypothesis is proposed based on growth—differentiation balance in southern pines (radial growth of stems versus synthesis and yield of oleoresin) and seasonal activity of the SPB based on knowledge from experimentation and observations reported in the literature. The spring appears to be particularly favorable for successful SPB attack because of the strong demand for available photosynthates by growth processes at that time, whereas, in the summer, strong resin flow increases the potential resistance of trees to attack.

Growth—differentiation balance provides a basis for understanding SPB-tree interactions, a rationale for commonly experienced problems in identifying consistent precursors to SPB outbreaks, and a philosophical basis for future research. The concept has potential application to other bark beetle—host conifer relationships.

INTRODUCTION

Bark beetles of the genus *Dendroctonus* kill pines by boring through the outer bark to the cambial layer, excavating egg galleries in the phloem, and effectively girdling the trees over much of the clear bole. These destructive forest pests have remained puzzling organisms despite more than 70 years of research in the United States. The southern pine beetle (SPB), *Dendroctonus frontalis* Zimmermann, is one of the more perplexing and serious bark beetle pests that has had an enormous impact on pine forests in southern United States, Mexico, and the Republic of Honduras (Beal et al., 1964; Price and Doggett, 1982; Thatcher and Barry, 1982).

Reviews of bark beetle research around the world by Rudinsky (1962) and Stark (1965) illustrate the complexity confronting students of bark beetle ecology. Rudinsky considered abundance of suitable breeding material to be the decisive factor in bark beetle outbreaks, and Stark indicates that water deficit is probably the most important single factor leading to conditions conducive to outbreaks. In recognition of the potential role of oleoresin as a defense mechanism against bark beetle attack, Stark discusses resin synthesis; its physical and chemical characteristics; exudation pressure, flow rate, and quantity produced; characteristics of the pine resin duct systems in trees; and the probability that oleoresins can be remetabolized. Loomis and Croteau (1980) provide ample evidence that monoterpenes, important components of pine oleoresins, are both rapidly synthesized and catabolized, and conclude that monoterpenes may play a dynamic role in metabolism. They suggest that synthesis, storage, and catabolism of monoterpenes are controlled by growth—differentiation balance relationships (Loomis, 1932, 1953).

The concept of growth—differentiation balance was offered by W.E. Loomis (1932, 1953) as a convenient and simplified scheme for predicting or explaining plant behavior. Loomis recognized the potential value of a growth—differentiation balance concept to replace the then popular carbohydrate—nitrogen balance, but did not consider it as a complete and final statement of developmental processes in plants.

Here, I propose that the growth—differentiation balance concept provides a rational basis for understanding SPB interactions with southern pines, that it helps to explain commonly experienced difficulties in attempts to identify consistent precursors to SPB outbreak (Coulson, 1980), and that it forms a philosophical basis for development of future research. The basic principle of growth—differentiation balance should apply to other bark beetle—tree species interactions as well as to the SPB and southern pines.

THE CONCEPT

Loomis (1932), following common practice, divided the development of plants into three more or less distinct but overlapping phases: cell division, cell enlargement, and cell differentiation. The first two are generally considered together as elements of growth involving increase in plant size. The third has to do largely with changes in morphology as a result of pre-existing chemical conditions in the cells or tissue involved. For the purposes of growth—differentiation balance, Loomis defined differentiation as the sum of the chemical changes that occur in maturing cells and of the morphological changes which result from these chemical conditions. Examples of differentiation processes, as provided by Loomis (1953) are: thickening and lignification of secondary cell walls, thickening of leaf cuticle, hardening of the protoplasm, formation of specific flowering substances, and the production of cellular inclusions such as gum, resin, essential oil, or similar products.

Growth, involving cell division and cell enlargement, depends upon an array of internal and external factors, including temperature, water, oxygen, sugar, inorganic nutrients, enzymes, and hormones. As long as all factors are favorable for growth, growth processes predominate over differentiation.

Differentiation is dependent primarily upon temperature and sugars and is dominant only when conditions other than temperature and photosynthate supply are below optimum for growth.

