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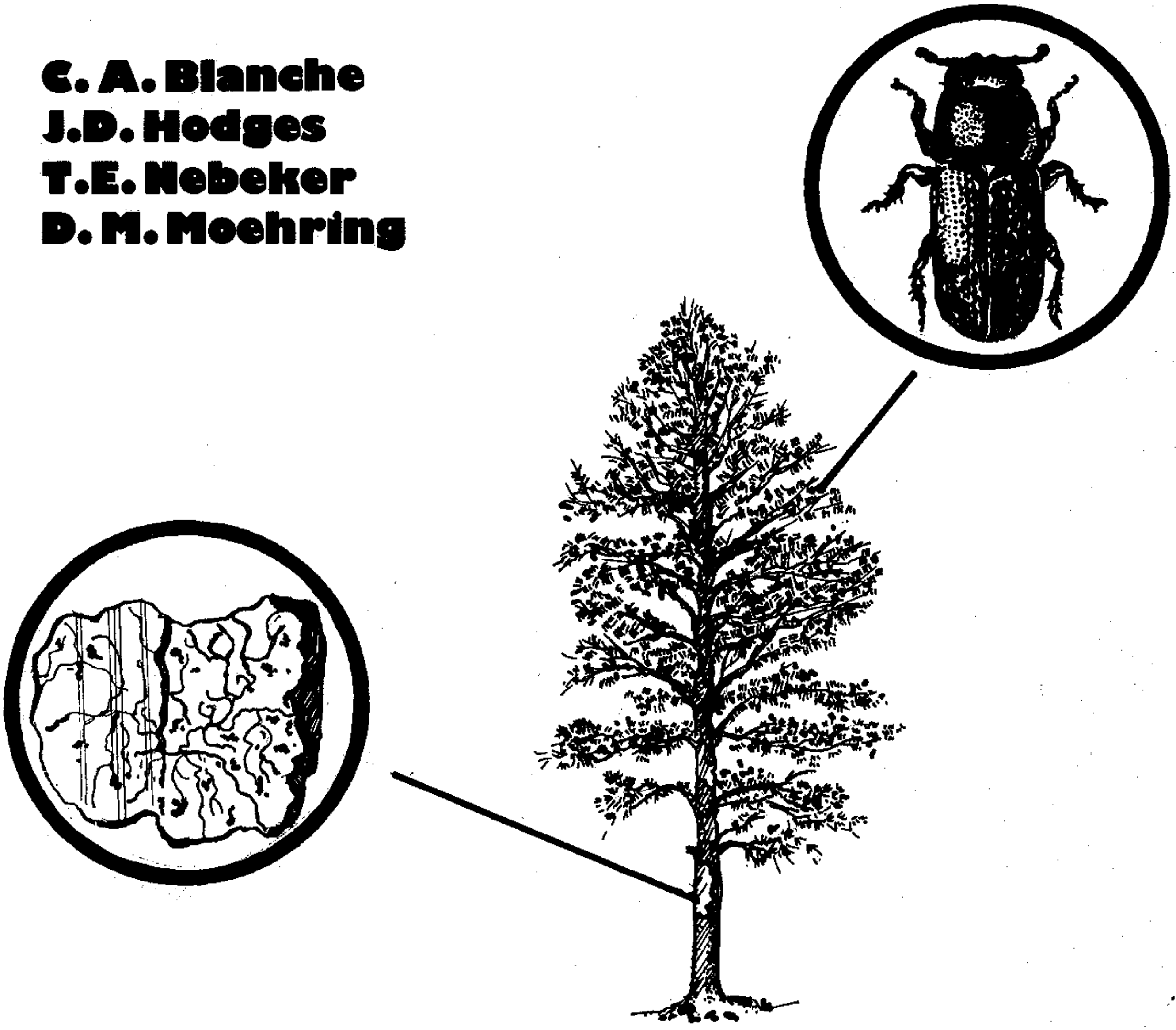
C. A. Blanche
J.D. Hodges
T.E. Nebeker
D. M. Moehring



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R. RODNEY FOIL, DIRECTOR MISSISSIPPI STATE, MS 39762

Mississippi State University
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SOUTHERN PINE BEETLE: THE HOST DIMENSION

C. A. Blanche, Research Associate,
Mississippi State University, Department of Forestry
J. D. Hodges, Professor and Forester,
Mississippi State University, Department of Forestry
T. E. Nebeker, Associate Professor,
Mississippi State University, Department of Entomology
D. M. Moehring (Deceased), Professor and Forester,
Mississippi State University, Department of Forestry

CONTENT

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SOUTHERN PINE BEETLE: THE HOST DIMENSION

INTRODUCTION

The southern pine beetle (SPB), *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae) is considered one of the most serious pests of southern pines. The first outbreak formally recorded in the southern United States occurred during 1882 in southeast Texas (Hopkins, 1903). Since then, infestations have recurred extensively, spreading to areas roughly coinciding with the geographic distribution of loblolly pine (*Pinus taeda* L.). A historic account of these outbreaks has been compiled by Price and Doggett (1978) for the southeastern United States.

Comprehensive reviews on this beetle were done by Thatcher (1960), Dixon and Osgood (1961) and Coulson et al (1972). An integrated presentation edited by Thatcher et al (1980) covered the life history and habits (Payne, 1980), natural enemies and associated organisms (Berisford, 1980), climatic, site and stand factors (Hicks, 1980), population dynamics (Coulson, 1980), sampling and predicting population trends (Hain, 1980), impacts of the SPB (Leuschner, 1980) rating of stands for susceptibility (Lorio, 1980), silvicultural guidelines for reducing losses (Belanger, 1980), direct control (Billings, 1980) and integrated management strategies (Coster, 1980). Intensive treatment of the host as it influences the SPB is non-existent, except for the initial efforts of McAndrews (1926) and Caird (1935). Hanover (1975) reviewed the physiology of tree resistance to insects with some emphasis on the mechanisms of resistance and host terpene physiology but with little reference to the SPB. This review is therefore aimed at consolidating scattered host-related information, particularly the physiological aspect, analyzing and synthesizing such information and identifying knowledge gaps with the ultimate objective of prioritizing research on the host-bark beetle relationship.

The review was done in a combined time sequence and topical organization approach. In other situations the approach was dictated by developmental logic.

In analyzing the literature we used the following terms as defined:

Susceptibility = degree of resistance of the host to insect colonization. We visualize resistance as a spectrum with one extreme described as susceptible and the other extreme as immune.

Suitability = host quality in relation to brood development and resultant brood quality.

Vigor = the overall state of the host as reflected in the different degrees of metabolic activities (synthetic and degradative processes). Radial growth is one example of a manifestation of the degree of synthetic processes.

Attractiveness = the quality of the host that draws the beetles to attack or go near.

HOSTS AND HOST CHARACTERISTICS

Hosts

The SPB can potentially attack and kill all pine species within its range (St. George and Beal, 1929; Dixon and Osgood, 1961). Payne (1980) suggested that loblolly pine is so highly preferred that the geographic distribution of the SPB is roughly approximated by the distribution of this pine species. However, in the three geographic regions of the South (Coastal Plain, Piedmont and Southern Appalachians), shortleaf pine (*P. echinata* Mill.) has been reported to be the most susceptible, while loblolly pine is the other most susceptible species in the Coastal Plain (Belanger and Malac, 1980). In Arkansas, shortleaf pine is the preferred host (Ku et al, 1980), probably because of its abundance. In the Georgia Piedmont, shortleaf pine is again the preferred host despite the fact that it is not the most abundant pine species in the area (Belanger et al, 1977). This latter preference for shortleaf pine has been attributed to the predisposing effect of littleleaf disease (Belanger et al, 1979). In the southern Appalachians, shortleaf and pitch (*P. rigida* Mill.) pines are the preferred hosts (Belanger and Malac, 1980; Belanger and Hatchell, 1981) with pitch pine considered more susceptible (Belanger et al, 1979). In another report, Kowal (1960) cited shortleaf, loblolly and Virginia (*P. virginiana* Mill.) pines as the preferred hosts, and slash (*P. elliotti* Engel.), longleaf (*P. palustris* Mill.) and spruce (*P. glabra* Walt.) pines as the less desirable hosts. Earlier, St. George and Beal (1929) reported loblolly and shortleaf pine to be much more susceptible than longleaf and slash pine.

The apparent preference for specific host species appears to be related to variation in oleoresin properties. In comparing the four major southern pines (loblolly, longleaf, slash and shortleaf), Hodges et al (1977, 1979) identified total resin flow as the most discriminating variable in classifying the least desirable (most resistant) host. Belanger et al (1979) observed that white pine (*P. strobus* L.) was the least preferred host in the southern Appalachians and this has been attributed to the ability of this species to "pitch out" the SPB.

To test if there was any preference for loblolly over shortleaf pine, Thomas et al (1981) assayed for biting responses of SPB to bark extracts of different polarities. Judging from the bioassay responses, there seems to be no preference for loblolly over shortleaf. However, when inner bark and outer bark extracts were separated, extracts from the outer bark of shortleaf pine elicited the greatest number of biting responses. In loblolly pine, White (1981) demonstrated, through a bioassay, that diethyl ether and methanol extracts of inner and outer bark influenced beetle tunneling. The positive and negative responses of SPB to the bark extractives were attributed to tree-to-tree variation in extractive concentrations. White viewed these positive and negative responses as indicative of responses to gustatory stimulants and deterrents.

Other coniferous species reported to be occasional hosts of SPB in the United States are table mountain pine (*P. pungens* Lamb.) (Knull, 1934), red spruce (*Picea rubens* Sarg.) (Payne, 1980), pond pine (*P. serotina* Michx.) (Payne, 1980) and ponderosa pine (*P. ponderosa* Dougl. ex Laws.) (Wood, 1963).

Table 1. Comparison of the four major southern pines.

Features	Longleaf Pine	Slash Pine	Shortleaf Pine	Loblolly Pine
Turpentine density[1/]	0.8618	0.8533	0.8452	0.8525
Turpentine index of refraction[1/]	1.4657	1.4631	1.4728	1.4700
Optical rotation of turpentine[1/]	+7.89°	-30.78°	+103.49°	+46.2°
% turpentine from oleoresin[1/]	22-23	22	16-20	14-19
d, dl α-pinene[1/] (%) (based on turpentine)	64	75	85	71
1- β-pinene[1/] (%) (based on turpentine)	31	21	11	22
Oleoresin viscosity[2/] (stokes)	60	306	24	18
Total flow (ml)[2/]	18	11	9	12
Rate of flow (ml/hr)[2/]	1.55	0.56	0.78	1.12
Flow at 8 hrs. (%)[2/]	66	38	67	77
Time to initial crystallization (hrs)[2/]	0.98	48	2.36	0.98
α-pinene (mg/100mg oleoresin)[3/]	21.18	16.44	14.30	16.56
Camphene (mg/100mg oleoresin)[3/]	0.18	0.22	0.18	0.20
Myrcene (mg/100mg oleoresin)[3/]	0.70	0.48	0.60	1.56
β-pinene (mg/100mg oleoresin)[3/]	5.23	4.22	12.06	8.58
Limonene (mg/100mg oleoresin)[3/]	0.49	0.25	0.93	1.68
β-phellandrene	0.22	2.86	0.90	1.04
Total monoterpene (mg/100mg oleoresin)[3/]	28.00	24.47	28.96	29.63
Pimaric acid (mg/100mg oleoresin)[3/]	3.79	3.76	3.77	5.11
S.C. Pimaric acid (mg/100mg oleoresin)[3/]	1.11	1.09	1.19	1.22
Palustric acid (mg/100mg)[3/]	12.21	15.10	8.40	12.18
Levopimaric acid (mg/100mg)[3/]	16.83	8.62	18.74	19.44
Isopimaric acid (mg/100mg)[3/]	10.98	17.40	10.05	7.15

(continued)

There are no reports to indicate that outbreaks have occurred in these occasional hosts.

SPB outbreaks in Central America have occurred in the following pine species as hosts: *P. oocarpa* Schiede (Coyne and Critchfield, 1974), *P. caribaea* Morelet (Coyne and Critchfield, 1974), *P. pringlei* Shaw (Hendricks, 1977 as cited by Payne, 1980) and *P. pseudostrobus teocate* Lindl. (Hendricks, 1977 as cited by Payne, 1980). The broad range of host species attests to the aggressive behavior of this species.

Host Characteristics: Comparison of the Four Major Southern Pines

Motivated by our desire to explore the possibilities of identifying relevant host characteristics for breeding and rating resistance of individual trees and stands to SPB attack, we have tabulated species characteristics of the four major southern pines (Table 1). We premised our characterization on the recognition that slash and longleaf pine are more resistant, and shortleaf and loblolly pine are more susceptible to SPB attack. A cursory look at the table provides no significantly consistent feature for the four species, except for oleoresin viscosity, which stands out as a possible distinguishing characteristic for resistance.

What Constitutes Host Resistance to SPB?

The preference for a particular host is a valid manifestation of resistance. When a particular host species is preferred at one location and not in another it indicates that induced resistance or pseudoresistance exists. Our discussion of resistance of southern pines to SPB does not distinguish between induced resistance and inherited resistance. Suffice it to say that host resistance to SPB exists.

Table 1. (continued)

Features	Longleaf Pine	Slash Pine	Shortleaf Pine	Loblolly Pine
Abietic acid (mg/100mg)[3/]	8.08	8.57	7.95	8.63
Dehydroabietic (mg/100mg)[3/]	3.76	2.67	4.20	3.82
Neoabietic acid (mg/100mg)[3/]	11.61	13.75	10.85	9.49
Total resin acids (mg/100mg oleoresin)[3/]	68.37	70.96	65.15	67.04
Radial resin duct width (u)[4/]	57.6	54.8	49.0	54.6
No. of resin ducts[4/]	32.6	43.9	35.5	35.3
Oleoresin viscosity (stokes)[4/]	55.7	241.0	20.9	16.2
Resin flow rate (ml/hr)[4/]	1.1	0.6	0.8	1.5
Most critical disease[5/]	brown spot	fusiform rust	littleleaf disease	fusiform rust

[1/] Mirov, 1961.

[2/] Hodges et al., 1977.

[3/] Hodges et al., 1979.

[4/] Hodges et al., 1981.

[5/] Dorman, 1976.

HOST RESISTANCE/ SUSCEPTIBILITY TO SPB

Any effective investigation of host resistance to insect pests must recognize the components of resistance. The resistance components according to Painter (1951) are *preference* or *non-preference, tolerance* and *antibiosis.* Indications from the literature show tolerance to play no important role in host resistance to SPB. The preference or non-preference component appears likely. Field observations of host preferences, the attractiveness of loblolly and shortleaf pine over longleaf and slash pine and the result of the biting response bioassay of Thomas et al (1981) tend to support this general cause of host resistance to SPB. Although tree-killing bark beetles apparently use both random and directed host selection (Wood, 1982), decisive studies leading to the identification of the basis for host selection are lacking (Cates and Alexander, 1982). For as long as the question of host selection remains unresolved, our understanding of host resistance to SPB will continue to

be shaky. The antibiosis component appears to play some role. Toxicity tests of substances in pine oleoresin demonstrated that several monoterpenes are toxic to SPB in the following order (Coyne and Lott, 1976):
limonene > α-pinene > β-pinene > myrcene > Δ-3-carene.

**Smith (1966), used pure terpenes in administering vapor toxity tests to other *Dendroctonus* spp. and obtained the following rating:
limonene > Δ-3-carene > myrcene > β-pinene $\neq$ α-pinene. There seems to be no doubt about the antibiotic and repellent properties of oleoresin (Callaham, 1966; Bordasch and Berryman, 1977).**

What then constitutes host resistance to SPB? Our current knowledge does not permit us to provide a definitive answer to this question. However, we know that the oleoresin system in pines is the primary defense mechanism against attack by bark beetles (Rudinsky 1966b; Reid et al, 1967; Anderson and Anderson, 1968; Berryman, 1972; Smith, 1975; Hodges et al, 1979). We also know that we can classify southern pines as to their resistance or susceptibility to SPB using physical properties of oleoresin such as total flow, flow rate, viscosity and time to initial crystallization (Hodges et al, 1979). Also, low OEP is consistently associated with successful SPB attack (Lorio and Hodges, 1968, 1977). At the gross structural level, we can identify trees that are susceptible to SPB by using radial growth as an indicator of vigor (Bennett, 1971; Hicks et al, 1978).

How the host resin system serves as a resistance mechanism to SPB is the more important but more difficult question to resolve. Establishing the threshold levels of the resistance factors is contingent upon the resolution of the above question. In general, however, the defense mechanism of a plant does not depend on any one structure, product or function, but on a combination of several (Roth, 1970). While the physical properties of pine oleoresin are strongly related to resistance to SPB (Hodges et al, 1977, 1979), the chemical constituents, particularly the volatile moieties of oleoresin, play some role too (Coyne, 1973; Hodges and Lorio, 1975; Coyne and Lott, 1976). In lodgepole pine (*P. contorta* var. *latifolia* Engelm.) and grand fir (*Abies grandis* Lindl.), resin deposition around each attack (hypersensitive or wound response) by mountain pine beetle (*D. ponderosae* Hopkins) serves as a mechanism of host resistance (Reid et al, 1967; Berryman, 1972; Shrimpton and Reid, 1973). In ponderosa pine, the toxic properties of the different terpenes to *Dendroctonus* spp. predominate as a mechanism of host resistance (Smith, 1963). Smith's conclusion may be open to question because bark beetles are co-adapted to survive in the resins of their hosts. Therefore, resin components cannot be very toxic (Berryman, Person. Comm.). Further investigation revealed that chemical and physical properties of ponderosa pine oleoresin have a direct effect on resistance to western pine beetle (*D. brevicomis* LeConte) in that, the greater the oleoresin flow and the higher the limonene content, the greater the resistance to beetle attack (Smith, 1975). In loblolly pine, Hodges et al (1979) demonstrated that the physical properties of oleoresin have a direct effect on host resistance to SPB. Although they were not able to demonstrate conclusively a direct effect of chemical composition on resistance, the possibility that high-limonene-content trees within a species are more resistant to the SPB cannot be ignored. For instance, in their induced attack studies, resistant trees contained slightly more limonene than susceptible trees (2.4% vs. 1.0%) (Hodges et al, 1979). However, limonene content as a basis for resistance assessment should be restricted to trees within a species, because loblolly pine, a susceptible species to SPB, has a higher limonene content (see Table 1) than slash pine, a relatively resistant species.

In looking at the differences in susceptibility or resistance to SPB attack, the beetle should be taken into account. First, they change in quality from generation to generation and even from season to season. Second, the level of beetle activity in a given area determines whether a host tree succumbs to attack or not. For instance, trees classified as susceptible could be overcome when attacks were less than 100 attacks/sq m of bark (Hodges et al, 1979). At higher density levels, all southern pines, regardless of species, can be successfully attacked and killed; and under such conditions, the location of the tree with respect to the beetle population is the thing that matters (Hodges et al, 1977). Under a mass attack situation, overcoming host resistance is rendered possible by a marked decline of OEP, total flow and flow rate above and below the infested zone and within the zone (Hodges et al, 1979).

Hypersensitive response as a basis for host resistance to SPB is currently being investigated in loblolly and shortleaf pines at N. C. State University, the University of Arkansas and Mississippi State University under the auspices of the IPM Bark Beetle Program.

Criteria for Assessment

The establishment of criteria for assessing host resistance or susceptibility may be different if one wishes to accomplish different objectives. For instance, Rudinsky (1961) and Vite and Wood (1961) utilized OEP to evaluate resistance of western conifers to bark beetle attack. Although, Lorio and Hodges (1968) have pointed out the role of OEP in physically resisting SPB attack, they did not determine the critical level of OEP at which SPB can become established. They suggested, however, that to satisfactorily assess physical resistance, a series of daily measurements of OEP should be taken. Also, pressures are greater at the base of the stem than at mid- and upper bole (Vité, 1961). Grosmann (1967) suggested that, for bark beetles to breed successfully in a tree, the OEP must be reduced to 60 psi and must be further reduced to 35 psi for bluestain fungi to thrive.

Oleoresin exudation rate (OER) should be a very desirable criterion for assessing resistance to SPB since this can be easily measured. A definite relationship between OER and the incidence and success of *Ips* attacks exists (Anderson and Anderson, 1968). No attacks succeed when OER exceeds 0.1 ml/hr. According to Lorio and Hodges (1977), when the resin flow measurements of unsuccessfully and successfully SPB-attacked loblolly pines are translated to OER values, two unsuccessfully attacked trees had OER values of 0.35 ml/hr and 0.23 ml/hr, while a successfully attacked tree had 0.07 ml/hr. It seems that the critical OER value for successful SPB attack to occur is below 0.1 ml/hr.

Total resin flow is another measureable criterion for assessment of resistance. Oleoresin flow is the most important variable for distinguishing SPB-resistant loblolly and shortleaf pines from the susceptible ones (Hodges et al, 1979). More than 90% of the variation in total flow is explained by the variation in OER (Hodges et al, 1977). Successfully attacked host trees had a total resin flow of 1.6 ml/24 hrs (Hodges et al, 1979). If our estimated OER value of 0.1 ml/hr is translated into flow, the critical resin flow then would be 2.4 ml for a 24 hour period, a value which is greater than the observed value (1.6 ml/24 hrs) of successfully attacked loblolly pine.

The use of plant water potential (plant moisture stress) is an indirect method for evaluating resistance or susceptibility of the host to SPB. Its utility is hampered by the relative difficulty of determination and the absence of critical values. In white fir, the moisture stress threshold of susceptibility to the fir engraver beetle appears to be about -20 bars (Ferrell, 1978).

The role of monoterpenes in southern pine resistance or susceptibility to SPB attack has not been quantitatively determined. A conclusive demonstration of direct involvement of limonene content with resistance to SPB must first be carried out before attempting to use it as a criterion.

Evaluating host vigor as indicated by gross structural features is simple and practical. In selecting declining loblolly pines for their experiments, Hodges and Lorio (1973) utilized morphological features such as short and yellowish needles, small cones and sparse crowns. Trees attacked by SPB were generally of poor vigor as indicated by smaller size, smaller crown, thinner bark and slower growth relative to healthy ones (Ku et al, 1976, 1980). Hicks et al, (1978) have effectively utilized periodic growth (last 10-year radial growth) as an indicator of vigor of loblolly pine. One drawback of this 10-year growth vigor indicator is that it does not represent the current condition. Since growth varies with site, age, soil moisture, density and other factors, a standardized method is difficult to develop. Stand vigor, expressed as basal area growth for the current year over sapwood basal area, plotted against beetle attack density is believed to provide a good measure of resistance of lodgepole pine stands to mountain pine beetle attack (Waring and Pitman, 1980).