R.S. Loomis (1983) explains how growth and differentiation balance relationships are helpful in understanding partitioning of photosynthates. With water not limiting, supplies are used principally in growth and the new tissue consists mostly of proteins and cellulose. Under mild stress, differentiation is favored and the tissue has a higher content of lignin, wax, and other materials. If the direct effect of a deficiency is on photosynthesis (e.g. low light, or leaf removal), or if the water deficit is severe, then both growth and differentiation are limited.

In forest tree growth, and particularly for southern pines growing in the southeastern United States, water deficit is a common limiting seasonal growth factor. The effect of water deficit on tree growth and development has been a subject of major interest in forest science (Zahner, 1968; Kozlowski, 1968—1981). However, water deficit has been given little attention as a possible beneficial effect when it prompts formation of differentiation products, such as the oleoresin of pines. These products are important in tree resistance to SPB attack.

In southern pines the network of horizontal (radial) and vertical resin ducts in the xylem tissue and the oleoresins contained in the network comprise the primary defense mechanism against attacking bark beetles (Hodges et al., 1979; Coulson, 1980). Growth—differentiation balance determines when during the growing season and in what tissues resin ducts are formed and oleoresins are produced. Factors that affect tree crown development and radial growth likewise affect the potential synthesis and flow of oleoresin from wounds; and large-crowned trees that produce large supplies of photosynthates usually demonstrate fast stem radial growth as well as the ability to produce defensive chemicals compared to smaller-crowned trees, such as those in intermediate and suppressed crown classes (Wyman, 1932; Clements, 1974).

Waring and Pitman (1980) and Waring (1983) suggest that growth efficiency (the ratio of stemwood production per unit of leaf area) may serve as an index of vigor and the susceptibility of trees to native insects, because the production of protective chemicals declines in parallel with wood growth. This approach apparently assumes that all vigorously growing trees are resistant to bark beetle attack at all times, and does not consider that growth and differentiation processes are competitive sinks for photosynthates.

The competition between wood formation and formation of oleoresin in pines, an example of growth—differentiation balance, is in apparent conflict with Waring's (1983) ideas concerning the parallel relationship between growth and the production of protective chemicals. However, one must recognize that the seasonal allocation of photosynthates, either to radial growth or to secondary metabolism of monoterpenes and resin acids, is much different from the total allocation of photosynthates to both processes on a yearly basis. For example, research on guayule, *Parthenium argentatum* A. Gray (Wadleigh et al., 1946; Veihmeyer and Hendrickson, 1961) and on the shrub, toyon, *Heteromeles arbutifolia* (Lindl.) M.J. Roem., (Mooney and Chu, 1974) indicate that growth processes and secondary metabolism processes (differentiation) compete for available photosynthates, and that carbon allocation to all functions cannot be met simultaneously. Application of the growth—differentiation balance concept provides a basis for understanding why the general population of trees in a pine forest, including vigorously growing trees, will vary in their resistance to bark beetle attack in relation to ongoing physiological processes.

GROWTH—DIFFERENTIATION BALANCE AND TREE RESISTANCE TO SPB ATTACK: A GENERAL HYPOTHESIS

Because of growth—differentiation balance relationships, well-hydrated, fast-growing trees may be quite susceptible to beetle attack in the absence of any unusual stresses, depending on the season of the year and the growth stages of the trees. The following is a proposed rationale that draws together growth and differentiation balance relationships and seasonal activity of the SPB, based on knowledge from experimentation and observations reported in the literature.

Other conditions (such as stand age, density, and tree crown size) being equal, the general population of trees should vary in their susceptibility to beetle attack through the seasons of the year as described in Table 1. The left side of the table presents a proposed generalized seasonal growth and differentiation balance representation for southern pines. The right side of Table 1 illustrates a generalized schematic pattern of seasonal SPB activity in relation to the growth and differentiation balance relationships described on the left. The seasonal activity of the SPB is known in general terms but varies considerably across its very large range, from Pennsylvania to Texas and from New Mexico and Arizona to the Republic of Honduras (Billings, 1979; Coulson, 1980; Payne, 1980; Thatcher et al., 1980; Thatcher and Barry, 1982).