Other means of assessing resistance may be warranted as we acquire more refined knowledge on this subject. The practical value of such methods will be contingent upon their costs and technical limitations. Regardless of the feasibility of use, the establishment of criteria for assessing host resistance or susceptibility is of long-term value in minimizing losses from the SPB.

HOST PHYSIOLOGY AND CONDITIONS UNDER STRESS

Under Deficient Moisture

Water stress influences the overall physiology of plants. In general, stress depresses physiological processes, but in some processes, such as those where differentiation is involved, they may be enhanced. Trees that greatly deviate from their normal physiology are highly vulnerable to pests and diseases. A broad overview of host physiology in relation to forest pests has been presented by Kozlowski (1969).

Water Stress and Host Attractiveness to SPB

Craighead (1925) must have been the first to associate rainfall deficiency with SPB outbreaks. He pointed out that late summer and fall deficiencies seemed to be more important in epidemic development than deficiencies in other seasons. A parallel observation has been shown with hickory bark beetle (*Scolytus quadrispinosus* Say) (Blackman, 1924). Rainfall deficiency was considered beneficial to hickory bark beetle adults and larvae while an excess checked the beetle's aggressiveness. In 1929, St. George also found that rainfall deficiency was correlated with SPB outbreaks. Probability of infestations appeared to increase with drought duration (St. George, 1930; Merkel, 1956). Knull (1934) associated SPB infestations in Pennsylvania with exceedingly high temperatures and drought conditions accompanied by mild winters. He suggested that such environmental conditions "lowered the vitality of many thrifty trees and actually reduced them to an over-ripe situation." Subsequent reports (Chapman, 1942; Hetrick, 1949b; and Merkel, 1956) further strengthened previous observations on the relationship between drought and bark beetle activity.

The decade of 1960 was a turning point in "host water relations-bark beetle activity" investigations. Thatcher (1960), in his review, emphasized the need for greater knowledge on host physiology especially the relationship of water status to SPB activity and brood development. Although Vité's (1961) work was on ponderosa pine, his finding that bark beetle success was correlated with low oleoresin exudation pressure (OEP) and that change in OEP was directly related to water stress caused others to wonder about similar phenomena in southern pines. It is interesting to note that response flights of SPB to attractants are highest between 1400 and 1800 h (Vité et al, 1964). This period coincides with the time of daily minimum OEP levels in loblolly pine (Lorio and Hodges, 1968b). Such low OEP coupled with the higher bark temperature has been thought to promote higher volatilization and diffusion of the attractant and cause beetles to aggregate in larger numbers (Gaumer and Gara, 1967). The increased daily flight activity of SPB around 1700 h during the summer has also been noted by Coster et al (1977).

When one considers tree susceptibility to attack by bark beetles, the intensity and duration of water stress must be taken into account (Lorio and Hodges, 1968). Despite the observations of different levels of bark beetle activity in various stands and areas, such differences are not readily attributable to differences in the hereditary insect-resistance of the host trees but are due mainly to differences in environmental conditions which alter the water balance of the trees (Schwenke, 1966). Lorio and Hodges (1977) demonstrated that water-stressed trees can be overcome by SPB more easily than unstressed ones. Investigations of the microrelief and associated soil characteristics in relation to soil water regime and diameter growth response of loblolly pines indicated that flat sites in the lower Gulf Coastal Plain (Louisiana) affected tree rooting characteristics and eventually tree susceptibility to SPB attack (Lorio and Hodges, 1971). The development of deficient root systems and intermittent severe moisture stress on flat sites contribute to premature tree decline (Lorio et al, 1972).

Increase in monoterpene hydrocarbons as a result of water stress is believed to increase the interaction of host chemicals with beetle-produced compounds to produce strong secondary attractants (Hodges and Lorio, 1975). The attractiveness of moisture-stressed trees is further enhanced on some sites by the loss of secondary root systems to rootlet pathogens. On the other hand, physiological observations on loblolly and shortleaf pine attacked and unattacked by SPB indicated no preference by the beetle for highly stressed trees (Brown and Michael, 1978). However, there seemed to be a preference for trees with milder xylem water potential. These observations tend to conflict with those of Lorio and Hodges (1977). Also, Brown and Michael (1978) showed that girdled and ungirdled trees exhibited the same daily patterns of xylem water potential for almost a year, but their results did not support the popular belief that the SPB kills its host by the girdling action during the gallery excavation period.

Oleoresin Exudation Pressure and Oleoresin Exudation Flow

Many of the earlier studies of oleoresin of southern pines were directed at gum yield improvement (Mergen, 1953; Schopmeyer et al, 1954; Mergen and Echols, 1955; Mergen et al, 1955; Schopmeyer and Larson, 1955; Bourdeau and Schopmeyer, 1958; Barrett and Bengston, 1964). Many of their findings, however, are relevant in the discussion of host oleoresin characteristics in relation to the SPB. For instance, OEP in slash pine was highest during high humidity and relatively low temperature and lowest when RH was low and temperature was high (Bourdeau and Schopmeyer, 1958). The activity of the SPB may relate to these changes in OEP.

The diurnal variations of OEP in slash pine, being high in the early morning and low in the afternoon (Bourdeau and Schopmeyer, 1958), are consistent with the findings of Barrett and Bengston (1964) on the same species, of Vité (1961) on ponderosa pine and of Lorio and Hodges (1968) on loblolly pine. Minimum daily OEP occurs in mid- to late afternoon when relative humidity is lowest and air temperature is highest. Phloem tissue temperature is also highest at this time (Gaumer and Gara, 1967). This period of minimum OEP coincides with the period of maximum flight response of SPB to chemical attractants (Vité et al, 1964).

Besides air temperature and atmospheric RH, soil moisture also affects OEP (Lorio and Hodges 1968). Under severe soil and atmospheric moisture stress, OEP was reduced more in loblolly pine trees on flat sites (50% loss of the daily average OEP) than in trees on low mounds (25% loss of the daily average OEP) (Lorio and Hodges, 1968b). Although soil moisture stress is related to microrelief, the contribution of a deficient fine-root system on flat sites to OEP reduction is significant (Lorio and Hodges, 1968b). Bourdeau and Schopmeyer (1958) indicated that under conditions of high temperatures, low humidities and direct sunshine, rapidly transpiring trees are likely to develop moisture stress even if soil moisture is adequate. Also, Barrett and Bengston (1964) reported that vapor pressure gradient accounted for 83% of the variation in OEP. Vapor pressure gradient exerts its effect on the water status of the tree, which in turn influences the OEP. Unfortunately, tree water potential could account for only 67% of the variation in OEP in loblolly pine (Hodges and Lorio, 1971).

Oleoresin exudation flow (OEF) may be a valuable property of oleoresin in the study of tree resistance to bark beetles (Mason, 1971). Lorio and Hodges (1977) demonstrated that reduced OEF is associated with successful attacks by the SPB. Their data showed a flow of 8.4 ml and 5.6 ml for unsuccessful attacks and 1.6 ml for successful initial attack. Mean OEF rate in loblolly pine is reduced more by overstocking in the stand than by temporary moisture stress (Mason, 1971), suggesting that other significant factors influence OEF rates. According to Mirov (1945) the role of the crown in oleoresin production is more involved than just producing a supply of sugars. Some growth substances are also produced in the crown.

A number of factors influence OEF. OEF may be expressed as (Schopmeyer et al, 1954)

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

where,

Y = yield of oleoresin over a fixed period of time
K = a constant
N = the no. of radial resin ducts per unit area of wound surface
a and b = the major and minor semi-axes of the duct cross section
P = OEP at the point of discharge
η = oleoresin viscosity.

Obviously, OEF is directly proportional to the number and size of resin ducts and OEP and inversely related to oleoresin viscosity. This relationship holds for slash pine (Schopmeyer et al, 1954; Bourdeau and Schopmeyer, 1958). However, doubts have been cast on this expression after Barrett and Bengston (1964) found no correlation between OEP and oleoresin yield in slash pine. Also, Hodges and Lorio (1971) found no correlation between OEF and OEP (r = .03) and that OEF was poorly correlated with water potential (r = .27) in loblolly pine. In addition, oleoresin flow was not correlated with resin duct size and number in shortleaf, loblolly and longleaf pines (Hodges et al, 1981). Thus, the expression developed by Schopmeyer et al, (1954) has very little utility in describing resin flow or yield in southern pines.

Within species, total resin flow is highly correlated (r = .90) with OEF rate (Hodges et al, 1977). OEF appears to be influenced more by oleoresin supply which is influenced more by crown size and competition (Mason, 1971) than by current soil moisture conditions (Lorio and Hodges, 1974). Slash and longleaf pines with large crowns have the highest gum yields (Schopmeyer and Larson, 1955). Mason (1971) reported that OEF responded to rainfall recharge only when about 50% of the available soil moisture had been depleted. Furthermore, mean OEF did not continue to decrease with increasing soil moisture stress, but a minimum level remained unchanged despite current moisture stress. Finally, Mason found that changes in soil moisture availability accounted for 34% of the summer variation in mean OEF. Despite the relatively minimal effect of moisture stress on OEF, its effect is principally directed at curtailment of oleoresin flow duration, which leads to favorable oviposition and rapid larval development (Lorio and Hodges, 1977).

Water Stress and Bark Moisture Content

Since a greater part of the life cycle of the SPB is spent in the bark, a substantial influence is exerted by the host on beetle development. Changes in the environment affect changes in the bark too. Phloem moisture content, for instance, decreases very rapidly as xylem water potential decreases (Wagner et al, 1979). The relative water content of inner bark has been shown to reflect soil moisture status as well as diameter growth response (Lorio and Hodges, 1968). Water potential in loblolly pine correlates nicely with the relative water content of the inner bark (Hodges and Lorio, 1971). Likewise, OEP is highly correlated with relative water content. On a diurnal basis, the minimum phloem moisture content occurs in late afternoon (Gaumer and Gara, 1967), paralleling the daily pattern of OEP (Lorio and Hodges, 1968b). Measurements of relative water content of inner bark can be utilized in the assessment of moisture stress in trees, since relative water content of the bark reflects moisture stress in trees regardless of whether stress was due to flooding or drought (Hodges and Lorio, 1969).

When loblolly pine stems are either infested by SPB or severed, the phloem rapidly dries, with the infested tree drying more rapidly (Gaumer and Gara, 1967). Wagner et al (1979) found that phloem moisture content decreases rapidly a few days after SPB attack. Following this dehydration process, the phloem becomes more moist during the late larval and pupal stages (Caird, 1935; Wagner et al, 1979). The rapid dehydration of the phloem and xylem has been attributed to the action of bluestain fungi (Caird, 1935; Bramble and Holst, 1940). The dehydration process cannot be easily explained and needs further investigation.

Water Stress, Vigor and Growth

The effect of water stress is readily translated to growth and eventually to the overall vigor of the tree. Bennett (1968, 1971) suggested that poor tree vigor, expressed as reduced radial growth, was consistently associated with SPB infestations. Hicks et al (1978) used the most recent five year radial growth of loblolly pine as a measure of tree vigor. Reduced radial growth rate has been correlated with SPB activity in the West Gulf Coastal Plain (Kushmaul et al, 1979). In a major southwide research effort, mean radial growth rate was shown to be one of the two most apparent factors related to SPB activity (Coster and Searcy, 1981).