In the winter, stem radial growth has ceased and oleoresin synthesis is low (Bishop and Marckworth, 1933), and flow of oleoresin from wounds is limited (Harper and Wyman, 1936; Barrett and Bengtson, 1964). Photosynthesis may be quite active (Kozlowski, 1971). Beetles are active intermittently in winter, and are found in all life stages from egg to adult (Thatcher, 1967; Franklin, 1970; Thatcher and Barry, 1982). Adult beetles respond readily to mild temperatures in the winter (Moser and Dell, 1979, 1980); broods apparently have high survival rates (Thatcher and Pickard, 1964; Thatcher, 1971, 1974), but relatively low fat content (Hedden and Billings, 1977). Although beetles fly readily in warm periods in all winter, Franklin (1970) believes that mild winters may be detrimental to beetles. He indicates that at the latitude of

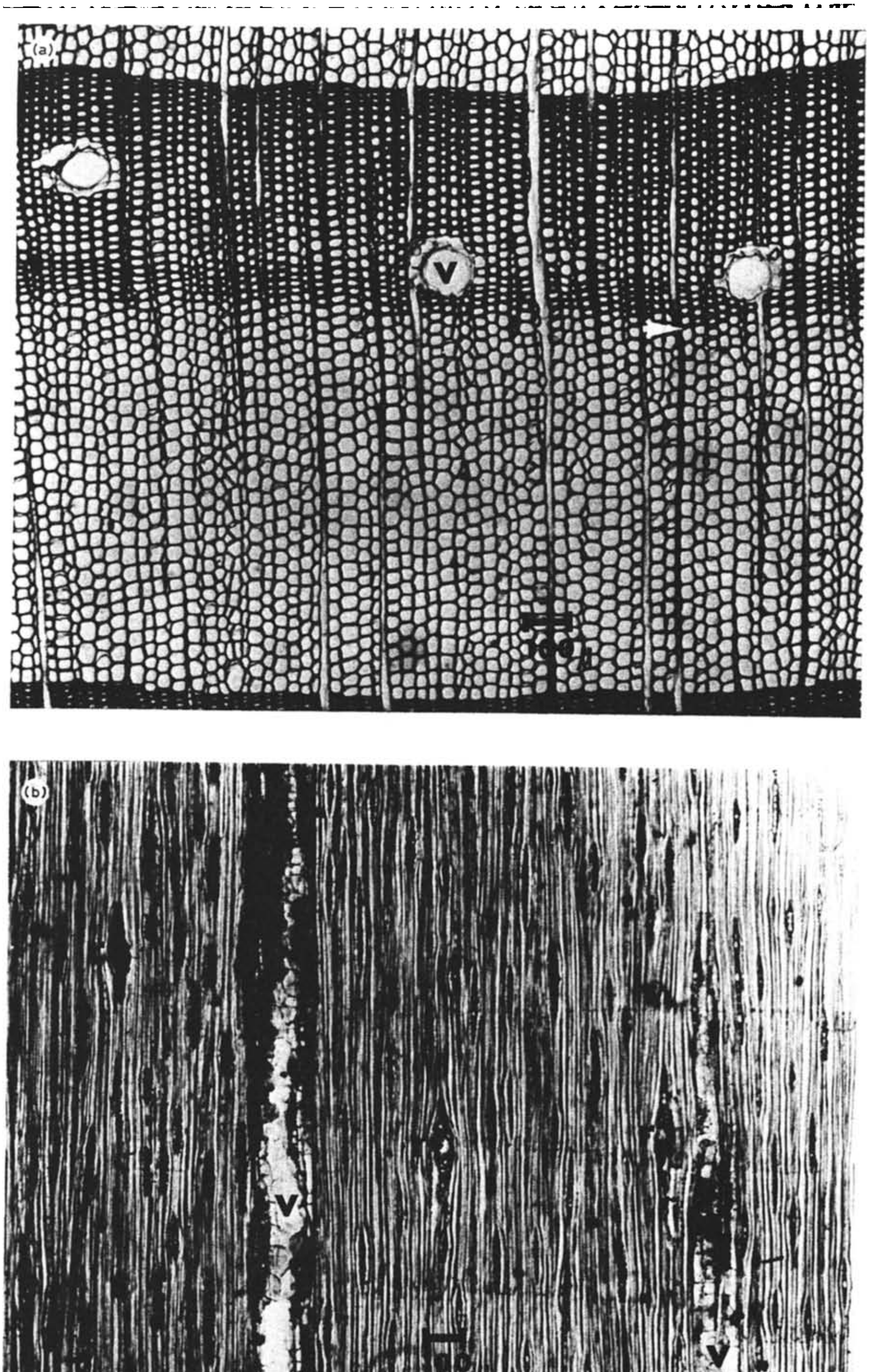
Athens, Georgia, rapidly falling temperatures in the late afternoon and evening limit the potential colonization of trees by the SPB.