Since about 80 to 90% of the variation in tree growth is attributed to water stress (Zahner, 1968), this should be a major predisposing factor affecting southern pine susceptibility to SPB attack. Moehring and Ralston (1967) pointed out that rates of change in moisture supply as well as moisture content are related to loblolly pine diameter growth. Bassett (1966) observed the same relationship. He further observed that diameter growth is also affected by the size and position of the crown. Dominant and codominant trees grew longer and faster in lightly stocked than in heavily stocked stands. The severity of water stress is reliably reflected through the differences in the cross sectional growth of loblolly pines exposed to flooding and drought, with the drought trees exhibiting the slowest growth (Lorio and Hodges, 1968). Moreover, chlorosis and needlefall proceed more rapidly on water stressed than on flooded trees. Besides diameter growth, water stress also decreases height growth. Height growth of loblolly and shortleaf pine seedlings is inhibited by matric potentials of -2 bars, stops completely at -3.5 bars and begins to wilt near -5 bars (Stransky and Wilson, 1964). These values are indicative only of the pattern of response and cannot be directly extrapolated to mature trees. The effect of water stress on tree growth is via the reduction in cambial cell division (Zahner, 1968). Hodges and Lorio (1969) demonstrated that loblolly pine subjected to drought produced only about half as many cells as control trees. Measurement of the amount of latewood cells showed that these made up 52% of the ring within control trees, 39% in flooded trees and 32% in sheltered trees.

Regression analysis of climatic data and SPB activity in east Texas indicated that the effect of water deficit upon the intensity of SPB activity was less significant than potential evapotranspiration and moisture surplus (Kalkstein, 1976, 1981). Earlier, Lorio and Hodges (1968) found that flooding effected more drastic reduction in OEP than drought did. These observations seem to indicate that growth alone does not completely reflect the true vigor of the tree. It is not surprising then to see certain trees under water stress that may not be attractive to the SPB.

The vigor of a tree is substantially conditioned by the environment. Chararas (1959) reported that the optimum osmotic pressure (OP) is closely related to the vitality of the tree and therefore to climatic, soil and silvicultural conditions. He claimed that trees with low vitality and low OP in the bark are often attacked. However, such primary pests as *I. sexdentatus* Born. on *P. pinaster* Ait. and I. *typographus* L. on *Picea abies (L.)* Karst., attack trees whose OP approaches the optimum. Also, the OP in the zone of attack is more important than the general vitality of the tree. Finally, Chararas (1959) stated that resin flow is closely related to tree vitality and responds to wounding associated with beetle attack.

Water Stress and Host Chemistry

Changes in plant metabolism caused by water stress are, in one way or another, accompanied by qualitative and quantitative changes in the chemistry of the plant. Knowledge of the chemistry of the SPB hosts as affected by water stress is very limited. Generalizations from other plants may apply to southern pines, but explicit demonstration of their validities must be a major future research consideration.

It is generally believed that there are two phases of protein response to water stress (Stocker, 1960). These are an initial decline in protein and a restitution phase with prolonged stress. Hodges and Lorio (1969), analyzing bark of 40-year-old loblolly pines subjected to drought, suggested that protein synthesis was initially depressed and then later the trend was reversed. The same study revealed that drought did not have any effect on amino N accumulation. Whether changes in the nitrogenous components of the bark have something to do with host preference or bark beetle development is unknown. We do know, however, that at least 10 essential amino acids are necessary for insect growth and development (Dadd, 1970, 1973; Hagen, 1974). Also, high nitrogen content favors greater fungal activity, particularly wood-rotting fungi (Merrill and Cowling, 1966).

The effects of water stress on plant carbohydrates are fairly well established. Iljin (1929) demonstrated that plants are much richer in saccharides when located in dry places than in more humid locations. Magness et al (1933) found the total sugar of irrigated apple trees to be lower than the corresponding dry trees based on bark, wood and fruit samples. And of the total sugar in dry trees, 80 to 90% is in the free reducing form. Using labeled carbon in his sugar analyses of yellow poplar sap, Roberts (1963) found that increased water stress causes translocation of glucose and fructose as individual hexose sugars, not as hydrolytic products of sucrose. Drought conditions basically lead to an increase in the sugar content of the cell sap (Schwenke, 1966). The finding of Hodges and Lorio (1969) for loblolly pine bark was no exception. Moisture stress caused an increase in reducing sugars, non-reducing sugars and total carbohydrates, and a decline in starch. Increased respiration resulting from severe moisture stress (Schneider and Childers, 1941; Stocker, 1960; Brix, 1962) may prevent the polymerization of sugar monomers. Related to these chemical changes were the observations of Chararas et al (1960) on the cellular and extra-cellular liquid of bark samples from sound and unhealthy trees of Norway spruce (*Picea abies* (L.) Karst.) and Scotch pine (*P. sylvestris* L.). They noticed that changes in OP were accompanied by changes in dry matter, sugars and water soluble organic acids. Free organic acids, such as malic, citric, quinic, shikimic and formic acids, were lower in the bark-beetle-attacked trees than in the healthy trees (0.6 ml/100 ml bark liquid vs. 9.01 ml/100 ml, respectively). These changes are associated more with the physiological condition of the tree than with the species.

Moisture stress caused an increase in the ratio of monoterpene to resin acids in loblolly pine xylem oleoresin (Lorio and Hodges 1974; Hodges and Lorio 1975). With time, all the resin acids decreased in moisture-stressed trees, with levopimaric and palustric acid accounting for most of the decline, while, in the control trees, all the resin acids increased. The bulk of the increase in monoterpene hydrocarbons in water-stressed trees was due to α - and β -pinene. These changes in monoterpene hydrocarbons and resin acids were further intensified by the physiological condition (healthy vs. declining) of the trees (Hodges and Lorio, 1975). Further examination of the test trees revealed that the greatest changes in these two oleoresin components were found in trees whose root systems had been infected with rootlet pathogens.

Water Stress in Relation to Stand Density and Thinning

High stand density has been consistently associated with SPB infestations (Bennett, 1968, 1971; Lorio and Bennett, 1974; Hicks et al, 1978; Belanger et al, 1979, Belanger, 1980; Coster and Searcy, 1981). The same stand condition has been found to be associated with high hazard for the fir engraver, *S. ventralis* Lec. (Schenk et al, 1977) and mountain pine beetle, *D. ponderosae* Hopkins (Sartwell and Stevens, 1975; Mahoney, 1978). Bennett (1971) suggested that overstocking causes reduced vigor of trees and therefore predisposes them to SPB attack. Coulson et al (1974) substantiated Bennett's suggestion, and Hicks et al (1978) further confirmed it. In fact, Hicks et al (1978) suggested that a cause and effect relationship may exist between stand density and tree vigor. Some competition indices incorporating basal area and distance (Hegyi, 1974; Daniels, 1976) tend to support a cause-and-effect relationship between stand density and tree vigor. Hedden and Billings (1979) obtained a positive correlation between spot growth (trees killed/day) on the one hand, and the number of active trees in the infestation and the stand basal area on the other. Generalizing from the results of his thinning and beetle introduction experiments, Nebeker (1981) reported that stand density plays a role in the success or failure of an attacking SPB population. Recognizing this close association between high density and SPB infestations, Belanger (1980) recommended thinning from below to 80 ft^2/acre basal area as a silvicultural strategy for reducing possible losses to SPB. Hicks et al (1979) recommended that the same strategy be carried out in early fall or winter and at times when beetle activity is low. The complication of annosus root rot in thinning during the recommended times should be given careful consideration. Too, the findings that summer thinning of loblolly pine plantations attracts large numbers of *I. avulsus* and *I. grandicollis* into logging slash (Mason, 1969) should not be overlooked. To develop an effective thinning recommendation for specific stand conditions and management objectives, a knowledge of the direct effect and scientific basis of thinning is necessary. The thinning study of Nebeker (1981) partly demonstrates the direct and indirect effect of stand density on an attacking SPB population.

The water relations of a stand are influenced by thinning. In Arkansas, the diameter growth (on an individual tree basis) doubled during the first year after thinning. The thinning treatment reduced the depletion of the soil moisture supply (Anonymous, 1955). Douglas (1960), in determining the available soil moisture in a thinned 16-year-old loblolly pine stand, found that soil moisture in the upper 4 feet was greater between trees than under trees. In unthinned stands, the soil moisture remained relatively constant between trees. Rates of soil moisture depletion are considerably reduced in thinned shortleaf pine stands. This slowdown in water use prolongs available soil moisture for extended seasonal growth (McClurkin, 1961). The same pattern has been observed in thinned pine plantations in other places. For instance, a thinned 39-year-old red pine (*P. resinosa* Ait.) plantation in lower Michigan exhibited increased diameter growth, and the initial supply of moisture was available for a longer period of time (Della-Bianca and Dils, 1960). In the West, Helvey (1975) reported that heavy thinning of a 50-year old ponderosa pine stand resulted in a radical reduction in soil moisture depletion, but growth was greatest in stands thinned to a 15-foot spacing (moderate thinning). In New Zealand, dense stands of Monterey pine (*P. radiata* D. Don) exhausted available soil moisture as early as November, and diameter growth stopped. Moisture was available in heavily thinned stands, and diameter growth continued until the following March or April (Butcher and Havel, 1976). In the same investigation, Butcher and Havel (1976) claimed that moisture limitations manifest themselves first in depression of diameter growth, second in predisposition to attack by *I. grandicollis*, and third in direct drought deaths.

It has been claimed that the immediate effect of thinning is to increase light levels in the bottom one third of the crown, providing a wider zone of high photosynthetic surface and increased production by older needles (Woodman, 1976). His light measurements at different heights along the crown showed that only 2% of full sunlight reached the needles on the bottom branches of 37-year old unthinned Douglas fir (*Pseudotsuga menziesii* (Mirb. Franco) trees. A correlation analysis indicated that almost all photosynthetic variations on the bottom one third of the crown were accounted for by radiation. However, other microclimatic factors, such as ambient air temperatures, vapor pressures and ambient CO_2 concentrations, play more significant roles in the upper crown. The paper further asserted that the secondary effect of thinning is to increase transpiration rates and nutrient uptake. This increase in transpiration rate is on an individual tree basis and should be compensated for by fewer numbers of trees utilizing the water supply.

Mason (1971) reported that the average OEF was 40% greater in loblolly pines in thinned plots than in trees in unthinned plantations. This should not be construed as a direct effect of thinning in enhancing OEF but rather the effect of eliminating individuals with low OEF. Overstocking in the stand was found to reduce OEF rates more than temporary moisture stress did (Mason, 1971). This is not surprising since flow rate is more a function of oleoresin reservoir (Hodges et al, 1977). And Schopmeyer and Larson (1955) have shown that oleoresin production is influenced by dbh, crown size, and position of trees in slash pine stands.

Under Excessive Moisture

Effects of Excessive Moisture on the SPB

Too much moisture could be beneficial or detrimental to the SPB depending on its stage of development. Craighead (1925) observed that heavy precipitation, while the young broods were developing under the bark, caused high mortality. He also noted that heavy precipitation effectively killed the beetles during periods of attack. He then concluded that excessive precipitation is one of the causes of rapid decline of SPB epidemics. Beal (1927), corroborating Craighead's observations, found heavy brood mortality of SPB in 1926-27 in Asheville, NC to be due to excessive rain in the fall of 1926 and high temperatures in January. On the other hand, regression analysis revealed that excessive moisture appeared to favor the reproduction and rapid development of SPB broods as expressed by the regression coefficients of the two moisture variables used (Kalkstein, 1976). Integrating excessive rainfall with season, Kroll and Reeves (1978) showed that periods of high summer rainfall were correlated with increased numbers of spots, while high spring and fall rainfall were correlated with reduced beetle activity. (More on this under host conditions in relation to brood development.)