As growth commences in the spring with a warming trend, water supply is usually optimum, food reserves are high, photosynthesis proceeds rapidly,

TABLE 1

A generalized schematic representation of growth and differentiation balance for southern pines and seasonal activity of the southern pine beetle

Season	Tree growth and differentiation conditions	Southern pine beetle activity
Winter	No stem radial growth and little or no differentiation; little oleoresin flow from wounds (Bishop and Marckworth, 1933; Harper and Wyman, 1936; Barrett and Bengtson, 1964); photosynthates accumulate (Kozlowski, 1971).	Beetles are active intermittently (Thatcher, 1967; Franklin, 1970); occur mostly in fall—winter initiated infestations (Billings, 1979; Payne, 1980); respond rapidly to mild temperatures and fly readily during warm periods (Franklin, 1970; Moser and Dell, 1979, 1980); survival rates are high in the deep South (Thatcher and Pickard, 1964; Thatcher, 1971, 1974); fat content may be low (Hedden and Billings, 1977).
Spring	Cambial growth predominates with rapid cell division and enlargement (Zahner, 1962, 1968); few or no vertical resin ducts are formed (Hobert, 1932; Koch, 1972; and see Fig. 1a); oleoresin yield increases gradually through the season (Harper and Wyman, 1936; Barrett and Bengtson, 1964).	Beetles are active and disperse from fall—winter initiated infestations (Billings and Kibbe, 1978; Billings, 1979; Payne, 1980); and establish new ones (Thatcher and Pickard, 1964; Franklin, 1970; Thatcher, 1971; Hedden and Billings, 1977).
Summer	Water deficits are established and latewood starts forming (Zahner, 1962, 1968); photosynthates accumulate (Hodges and Lorio, 1969); oleoresin flows freely from wounds and production maximizes (Harper and Wyman, 1936; Barrett and Bengtson, 1964) in correlation with an increase in potential evapotranspiration (Moser and Dell, 1980).	Beetles are active and tend to mass attack trees on periphery of existing infestations (Billings, 1979; Payne, 1980); high temperatures may inhibit flight and activity (Moser and Dell, 1979; Coulson, 1980); and survival may be low (Thatcher and Pickard, 1964, 1967; Thatcher, 1971, 1974).
Fall	Stem radial growth stops (Zahner, 1962, 1968); oleoresin flow from wounds drops and production declines (Bishop and Marckworth, 1933; Harper and Wyman, 1936).	Beetles are active, are said to disperse from existing infestations and establish new ones that tend to remain small (Hedden and Billings, 1977; Billings, 1979); development of broods proceeds slowly (Thatcher and Pickard, 1967; Billings and Kibbe, 1978).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and cell division and enlargement take place with production of earlywood-type cells (Zahner, 1962, 1968). Few or no vertical resin ducts are formed (Hobert, 1932; Koch, 1972). Oleoresin yield gradually increases through the season (Harper and Wyman, 1936; Barrett and Bengtson, 1964). In the spring, beetles emerge in large numbers from fall—winter initiated infestations and are said to disperse widely (Thatcher, 1974; Hedden and Billings, 1977; Billings and Kibbe, 1978; Billings, 1979; Payne, 1980). Attacking beetles encounter trees in the grand growth phase when little photosynthate is being converted to oleoresin, and this defense mechanism is ineffective (see left side of the table). Resin that flows from wounds must come from a reservoir somewhat remote from the cambium and flow relatively long distances through the very small diameter radical canals (Fig. 1a and 1b). Warm temperatures favor beetle flight and general activity, and dispersed beetle populations may overcome even healthy, vigorous trees.