Effect on the Host and Host Characteristics

The overall effect of excessive moisture on SPB hosts was expressed by Hetrick (1949) when he wrote "the most susceptible hosts are pines weakened by excessive precipitation." The key point in this statement is that tree vigor is influenced by surplus moisture, and not tree growth since drought is more effective than flooding in reducing cross-sectional growth of loblolly pines (Lorio and Hodges, 1968). Despite the slower radial growth of pines in dry or droughty conditions, trees growing in wet or waterlogged soils are more susceptible to beetle attack (Hicks et al, 1979). Reduced vigor of trees growing along Kerr Reservoir in North Carolina was believed to be due to periodic flooding (Hicks, 1980; Maki et al, 1981). Lorio (1968) reported that pines growing on poorly drained sites are particularly susceptible to SPB attack. Kalkstein (1976, 1981), in his attempt to identify significant climatic variables associated with SPB outbreaks, suggested that the vigor of loblolly pine is adversely influenced by moisture surplus since the areas under study are often waterlogged.

Why are loblolly pines that are subjected to flooding more vulnerable to SPB attack than those under droughty conditions? We do not fully understand this phenomenon, but we do know that

a) flooding significantly reduces the bark-water potential of loblolly pine just as drought does (Hodges and Lorio, 1969);
b) continuous flooding adversely affects both OEP and relative water content of loblolly pine (Lorio and Hodges, 1968);
c) flooding noticeably reduces the rate of growth of conifer terminals (Ahlgren and Hansen, 1957);
d) flooding increases the mortality of secondary roots (Hosner, 1959);
e) loblolly pine growing on flat or concave sites (periodically waterlogged) have fewer fine roots than those on comparable trees on mounds (Lorio, Howe and Martin, 1972);
f) loblolly pine subjected to continuous flooding exhibits a remarkable increase in sugars, but the increase occurs later relative to sugar increase in drought stressed trees (Hodges and Lorio, 1969);
g) under anaerobic conditions, the roots of many species produce compounds such as ethanol and acetaldehyde (Fulton and Erikson, 1964), ethylene (Kawasi, 1972) and cyanogenic compounds (Rowe and Catlin, 1972);
h) summer flooding is more injurious to woody plants because oxygen is less soluble at higher temperatures (Verentennikov, 1964);
i) under flooded conditions, transpiration is much lower (McColl, 1973; Veretennikov, 1964), but trees on moist soils are capable of increased transpiration activity when their root systems are not completely flooded (Veretennikov, 1964);
j) under temporary cessation of respiration (due to anaerobiosis) plant cells lose a significant portion of their water, and the water retaining ability of the leaves drops (as reviewed by Samuilov, 1965);
k) flooding increases the glycolytic rate of intolerant trees (Crawford and McMannon, 1968);
l) glycerol accumulates in the roots under flooded conditions (Crawford, 1976) and
m) OEP is high in the early morning in all control and drought-stressed trees, but flooded trees exhibit low pressures as well as the drastic and prolonged reduction in OEP all day (Lorio and Hodges, 1968).

This last observation (m) is interesting in that it appears to implicate OEP in the greater susceptibility of flooded trees than drought-stressed trees.

Effects of Flooding on the Soil and Microorganisms

A knowledge of the effects of flooding on soil provides us better insight into the SPB/host interaction since these effects are eventually translated into host and finally into beetle response (survival). We know that flooding causes oxygen deficiency. Very often anaerobiosis may develop within a few hours after flooding due to displacement of gas from the soil pore space (Coutts and Armstrong, 1976). Under such reduced conditions, phosphorus availability usually increases but nitrogen availability is diminished (Patrick, 1978). Ahlgren and Hansen (1957) pointed out that the soil carbon dioxide-oxygen ratio and nitrate availability are altered by flooding and that such alterations may cause growth retardation. Waterlogged soils have been known to produce harmful substances such as sulphides (Culbert and Ford, 1972), high CO_2 concentration (Hook et al, 1971) and soluble iron and manganese (Jones, 1972). The production of hydrogen sulphide (H_2S) brought about by the reducing conditions in soils may not only affect the host trees but may attract the beetles. All and Anderson (1974) have shown that pioneer beetles of *I. grandicollis* are attracted to such odors as carbon disulfide (foul odor).

Mycorrhizal fungi do not grow anaerobically (Coutts and Armstrong 1976). Under flooded conditions, the mycorrhizal association may be entirely absent. Mycorrhizal surface area appears to be related to water regime. When the soil becomes drier, mycorrhizal surface area is reduced on mounds and increases on flats. The surface area is greatly reduced on flat sites during most of the wetter period (Lorio et al, 1972). The forms of mycorrhizae also appear to change with soil moisture conditions. The nodular types become common when there is excessive soil moisture, and the bifurcate and branched types predominate under moisture stress (Lorio et al, 1972).

Lightning-struck Trees

Lightning and Extent of Damage

Lightning is a very powerful change agent in a forest ecosystem. It starts forest fires, acts as a nitrogen fixer and predisposes trees to other agents of deterioration (Taylor, 1969, 1971, 1974). A lightning bolt can produce as many as 345,000 amperes of electricity (Anonymous, 1966) and can develop peak color temperatures of the channel in air from 21,000° to 31,000°K (Prueitt, 1963; Uman, 1964). Although very little is known about the peak temperature developed by a lightning discharge at the ground level, it is believed to develop energy sufficient to melt some metals and to ignite forest fuels (Taylor, 1969). Coupled with these energy characteristics is its frequency; it is estimated that about 8 million lightning discharges strike the earth each day, and if these were evenly distributed, roughly half a million would be striking the world's forests (Taylor, 1969).

Lightning damage has been reported in the swamp forests of Southeast Asia (Anderson, 1964; Brunig, 1964), the rubber plantations of Sumatra (LaRue, 1922), the banana plantations of Honduras (Reinking, 1930), the Valdivian rain forest of Chile (Wilhelm, 1968), the Trans-Saharan regions of Africa (Phillips, 1965), the radiata pine stands in Australia (Minko, 1966), the forests of Scotland (Murray, 1958) and the coniferous forests of the U. S., particularly the western states (Taylor, 1969). Forest wildfires could be the most destructive direct effect of lightning on the temperate coniferous forests of North America. Each year, lightning causes some 10,000 forest and range fires in the U. S. alone (Fuquay et al, 1967). Timber mortality caused by lightning probably ranks second in severity. Ffolliott and Barger (1967) examined 634 sawtimber trees in northern Arizona and found 10% of these to have been damaged by lightning. Johnson (1966a) claimed that lightning was responsible for 4% of the mortality of old-growth ponderosa pines in western Montana. Reporting from the northeastern U.S., Nelson (1958) found that lightning caused 25% mortality of 1,300 mature eastern hemlock trees. From the South, Trousdell (1955) indicated that lightning was one of the most important single causes of mortality of loblolly pine seed trees.

Lightning that strikes the forest does not necessarily cause a wildfire, but often causes structural damage to the struck tree. Occasionally, such damage extends to a nearby tree (Schmitz and Taylor, 1969). Structural damage ranges from the removal of the cambium or sapwood (Fuquay et al, 1967; Taylor, 1969; Hodges and Pickard, 1971) to splitting and ejection of slabs from the most severely damaged trees (Fuquay et al 1967; Taylor, 1969). Loosening of bark of struck trees has been observed in loblolly pine (Howe et al, 1971). Severance of lateral roots (Minko, 1966; Schmitz and Taylor, 1969), exposure of main roots (St. George, 1930) and excavation of the soil at the base of the lightning scar (Schmitz and Taylor, 1969) have likewise been reported. Crown injuries, in the form of ruptured branchlets and needles, by flying bark and wood debris (Taylor, 1969) and ignition of crown foliage and upper stem (Fuquay et al, 1967) are common in lightning-struck ponderosa pine. Sometimes, a struck tree literally explodes (Johnson, 1966b) causing its virtual disappearance. It appears that all parts of a tree are vulnerable to lightning injury.

Attractiveness of Lightning-struck Trees to Bark Beetles

Conifers that are structurally damaged by lightning are very attractive to bark beetles (Hopkins, 1909; St. George, 1930; Knull, 1934; Beal and Massey, 1945; Hetrick 1949; Thatcher, 1960; Anderson 1960; McMullen and Atkins, 1962; Rudinsky, 1962; Thatcher and Pickard, 1964; Johnson, 1966b; Anderson and Anderson, 1968; Schmitz and Taylor, 1969; Hodges and Pickard, 1971; Howe, et al, 1971; Lorio and Bennett, 1974; Lorio and Yandle, 1978). Johnson (1966b) reported that about 80% of all mature ponderosa pine struck by lightning were attacked and killed by the western pine beetle. Of the 2,100 SPB infestations over a three-year period in south-central Louisiana, 31% were associated with lightning-struck trees, and 75% of the beetle spots found in August alone of those years had lightning-struck trees (Hodges and Pickard, 1971).

Studying the spatial-temporal distribution of SPB infestations near Oakdale, Louisiana, Lorio and Bennett (1974) found that lightning was associated with 29% of the infestations tallied from April, 1965 to March, 1969. And in August 1965 alone, 77% of the infestations included lightning-struck trees. Available information indicates that lightning plays a very important role in the SPB population dynamics. In late summer and early fall, when beetle populations are normally low (Thatcher and Pickard, 1964), lightning-associated infestations peak (Lorio and Bennett, 1974; Lorio and Yandle, 1978). A southwide survey of SPB-infested plots showed that 39.0%, 31.6% and 23.0% of the attacked plots in Arkansas, Texas and Georgia, respectively, contained lightning struck trees as opposed to 0.4%, 0.9%, and 1.0% of the corresponding non-attacked plots (Hicks, 1980). Also, trees around a struck tree often become vulnerable. For instance, a study by Schmitz and Taylor (1969) revealed that 76% of the ponderosa pine trees within an 80-foot radius of the struck tree were infested by the pine engraver (*I. pini* Say) in the upper two-thirds of the stem, with some mountain pine beetle at 50 feet and western pine beetle in the lower 20 feet. Whether such increased susceptibility of neighboring trees is directly attributable to lightning is uncertain. However, reports of declining trees around struck stems have been published (Jackson, 1940; Murray, 1958; Anderson 1964; Komarek, 1964; Minko, 1966b). Schmitz and Taylor (1969) suggested that lightning causes unobserved physiological injury to trees surrounding a struck tree, making them susceptible to beetle attack.

What makes a struck tree highly

attractive to bark beetles is not fully understood, but hypotheses have been stated as follows:

a) Fermentation of the phloem, whether by anaerobic respiration or from external microorganisms, could be a product of the wounding of ponderosa pine trees by lightning. Volatile odors from this fermented phloem attract newly emerged beetle adults (Johnson, 1966b);
b) When lightning strikes a pine tree and ruptures the bark, certain host volatiles are released from the exposed wood and phloem. Some of these volatiles are attractive to *Ips* spp. flying through the forest (Anderson and Anderson, 1968);
c) The sudden release of ozone following a lightning strike attracts beetles (Howe et al, 1971);
d) Microorganisms invading a lightning wound produce beetle attractants (Howe et al, 1971);
e) The black turpentine beetle may respond to an attractant(s), produced as a result of the strike, and in turn produce a secondary attractant responsible for attack by the SPB (Hodges and Pickard, 1971);
f) The ejection and deposition of the debris shower from the struck tree on neighboring trees provide a means for short-term oleoresin release that enhances the probability of discovery and attack by pioneer beetles in an otherwise marginal olfactory search situation (Taylor, 1974).