Development of water deficits and a decline in auxin levels in summer cause a shift from earlywood-type to latewood-type growth (Zahner, 1962, 1968) with the accompanying development of vertical resin ducts (Hobert, 1932; Koch, 1972), and an increase in oleoresin synthesis and yield (Harper and Wyman, 1936; Barrett and Bengtson, 1964). The rate of development and severity of water deficits determine the degree of gradual or abrupt transition from earlywood to latewood and how much latewood is produced, as well as the amount of oleoresin synthesis and yield. Carbohydrate and nitrogen fractions in the inner bark of loblolly pine (*Pinus taeda* L.) change dramatically through the seasons in relation to stem radial growth rates and the degree of water deficit that trees experience (Hodges and Lorio, 1969). Emerging beetles tend to attack trees at the periphery of existing infestations so that infested areas become quite large while the number of new infestations decreases (Billings, 1979; Payne, 1980). Under endemic conditions, beetle attacks would likely fail, but concentrated attack of many beetles over a short time span generally assures successful colonization of trees (Franklin, 1970). Lightning-damaged trees provide easily colonized hosts at this time, when undamaged trees are relatively resistant to attack (Hodges and Pickard, 1971; Thatcher, 1971; Lorio and Bennett, 1974; Lorio and Yandle, 1978). However, high temperatures may inhibit flight and activity (Moser and Dell, 1979, 1980; Coulson, 1980), and survival and activity may be low (Thatcher, 1974).

Fig. 1. Resin ducts in loblolly pine stem wood: (a) cross section through annual ring showing vertical ducts (V) in the latewood (× 40). In this specimen, a total of 48 rows of tracheids form the ring, 22 rows of earlywood and 26 rows of latewood. Note that 25 rows of tracheids were formed before formation of the first vertical resin duct. Section prepared by E.T. Howard; (b) freehand tangential section in the latewood showing radial ducts, r, and portions of two vertical ducts, v, (× 40). Note that the vertical ducts are several times larger in diameter than the radial ducts. Section mounted in lactophenol with aniline blue stain.

In the fall, shortening day length and cool temperatures bring growth to a halt (Zahner, 1962, 1968). Oleoresin synthesis and yield decline, dropping to very low levels in the winter (Bishop and Marckworth, 1933; Harper and Wyman, 1936). Beetles are said to disperse in the fall (Billings, 1979; Hedden and Billings, 1977; Payne, 1980), coincident with the decline in oleoresin synthesis and yield in trees. Decreasing temperatures result in reduced flow of resin from wounds and presumably fewer beetles are required to successfully attack and overcome trees. New infestations tend to remain small (Billings, 1979) and broods develop slowly (Thatcher and Pickard, 1967; Billings and Kibbe, 1978).

SUPPORTING EVIDENCE

It might be helpful to more fully discuss evidence that supports the proposed general scheme of seasonal behavior of the SPB in relation to tree growth and differentiation balances. Thatcher (1967) observed brood development in a total of 132 trees from December through February of 1959—1960, 1961—1962, and 1962—1963 in southeast Texas. In December at least 28% of the study trees contained attacking adult beetles and their eggs at breast height (1.4 m), and more than 50% had more advanced brood development. By mid-February brood adults were found in many trees, and Thatcher states that "Emerging adults attacked basal stems and lower crown areas of trees which had not been attacked, or had been abortively attacked, the previous fall." Thatcher (1974) subsequently concluded, on the basis of studies in southeast Texas and central Louisiana (Thatcher and Pickard, 1964; Thatcher, 1967, 1971), that highest survival occurs in trees infested during the fall through early spring, that severity of outbreaks is greatest in the spring, and that survival and activity are lowest in the summer.