Vité and Gara (1962) and Howe, et al (1971) presented convincing evidence against hypotheses *a* and *d*. Both studies concluded that microorganisms do not have a role in the initial attraction of the SPB to struck trees. However, Howe, et al (1971) stressed that the microorganisms may play a major role in modifying the condition of trees and enhancing their suitability for brood development. Hypothesis *b* appears promising. For instance, Werner (1972) demonstrated that *I. grandicollis* is attracted to volatile terpenes released from host tree phloem. All and Anderson (1974), working on the same species of bark beetle, provided further support for the hypothesis that *I. grandicollis* initially selects and attacks host trees as a chemotactic response to olfactory stimuli. The initial attack by SPB was hypothesized to be in response to volatiles emitted by dead pines (Heikkenen, 1977). Heikkenen's data were collected in an area of endemic beetle populations. The problem with hypothesis *b* is the difficulty of designing a decisive experiment to test it. To date no experiment has ever attempted to collect volatilized compounds from a lightning struck tree. The other complication is the pheromone produced by the first beetles attacking a struck tree. At this point, the issue of host selection as being random or directed inevitably causes argument between individuals. Whether pioneer beetles attack a host tree in a random manner (Vité, 1961; Vité and Wood, 1961; Gara, Vité and Cramer, 1965; Franklin, 1970; Berryman and Ashraf, 1970; Howe et al, 1971; Hynum and Berryman, 1980; Moeck et al, 1981) or initial attacks result from attraction to odors emanating from susceptible host trees (Person, 1931; Anderson, 1948; Chapman, 1963; Rudinsky, 1966; Heikkenen and Hrutfiord, 1965; All and Anderson, 1974; Heikkenen, 1977) remains unresolved. There is no doubt that host selection by the SPB is extremely complicated and very likely species specific. However, it is possible that host selection is a catenary process (Kennedy, 1965). At the ecosystem level, it is the arrestant property of pine trees that holds the SPB from getting outside its host range. At the individual tree level, it is the distribution, duration, and concentration of potential host attractant(s) that provides a sphere of influence that directs the SPB to its susceptible host. After a successful initial attack, a stronger secondary attraction (pheromone effect) leads to mass attack. Therefore, the host selection catena for SPB may be composed of orthokinesis (host finding movement with an arrestant), olfactory, biting and gustatory responses. Hypothesis *c* at first appears attractive (Howe et al, 1971), but observations in north Florida, strongly suggest that ozone produced by lightning strikes is at best insignificant, and even declines regardless of intensity and severity of the lightning activity (Davis, 1974). Hypothesis *e* proposes that the black turpentine beetle responds to a primary (host) attractant, produced as a result of the strike, and in turn produces a secondary attractant responsible for the attack by the SPB (Hodges and Pickard, 1971). This hypothesis is based on the observation, by the same authors, that the black turpentine beetle usually attacks first, *I. grandicollis* and SPB at about the same time and *I. avulsus* last. Merkel (1981) also noted that pines attacked by the black turpentine beetle are subsequently attacked by other bark beetles. Furthermore, the black turpentine beetle exhibits a strong preference for wounded trees, which provide strong initial attractancy for the pioneer beetles (Goldman, Cleveland and Parker, 1979). The attraction of black turpentine beetles to oleoresin liberated by lightning strikes was observed earlier (Hopkins, 1909). Vité et al (1964) demonstrated that black turpentine beetles respond to uninfested log sections and to various resinous compounds. Also, the possibility of beetles of one species being attracted by the aggregation pheromone of another species (Vité et al, 1964) is worth considering. Hypothesis *f* is the same as hypothesis *b* except that a means of oleoresin release and distribution is specified. This hypothesis also attempts to explain the "group kill" associated with lightning strikes.

Chemical and Physiological Changes in Struck Trees

Reports on the chemical and physiological changes in lightning-struck trees are scarce. The suggestion by Johnson (1966b) that fermentation of the phloem by anaerobic respiration or by external microorganisms occurring as a result of wounding by lightning has never been validated.

The water relations of lightning-struck trees have been shown to be markedly altered (Anderson and Anderson, 1968; Hodges and Pickard, 1971). The relative water content of the inner bark of struck loblolly pines is much lower than in green trees, and the difference increases with time (Hodges and Pickard, 1971). Anderson and Anderson (1968) found that the hydrostatic condition of the struck trees deteriorated first in the crown and progressed gradually down the stem. Since the turgor of the epithelial cells regulates the OEP (Vité and Rudinsky, 1962), a reduction in hydrostatic pressure is accompanied by a decrease in OEP. Hodges and Pickard (1971) reported that the average OEP for control trees was 7.7 atm. as against 2.3 atm. and 0.4 atm. on the undamaged and damaged sides of struck loblolly pines, respectively. Concommittant with the reduction in OEP was the reduction in OER. Anderson and Anderson (1968) obtained OER values ranging from 0 to 0.9 ml/hr for a struck loblolly pine, with the lowest values occurring nearest to the lightning-caused fissure. Their data on the water content of the inner bark did not show any direct effect upon *Ips* attacks or brood development, except in cases of extreme water loss.

The chemistry of lightning-struck trees and subsequent changes with time have not been adequately investigated. Some changes in reducing and non-reducing sugars, starch (Hodges and Pickard, 1971), amino N and total N (Smith, 1968; Hodges and Pickard, 1971) have been reported. Amino N and total N were little influenced by lightning strikes (Hodges and Pickard, 1971), but with time, total N increased while amino N decreased (Smith, 1968). Smith (1968) attributed this increase in total N to microorganisms colonizing the lightning wounds. Howe et al (1971) isolated and identified microorganisms from lightning wounds. In addition, Bridges (1978) isolated nitrogen-fixing bacteria from *D. frontalis, D. terebrans, I. avulsus* and *I. calligraphus*. After these beetles attacked struck trees, total N increased while amino N decreased (Hodges and Pickard, 1971). Whether the increase in total N and decrease in amino N were due to attack or would have happened anyway is uncertain. However, a closer look at Smith's data (Smith, 1968, Tables 3 and 4, pp. 18 and 19) indicates some increase in total N and decrease in amino N even before attack took place.

Lightning strikes apparently cause marked reduction in non-reducing sugar, which is further reduced after beetle attack. The reducing sugar is increased by the strike slightly over the control (Hodges and Pickard, 1971). The starch level is unaffected by the strike but declines slightly after the beetles have attacked. Other chemical changes (e.g., volatilization of terpenoids, oxidation of monoterpene compounds, electrolysis of water) which may play some role in host selection, have not been examined.

The effect of lightning is subsequently reflected in the growth of the tree as loss in increment and volume (Wadsworth, 1943). All things being equal, most of the lightning-struck trees die sooner than non-struck trees (Baker, 1974).

Role in Brood Development and Population Dynamics

Apparently, lightning renders a tree favorable for brood development and survival. To wit, the breeding potential of *D. brevicomis* was estimated to be greater in lightning struck ponderosa pines than in living ponderosa pines that were normally attacked (Johnson, 1966b). For example, the mean number of emergence holes in struck trees was estimated to be from 150 to 200/ft^2 of bark as against a mean of 63 holes/ft^2 in normal host trees. With *D. frontalis*, a record emergence of 950 beetles/ft^2 was estimated in a struck tree as against an average emergence of 250/ft^2 in unstruck infested trees (Hodges and Pickard, 1971). This increased suitability of struck trees may be attributed to lower resinosis (Berryman, 1976), greater amounts of available energy substrates and other essentials for insect growth and development, since lightning-struck trees are often the largest and most vigorous individuals in a stand. Also, the reduction of the relative water content of the inner bark improves the brood environment of the beetles. Although Anderson and Anderson (1968) claimed that the moisture content of the inner bark did not have a direct effect on brood development of *Ips* spp., the moisture content of their experimental tree did not go below 100%. Earlier, Anderson (1948) pointed out that heavy brood mortality of *Ips* occurred when bark moisture content was below 100%. Anderson and Anderson (1968) attributed the successful brood development of *Ips* in a lightning-struck tree to a markedly reduced OER. Despite limited data, Hodges and Pickard (1971) demonstrated a positive correlation between SPB emergence and carbohydrate content of struck trees. Earlier, it was indicated that hexose sugars were more readily utilized by the SPB (Barras and Hodges, 1969).

The attractiveness of lightning-struck trees to beetle attack and their suitability for brood development may play a major role in the dynamics of SPB populations. Struck trees have not only served as centers for spot infestations (Lorio and Bennett, 1974) but have sustained beetle populations during periods of low seasonal activity (Hodges and Pickard, 1971). It is apparent that the effect of lightning is more pronounced during endemic periods and generally masked during epidemics.

Under Biotic Stress (Diseases and Other Pests)

The association of root injury due to microorganisms and other agents with increased attractiveness to SPB attack was first pointed out by Hetrick (1949). He asserted that any disturbances that interfere with the normal functioning of the root systems of pines may induce bark beetle attack. His observation of the mushroom root rot (*Armillaria mellea*) on SPB-infested trees clearly indicated that the fungus preceded the bark beetle attack. The attractiveness of flooded and lightning-struck pines, as described earlier in this paper, lends support to this claim.

Root pathogens play some role in predisposing southern pines to SPB attack. Lorio (1966) reported that *Phytophthora cinnamomi* Rands. and *Pythium spp.* were associated with declining 40-year old loblolly pines in the lower Gulf Coastal Plain of Louisiana. Observations on Monterey pine by Hartigan (1964) indicated that root destruction by *Phytophthora cinnamomi* and other organisms may predispose trees to insect attack. Prolonged wet conditions on flat sites (common in the lower Gulf Coastal Plain) are believed to favor the distribution and development of rootlet pathogens (Lorio and Hodges, 1971). Pines on intermound areas have been observed to form rough bark on roots, and this has been associated with phloem starvation due to impeded synthesis or translocation of food by root diseases (Jackson and Hepting, 1964). The dynamics of mycorrhizal associations (abundance and types) in these flat sites and mounds (Lorio, et al, 1972) may find some value in the maintenance of tree vigor. Mycorrhizal roots have been shown to be resistant to certain pathogens (Marx, 1967; Marx and Davey, 1969; Zak, 1964). Very recently, the vesicular-arbuscular mycorrhizal fungi have been pointed out to affect plant parasitic nematodes by physiologically altering or reducing root exudates responsible for chemotactic attraction of nematodes or directly retarding nematode development or reproduction within the root tissue (Hussey and Roncadori, 1982).

In the Georgia Piedmont, littleleaf disease has been implicated as an agent predisposing shortleaf pine to beetle attack (Belanger et al, 1977). A study of this disease by Copeland (1952) indicated that mortality of roots less than one-fourth inch in diameter contributes to the rapid decline of shortleaf pine. Also, when 18 to 34% of the roots are infected, normal growth stops and the tree declines very rapidly.

Under certain conditions, particularly on the Coastal Plain, annosus root rot (*Heterobasidion annosum* (Fr.) Bret.) is an important predisposer of pines to SPB attack in thinned loblolly pine stands (Alexander, 1977; Alexander et al, 1978; Alexander et al, 1980). This is very true on high-hazard annosus root rot sites, but not in low-hazard sites such as the Piedmont (Belanger, 1981). Skelly (1976) found that about 30% of the roots of SPB-attacked trees had annosus root rot infection compared with 20% for unattacked trees. In an extensive survey of the Coastal Plain, Skelly et al (1981) and Alexander et al (1981) noted that annosus root rot is significantly associated with trees infested by the SPB. The same studies suggested that the disease stressed the SPB-attacked trees as indicated by reduced mean annual radial growth in the last 5-10 years. Kuhlman (1970) identified isolates of annosus root rot with varying degrees of virulence, hence causing different degrees of infection of living pine roots and, in turn, varying effects on tree growth (Bradford and Skelly, 1976).