Hedden and Billings (1977) found that average fat content and pronotal width of newly emerged adult beetles varied with season in east Texas, with fat content being highest in the fall and spring, and lowest in summer and winter. Beetles were smallest during July, August, and September. Hedden and Billings suggest that fat content is correlated with dispersal capacity, and that the abrupt decline in the number of new infestations detected in mid-summer indicates reduced beetle dispersal capacity. Further, they suggest that the long-range dispersal of SPB in east Texas, followed by the initiation of new infestations, occurs primarily during the spring and fall when fat reserves are high, environmental conditions are optimal for flight, and intermittent cool weather interrupts pheromone production in old infestations.

Moser and Dell (1979) reported trapping large numbers of flying SPB in January, May, and October of 1975, with peak catches occurring in October. In another study in 1978, more beetles were trapped in the first week in January than any other week of the year (Moser and Dell, 1980). Beetles were caught in least numbers during very cold periods of January and February, and the hot summer months.

Billings and Kibbe (1978) studied brood development in infestations in loblolly pine stands in several counties in southeast Texas from September 1976 through August 1977. They concluded that broods in winter-infested trees developed rapidly as temperatures rose in March and April, and that broods which took 17 weeks to develop from 1 December to 1 April, emerged within a 5-week period from the last of April through the end of May.

The works cited above (Thatcher, 1967, 1971, 1974; Thatcher and Pickard, 1964; Hedden and Billings, 1977; Moser and Dell, 1979, 1980; Billings and Kibbe, 1978) all support the proposed seasonal activity illustrated in Table 1. Payne (1980), in discussing the seasonal behavior of the SPB, cites some of these same works and does not indicate disagreement or propose alternative behavior. Coulson (1980) reviews a large body of work by himself and co-workers, directed primarily at beetle population parameters and individual infestation growth from May through October in southeast Texas. He does not consider the dispersion of SPB populations per se in his review, but indicates that the first phase of attack, involving host selection by "pioneer beetles", is dependent on sophisticated behavioral mechanisms, because it is assumed that beetles must be able to identify relatively rare susceptible hosts to ensure the perpetuation of the insect. Coulson acknowledges that information on what happens to adult beetles after emergence and flight from colonized trees has been extremely difficult to obtain.

Based on the anatomical characteristics of southern pine wood, and especially the earlywood—latewood transition (including the development of vertical resin ducts), oleoresin synthesis would be expected to occur primarily in the summer, or whenever water deficit checks growth and induces differentiation. Harper and Wyman's (1936) study supports this idea, in that oleoresin yield was closely related to temperature and that maximum first-day yields for 70 longleaf pines (*Pinus palustris* Miller) occurred in July in central Florida. Moser and Dell (1980) subsequently showed that the seasonal yield of oleoresin reported by Harper and Wyman followed the potential evapotranspiration curve closely (Fig. 2). Fourteen-day yields of oleoresin from 315 slash pines (*P. elliottii* Engelmann var. *elliottii*) (Barrett and Bengtson, 1964), and first-day yield from 10 loblolly pines in central Louisiana (R.A. Sommers, personal communication, 1984) followed similar trends, with peak yields shifted to late summer. The results of these studies strongly support an inverse relationship between growth processes and oleoresin synthesis and flow from wounds. Competition for available photosynthates, as described by the growth—differentiation balance concept, appears to be the basis for the inverse relationship.

In the lower West Gulf Coastal Plain of Louisiana and Texas, pines on flat, poorly drained sites commonly are attacked first in the development of SPB infestations and those on slightly elevated mounds are not attacked, or are attacked later as an infestation develops (Lorio, 1968; Thatcher, 1971).

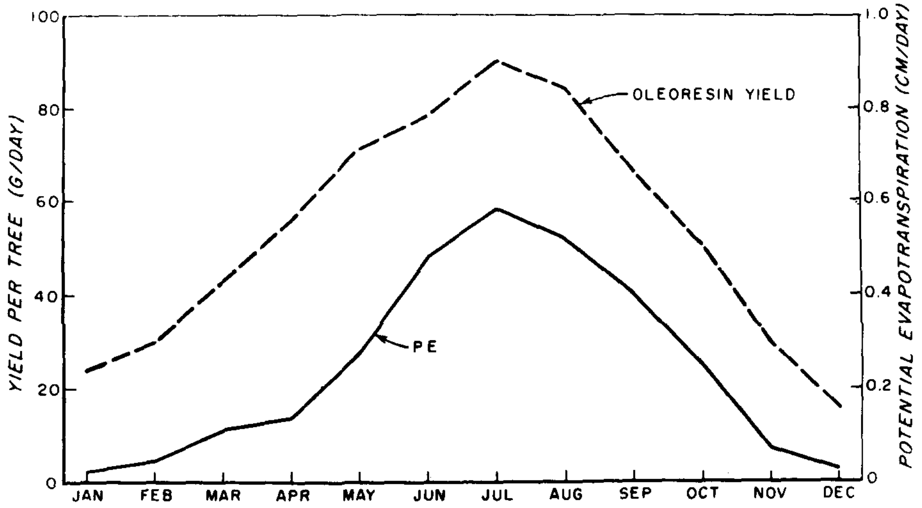

Fig. 2. Seasonal curves for potential evapotranspiration for Starke, Florida (solid line), and average gum yield for 70 longleaf pines (dashed line) the first day after chipping in 1928. Yield data from Harper and Wyman (1936). (After Moser and Dell, 1980.)

Lorio and Hodges (1971) reported greatly different growth patterns for loblolly pines on the slightly different microrelief, with trees on the intermound areas continuing fast diamater growth much longer in the spring than neighbors on mounds. Pines on intermound sites also demonstrated strong growth responses to intermittent rainfall in the mid to late summer, and tended to produce false rings within annual rings. The prolonged, accelerated growth on intermound sites, with little or no resin production, is synchronized with the spring surge of SPB activity (Thatcher, 1971; Billings and Kibbe, 1978).

Lightning is recognized universally as a most important factor in SPB ecology (Blanche et al., 1983), and some researchers believe that a fundamental relationship exists between epidemiology of the SPB and the occurrence of lightning (Coulson et al., 1983). However, available information in the literature strongly supports a relationship between lightning-damaged trees and SPB activity that varies with seasons of the year (Thatcher, 1971; Hodges and Pickard, 1971; Lorio and Bennett, 1974; Lorio and Yandle, 1978). For example, the data of Lorio and Yandle (1978) show that SPB infestations associated with lightning-struck trees over a 4-year period in southwest Louisiana followed a trend of low association in the winter and spring months and a very high level of association in the mid- to late-summer months.

Growth—differentiation relationships in southern pines indicate strong resin flow in summer months and relatively low flow in the fall, winter, and spring. Experience and literature on the subject support the expected relationships (Harper and Wyman, 1936; Barrett and Bengtson, 1964; R.A. Sommers, unpublished data), and indicate that lightning-struck trees should be most important in SPB ecology during the summer months when undamaged trees have high potential for resin flow. Conversely, lightning-struck trees should be of considerably less importance in the late fall, winter, and spring when ontogenetic changes in host trees enhance the potential success of SPB attacks.

Although the proposed general seasonal activity for the SPB in relation to growth and differentiation balances described in Table 1 appears reasonable, it should be recognized that this is a general scheme, and that much of the literature supporting it with regard to the SPB is limited in scope. Especially, one should expect considerable variation in host-tree responses and SPB activity in relation to latitude and altitude variations across the range of loblolly pine and other host species.

FUTURE RESEARCH NEEDS

Application of the growth—differentiation balance concept provides a most useful framework for planning future research on SPB—host interactions and beetle population dynamics. The concept furnishes a rationale for developing studies of ontogenetic changes that alter tree susceptibility to insect attack, an approach that Kozlowski (1969) suggested was especially needed. For example, studies of SPB—host interactions and population dynamics during the late fall, winter, and early spring are urgently needed to complement the intensive population dynamics research conducted primarily through the summer months in recent years (Coulson, 1980). Studies by Thatcher (1967, 1971), Thatcher and Pickard (1964, 1967), Franklin (1970), Hedden and Billings (1977), Moser and Dell (1979, 1980), and Billings and Kibbe (1978), provide abundant evidence of important behavioral and biological changes associated with seasons of the year that demand more intensive study.