Aside from these pathogenic organisms, other pests may initiate the decline of the host. Lorio (1973) suggested that black turpentine beetle may contribute indirectly to SPB epidemics by weakening trees and rendering them more attractive to other beetles. Lorio and Hodges (1977) observed black turpentine beetles attacking their flooded and drought-stressed trees before they could induce SPB attacks.

In most instances, these biotic factors act in concert with environmental factors so that their true effects are hard to isolate. Regardless of how they affect the trees, the obvious consequence is the alteration of normal host metabolism resulting in reduced growth and vigor.

Other Stress Forms (Harvesting, Wind, Fire, Etc.)

Any stress that causes elastic or plastic strain is bound to alter the normal physiology of the host. Unfortunately, we know very little about host physiology under stress due to harvesting, thinning, wind, ice, etc. However, we do know that above- and below-ground injuries from harvesting and thinning operations serve as infection courts for organisms causing decay and discoloration. In fact, thinning increases the incidence of annosus root rot on deep sandy sites underlain with clay (Powers and Verrall, 1962; Froelich et al, 1977). Other stress forms, such as windthrow (St. George, 1930; Knull, 1934), recent fire (Knull, 1934) and logging disturbance (Ku et al, 1976; Porterfield and Rowell, 1981), have been associated with SPB outbreaks. In some areas, however, fire has never been associated with SPB infestation (Ku et al, 1980). Between water-stressed and wounded trees, the wounded ones tend to be attacked more frequently by the SPB (Brown and Michael, 1978).

We need more thorough investigations of these stress-causing influences as they affect SPB population dynamics. Studies geared towards cause-and-effect relationships should have high priority.

HOST PHYSIOLOGY AND CONDITIONS IN RELATION TO BROOD DEVELOPMENT

Requirements for Brood Development

The food and microenvironmental requirements for SPB brood development have received little attention. We do not yet have a good handle on its nutritional needs. Initial attempts at mass rearing, providing a number of nutritional compounds, met with a limited success (Clark and Osgood, 1964). Mott et al (1978) aseptically reared SPB from egg to adult on 3% nutrient agar with loblolly pine callus initiated on Brown and Lawrence nutrient medium. When they added β -sitosterol to the medium, adult production increased from 14 to 26% of hatched larvae. It is intuitively obvious, though, that in nature, the two basic brood requirements of the beetle are a bark which serves as a habitat and substrate and a favorable environment. The environment can have a direct effect on brood development and survival of the beetle or an indirect one through its effect on the host. The bark offers the best medium for establishing the nutritional requirement (qualitatively) through chemical characterization. Such bark chemical characterization must be guided by established knowledge of nutritional requirements necessary for insect growth such as that given by Dadd (1970, 1973) and Hagen (1974) as follows:

1. water
2. minerals (salts)
3. 10 essential amino acids
4. 7 to 10 water soluble vitamins
5. vitamin C
6. a sterol
7. carbohydrate.

The water, amino acid and carbohydrate components of the bark have been investigated (Gaumer and Gara, 1967; Hodges et al, 1968; Lorio and Hodges, 1968; Barras and Hodges, 1969; Hodges and Lorio, 1969; Hodges and Pickard, 1971; Lorio and Hodges, 1977; Webb and Franklin, 1978; Wagner, et al, 1979). The other nutritional components have not received any research attention.

Host Conditions Affecting Brood Development and Mortality

The larval stage is a critical period in the life of the SPB. In fact, larval mortality is greater than mortality in any of the other life stages (Coulson et al, 1976; Goldman and Franklin, 1977; Wagner et al, 1979). Since the larval stages are primarily spent in the inner bark and with a short time in the outer bark for pupation, host conditions in the inner bark must have a strong influence on the development and survival of the brood. For instance, the high mortality (70.7%) from egg to the first and second larval instars could be attributed to host-tree conditions, since there are so few predators and parasites associated with these first two instars (Goldman and Franklin, 1977). Anderson (1948) obtained the best brood survival with pine engraver when the inner-bark moisture content did not deviate much from that found in vigorous trees. He also found that heavy brood mortality occurred when the inner-bark moisture dropped below 100%. Gaumer and Gara (1967) identified an optimum rearing environment for SPB from infested bolts to be from 20 to 22°C and RH of 50 to 60%---conditions that approximate the natural events occuring in infested trees. In general, high phloem moisture is associated with the formation of elongate larval mines and reduced survival (Thatcher, 1960; Clark and Osgood, 1964; Webb and Franklin, 1978). The rapid dehydration of the phloem to a moisture content below 200% appears essential to brood survival (Gaumer and Gara, 1967). The importance of this initial decline in moisture content to brood survival has been corroborated by Wagner et al (1979). Anderson (1967) on the other hand, employing techniques of girdling and bark isolation to produce a variety of physiological conditions, observed that the moisture content of the inner bark was not critical to either the success of *Ips* attacks or brood development under his experimental conditions. Anderson and Anderson (1968) concluded that the inner bark moisture content limited *Ips* brood development only where severe dessication occurred.

Investigations on the changes in

moisture status of the tree through time revealed that xylem water potential, xylem moisture and phloem moisture influenced SPB development (Webb and Franklin, 1978; Wagner et al, 1979; Coulson, 1980). Egg and early larval development proceed with xylem and phloem dehydration. As soon as the phloem and xylem moisture approaches the minimum, the larvae migrate to the outer bark, and the rehydration of the phloem takes place at about the time brood adults emerge (Wagner et al, 1979; Coulson, 1980). Webb and Franklin (1978) on the other hand reported an earlier time of phloem rehydration, which occurred about the time the larvae reached the outer bark. This phenomenon of phloem rehydration has not been elucidated. Changes in phloem moisture content elicit varying responses from the different beetle life stages. Wagner et al (1979) demonstrated that eggs and first-stage larvae of SPB are unaffected by changes in phloem moisture, while development of 2nd and 3rd instar larvae is slowed by phloem moisture above 170%. High bark-moisture content also slows the development of 4th instar larvae and pupae.

Environmental stresses are believed to cause chemical changes in the inner bark, which in turn influence the nutritional quality of the tissue. Water stress causes an increase in reducing sugars, which are readily used by the SPB and associated microorganisms (Barras and Hodges, 1969). Using cellular and extra-cellular liquid of bark samples from sound and unhealthy trees of *Picea abies* and *Pinus sylvestris*, Chararas et al, (1960) observed that the rate of development of Scolytidae is closely related to the amount of soluble sugars. Adequate hydration of tree tissues maintains a high level of oleoresin flow which prevents effective egg and larval development (Lorio and Hodges, 1977). Anderson (1967) showed that high OEP, a variable highly correlated with tissue hydration, reduces the suitability of the host tree for *Ips* attack and brood development. Unless the water balance of the tree is disturbed and its OEP reduced to 60 psi, the bark beetles cannot breed successfully (Grossman, 1967).

It is apparent that host suitability for brood development is one of the final determinants of the subsequent population status of SPB with respect to quality and quantity. Unfortunately, host suitability is not a constant property of the host but is related to a number of factors, such as the levels of readily assimilated compounds (Chararas et al, 1960; Hodges et al, 1968; Barras and Hodges 1969; Hodges and Lorio, 1969), rate of tissue dessication (Gaumer and Gara, 1967; Webb and Franklin, 1978; Wagner et al, 1979), initial host vigor (Lorio and Hodges, 1977), inner bark temperature (Gaumer and Gara, 1967; Powell, 1967), host tree species and age (Coulson, 1980), diameter of the host tree (Fargo et al, 1979), presence of microsymbionts (Howe et al, 1971; Barras, 1973) and an array of environmental factors.

HOST-SPB-MICROORGANISMS COMPLEX: THE ROLE OF THE ASSOCIATED MICROORGANISMS

The Beetle-Microorganism Association

The relationship between the SPB and the blue-stain fungi is considered symbiotic, but the demonstration that the beetle can complete its life cycle without the blue-stain fungi (Barras and Bridges, 1976) indicates that the relationship is protocooperative. Grossman and Hamburg (1965) believe that the relationship between bark beetles and the blueing fungi in general is optional. In fact, the absence of the fungi has no effect on the number of attacks, ovipositional gallery length and number of egg niches, but the number of progeny decreases, and the emergence is delayed 13 to 24 days (Barras, 1973). Also, laboratory observations show that the blue-stain fungi are detrimental to SPB development (Barras, 1970; Franklin, 1970). The fungi are thought to reduce the nutritive value of the inner bark and may even be toxic or repellent to larvae and adults (Franklin, 1970). However, the presence of other microorganisms prevents the expression of this detrimental effect (Barras, 1969). The reduction of progeny in SPB in the absence of blue-stain fungi can have greater implications for beetle population status. This reduction can perhaps spell the difference between an endemic population and a population outbreak. Unfortunately, the above studies were conducted on bolts or bark tissues; therefore, the relationships observed between the fungus and the beetle do not necessarily reflect the relationship between them in standing trees.

The blue-stain fungi and some

associated bacteria have some beneficial effects on the beetle. The presence of the mycangial fungi can increase the level of nitrogen compounds for beetle nutrition (Becker, 1971). Bridges (1978) demonstrated the presence of nitrogen-fixing bacteria in the SPB-microorganism association. Comparison of the levels of lipids in the phloem without mycangial fungi with phloem colonized by the fungi shows that lipids increase over time in the fungi-colonized phloem (Berisford, 1980). Kok et al, (1970) suggested sterol metabolism as a basis for mutualistic symbiosis.

From the standpoint of beetle behavior, the mycangial fungi appear to play some regulatory role. Brand et al (1976) showed that mycangial fungi are capable of transforming trans-verbenol to verbenone. Some yeast metabolites have also been shown to enhance the attractiveness of the attractant mixture of frontalin, trans-verbenol and host odor (Brand et al, 1977). A bacterium, *Baccillus cereus*, isolated from southern pine bark beetles is capable of producing verbenol (Brand et al, 1975). A mycangial basidiomycete has been reported to produce isoamyl-alcohol, 6-methyl-5-hepten-2-one and 6-methyl-5-hepten-2-ol (Brand and Barras, 1977).

Effects of the Associated Microorganisms on the Host

The blue-stain fungus (*Ceratocystis minor* (Hedge.) Hunt) is considered the principal tree-killing agent (Coulson, 1980). This claim has not been fully elucidated in SPB infested southern pines. Attempts to verify the role of the fungus have been unsuccessful (Hare, 1969; Brown and Michael, 1978). Earlier investigations, however, implicated the blue-stain fungus in accelerating the death of the beetle-infested host (Caird, 1935; Craighead and St. George, 1938; Bramble and Holst, 1940). How the associated fungi kill the host tree has remained a subject for further investigation. Caird (1935) noted that, after attacks by the bark beetles, the outer rings of shortleaf pine trees lose their capacity to translocate water in the sapwood. He attributed this to the invasion of the vascular elements by the fungi. This was later corroborated by Bramble and Holst (1940). Mathre (1964), using dye indicators, showed that water is conducted around but not through fungal infected areas of the sapwood. He suggested that pathogenecity may involve entry of air into the sapwood. Anderson (1960) suggested several mechanisms by which the associated fungi cause rapid host death. These include

a) toxin production,
b) mycellial plugging of the tracheids,
c) release of gas bubbles into the tracheids and
d) production of particles that block the pit openings by causing tori aspiration.

The study of blue-stain fungi associated with the mountain pine beetle by Shepard and Watson (1959) indicated that the fungi probably reduce stored food in the parenchyma cells and restrict water conduction by destroying the ray parenchyma cells, which partly control water movement. Pathogenecity tests of some blue-stain fungi revealed that stain penetrates into the sapwood and can kill loblolly pine seedlings (Basham, 1968). Dye conduction tests also revealed no dye in stained sapwood. The possibility of toxin production by these associated fungi exists. For instance, the isolation and identification of phenolic metabolites, especially 6, 8-dihydroxy- 3-hydroxymethyl isocoumarin, from *Ceratocystis minor* (McGraw and Hemingway, 1977) appear to support this hypothesis.

Host Response to Invasion by Associated Fungi

Observations of failures of bark beetle colonization are common. These are often attributed to pitch flow. However, the possibility exists that this is due to the failure of the fungi to establish themselves. Kulman (1964), for instance, observed that unsuccessful *Ips* colonization of red pine did not have blue-stain in the wounds. Basham (1970) noted a zone of phenols and resins in the region of fungal invasion of resistant loblolly pine trees but not in trees killed by the fungi. Berryman (1972) reported that resistant trees produce a hypersensitive reaction, causing a wound periderm to form around the necrotic lesion caused by fungal infection. When there is no hypersensitive reaction, the tree may die. The production of polyphenols and other toxic compounds may also serve as a host defense system to *Ceratocystis* infection (Shrimpton, 1973). However, some known toxic compounds such as flavonoids and stilbenes have been shown to be degraded by *Ceratocystis minor* (Hemingway et al, 1977). Therefore, such compounds could not be considered a host resistance factor against *Ceratocystis*.

STATE OF KNOWLEDGE ANALYSIS AND RESEARCH NEEDS

The SPB attacks all pine species within its natural range. The physical properties of the oleoresin system appear to be the primary defense mechanism against attack by this beetle. However, other factors influence this resistance mechanism either directly or indirectly. Hence, the host resistance (R) to SPB may be briefly described as

$$R = f\left(\frac{\text{GR, } O_f\text{, OEP, OER, HR}}{\text{Age, stress, stand BA, beetle density}}\right)$$

where,

Gr = radial growth rate

O = oleoresin quantity

OEP = oleoresin exudation pressure

OER = oleoresin exudation rate

HR = hypersensitive response.

Although some of these variables are expected to be autocorrelated, the above representation is presented as a form of synthesis of the qualitative information we now have on host resistance to SPB. Host physiology and conditions are inextricably intertwined with all these variables. Integrating these variables simplifies the host resistance (R) equation into

$$R = f\frac{\text{vigor}}{\text{beetle density}}$$

Based on current knowledge, the attack process of the SPB is summarized in a flow diagram (Figure 1). The flow diagram emphasizes the importance of the host (susceptibility and suitability) in the attack process. The level of the beetle population is also emphasized, and its interaction with the host is shown in Figure 2. Combining these host variables and the beetle-attack density in a host-by-beetle matrix, the beetle population consequences can be conceptualized as shown in Table 2.

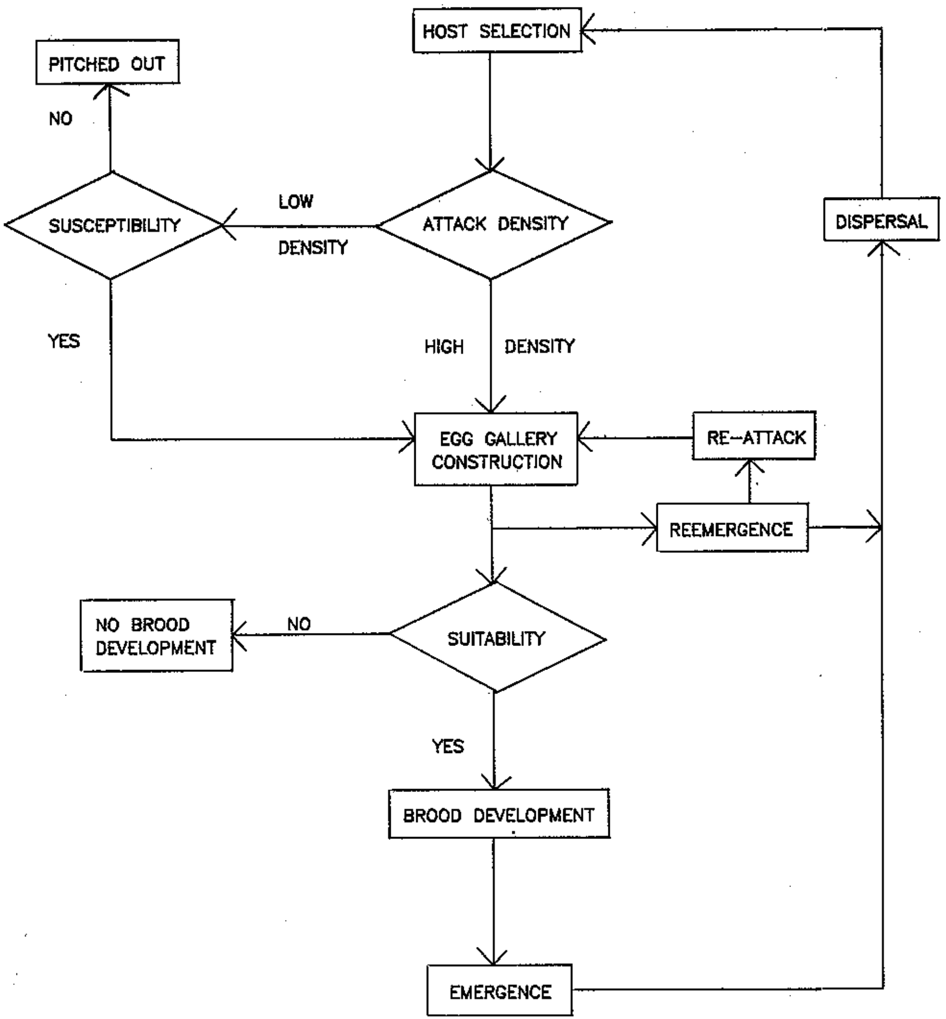

Figure 1. Flow diagram of the southern pine beetle attack process.

The susceptibility/resistance components of the host have been fairly well researched, and a number of relationships have been uncovered. Unfortunately, we do not have the critical values of the variables associated with these relationships to make full use of them. Hence, the establishment of the threshold levels of these variables, such as oleoresin flow, OEP, OER, rate of crystallization, bark or tree water potential, etc., for successful colonization of host to occur, is a high priority need.

The suitability component of the host has not been adequately investigated. We feel this ranks second in research priority since this may finally determine the consequent beetle population.

The beetle-inoculated blue stain fungus, *Ceratocystis minor*, is recognized as the principal tree-killing agent. How the fungus kills the tree is not fully understood. Investigation along this line will not only lead us to a better understanding of the host-SPB-microorganism complex but will provide us with alternative methods of control.

Other aspects of the host that demand investigative attention include:

a) host chemistry and physiology as affected by different forms of stress (excess water, deficient water, logging damage, wind, fire, lightning, disease, etc.);
b) the synchronization of seasonal host physiology with seasonal beetle activity; and
c) the development of host vigor indices.

Table 2. Conceptualization of relationship between host conditions and beetle attack density.

Degree of Resistance	Host Suitability	Beetle Attack	
		Low Density	High Density
Susceptible	Low	endemic population	population may collapse
	High	may lead to epidemic	explosive
Resistant	Low	endemic, dispersal	endemic, dispersal
	High	endemic but may build-up upon host predisposition	explosive

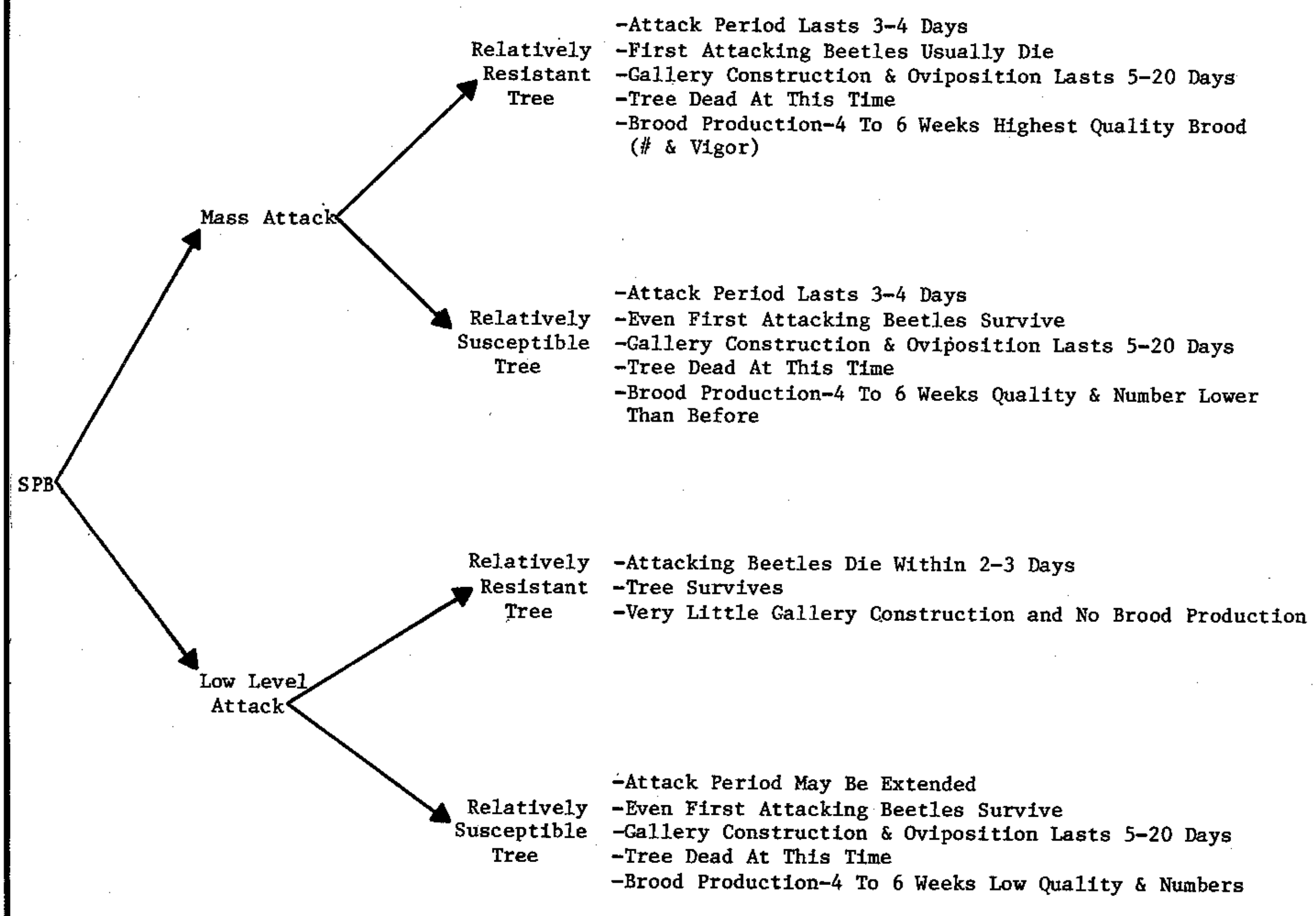

Figure 2. Consequences of southern pine beetle attack density and host resistance interaction.

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