Several important problems can be attacked effectively with an appreciation for growth and differentiation balance relationships. For example, Hodges and Lorio (1969) showed that loblolly pine inner bark underwent dramatic changes in carbohydrate and nitrogen fractions from April through October. How do such changes relate to SPB attack and brood development? What are the relationships through fall, winter, and spring? Studies can be designed to determine SPB—host relationships seasonally in the field, in controlled laboratory experiments, or in both.

Can it be demonstrated that loblolly pine oleoresin yield from small wounds does in fact increase when growth is curtailed by water deficit? A study by R.A. Sommers (unpublished) showed that oleoresin yield over 24 hours maximized when soil water deficit maximized. Study is in progress to quantify the relationships among stem radial growth, potential evapotranspiration, soil water balance, vertical and horizontal resin duct density and distribution, carbohydrate status of the inner bark, and oleoresin yield. Such basic information is required to develop meaningful studies of SPB—host interactions that will lead to improved population dynamics models.

Studies of microorganism—host interactions are especially suited to design with growth and differentiation balance relationships in mind. For example, the hypersensitive response (Berryman, 1972) is dependent on synthesis and/or deposition of oleoresin, which in turn would be greatly influenced by the growth status of the tree. In relation to such studies, Chou (1982) emphasizes the need to consider pre-inoculation conditions in planning inoculation trials, whether for pathogenicity tests or for any other purposes.

Lorio and Hodges (1985), in discussing theories of SPB, microorganism, and tree interactions point out that although something is known of seasonal changes in bark carbohydrates in loblolly pine, more studies are needed that span all seasons of the year. Such studies can be used effectively to clarify inner bark carbohydrate relationships with the relative success of SPB attack, responses of trees to fungal inoculation, and the quantity and quality of brood development. These studies alone offer significant challenges to researchers in several complementary disciplines.

SUMMARY AND CONCLUSIONS

Interrelationships between the SPB and its host pines are explained in terms of the growth—differentiation balance concept, and a general hypothesis is proposed that correlates pine growth and differentiation balance relationships with seasonal activity of the SPB. Experimentation and observations reported in the literature on the SPB are presented in support of the general hypothesis, and it is proposed that the growth—differentiation balance concept provides a useful framework for developing future research.

Based on growth and differentiation balance relationships in southern pines, the spring appears to be particularly favorable for SPB attack success because of the strong demand for available photosynthates by growth processes and the low potential for oleoresin synthesis and yield at that time. In the fall, decline in oleoresin synthesis and yield also favors beetle attack. Although the general population of trees should be quite susceptible to attack during the winter, environmental conditions may be unfavorable for beetle activity. In the summer, strong resin flow increases resistance to beetle attack.

Excessive crowding of trees that results in small crowns, slow growth, and limited synthesis and flow of oleoresin will produce conditions that favor success of bark beetle attack. Because the production of protective chemicals is reduced in parallel with wood growth, Waring (1983) suggests that growth efficiency (the ratio of stemwood production per unit of leaf area) may indicate the susceptibility of trees to native insects. However, Waring's growth efficiency cannot provide a basis for understanding why the general population of trees in a pine forest, including vigorously growing trees, will vary in their resistance to bark beetle attack in relation to ongoing physiological processes, as can application of the growth — differentiation balance concept.

The focus of this paper has been on the application of the growth—differentiation balance concept toward better understanding of the SPB and its interactions with southern pines. However, it would be unlikely if similar applications do not apply also to closely related bark beetle and tree species.

Finally, I propose that the growth—differentiation balance concept provides a basis for understanding SPB—tree interactions, a rationale for explaining commonly experienced problems in identifying consistent precursors to SPB outbreak, and a philosphical basis for future research — including other bark beetles and tree species.

ACKNOWLEDGEMENTS

Preliminary drafts of this paper were reviewed by numerous colleagues whom I truly thank for their constructive criticisms. Special thanks is extended to Dr. P.J. Kramer, Duke University, and Dr. R.S. Loomis, University of California, Davis. Drs. J.D. Hodges, Mississippi State University; R. Zahner, Clemson University; F.W. Whitmore, The Ohio State University, Division of Forestry; and D.P. Miles and W.D. Loomis, Oregon State University, gave generous assistance in discussions and correspondence.

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