se already seen. It is ritical photoperiod of cre is no modification ory it could place the

ysiological results of licit) conclusion that is. For under natural, photoperiod has the

ie emergence of the pae. Ann. appl. Biol.

exp. Biol. 27: 218-23 i., Hylemya brassicae

the cabbage root fly

phal de Chortiphila se. C.R.Ac.Sc., Paris

x diptères muscides uché. DSc. Thesis,

e maggot, Hylemya

Pegomyia hyoscyami Lussian). Rev. Ent.,

PHYSIOLOGICAL ASPECTS OF HOST TREE FAVOURABILITY FOR THE WOODWASP, SIREX NOCTILIO F.

by

J.L. Madden

Sirex noctilio F. is an exotic pest of softwood plantations in New Zealand and the Australian states of Victoria and Tasmania.

The National Sirex Committee was established in Australia in 1961 and a programme of search and eradication and basic studies on the insect, the host tree and asymbiotic fungus were commenced. Host tree attractiveness and attack have been considered by the Division of Entomology, C.S.I.R.O., and host tree susceptibility and resistance by the Forest Research Institute. All investigations have been conducted in predominantly *Pinus radiata* regeneration at Pittwater, Tasmania.

Sirex noctilio lays its egg in the outer sapwood of the host tree and the subsequent development of the eggs and larvae depends on the modification of the physical and chemical properties of the woody tissue by the symbiotic fungus, Amylostereum sp.. The tree is inoculated with the arthrospores of this fungus during oviposition.

Individual trees differ markedly in their attractiveness and reaction to Sirex, and favourability is determined by the physiological processes which affect (1). host tree selection, and (2), resistance to attack.

1. Host tree selection

Host tree selection involves (a) the attraction of female wasps to potential breeding material, and (b) subsequent assessment of this material as an oviposition substrate.

(a) Attraction

S. noctilio is attracted generally to suppressed trees but attraction may be induced by physically damaging trees or by conditioning healthy trees using caged insects.

The attraction of Sirex to trees under natural conditions is sustained with recruitment of other females. However, in some instances, and generally associated with more dominant trees, the initial attractive period may be short. These trees may or may not be conditioned to become attractive again after a suitable time lag.

When trees are felled or severely scorched attraction occurs soon after. Trees, completely defoliated or which have been pruned and then girdled (i.e. by removal of a 2 in band of phloem) below the remaining branches, are not consistantly visited until some 10-14 days after the treatment. Conditioned trees also become attractive after a similar time lag.

Comparable aberrant changes occur in host tree metabolism in these inductive treatments. Translocation of soluble solids to the stem is interrupted. In the defoliation and girdling treatments translocation is physically interrupted. There is a similar metabolic effect in conditioned trees as starch accumulates in the needles (Coutts 1968) with a corresponding increase in needle dry weight. In addition, the respiratory activity of the phloem tissue is markedly increased, leading to a depletion of reserve foods, and dendrograph recordings indicate that growth is checked at the onset of sustained attraction. This growth check occurs, on average, 10 days after treatment and coincided with a distinctive decline in respiratory rate.

These changes may be produced experimentally by wounding trees and, following attack, are accentuated by small quantities of a mucopolysaccharide secreted into the tree by the female during attack. This biologically potent material, which in saplings affects metabolism at a dosage rate of 3-4 microlitres, sustains the initial stress condition of the tree and favours attractiveness. The tree receives a cumulative dosage and Coutts (pers. commn.) has demonstrated that the material alone may be phytotoxic.

The immediate attraction of Sirex females to felled trees and freshly disturbed phloem suggested that the attractant was present in that tissue or the cambial sap. Solvent extracts of fresh phloem have resulted in positive responses to extract baits placed on healthy trees in field bioassay.

The attractant is released from trees when growth is static, as occurs in severely suppressed or temporarily checked trees. This latter condition may follow physical damage or environmental stress which result in demand exceeding the supply of translocate to the stem. Present evidence suggests that a deficit of auxin is involved in the release mechanism as permeability, transport and growth processes are affected. The diffusion of carbon dioxide from attractive stems is more rapid than from healthy ones and phloem slices from attractive trees display a greater degree of enzymatic oxidation or browning. These changes indicate an alteration in permeability properties.

whŝ

bee

pro

mu

me

mai

the

Cot

Co

Dr CS

Ta: Ho

Pre

The duration of attractiveness is determined by the events occurring within the tree. The attractiveness of felled material is limited by the rapid drying of the wood and phloem whereas in girdled trees, the attractive condition may carry over into a second season. In the latter case, the girdling operation has divided the tree into an upper, supra healthy and unattractive and unacceptable region and a lower, unthrifty and attractive region. If the vigour of the upper stem is sufficient to buffer the effects of Sirex attack and there is sufficient reserve food to maintain root and stem function, transpiration continues, the phloem remains moist although non functional, and the attractive condition is retained below the girdle.

The release of the attractant from naturally attacked trees is limited by the restoration of normal phloem function or, in susceptible trees, by excessive dessication following tree death.

(b) Attack

The Sirex female having located a potentially suitable tree assesses its vigour by drilling with its ovipositor. If the tree is acceptable then true oviposition begins. Vigozous trees may be rejected before the ovipositor has penetrated beyond the cambium.

The sites chosen by the female on the bark surface for drilling are at random, although the number of drills and, in turn, the number of eggs, at any one site is influenced by the properties of the phloem-cambium at that site. The number of drills may vary from one to five.

Fungus arthrospores and mucilage are deposited in at least one drill at all sites. The occurrence of a single drill, which is variable in length, and rarely contains eggs, indicates that the site has been rejected as an oviposition site. These drills function to assess and further condition a tree.

In the initial stages of attack most of the drills are single. As the attack progresses the proportion of double and treble drills increases, which indicates a change in the properties of the substrate. A similar change in proportions was found to occur on attacked, clean stemmed, mature trees. Single drills predominated in the upper regions of the tree and treble and higher multiples in the lower regions. The proportion of double drills remained relatively constant. The sensing of a tree's vigour favours egg economy. To determine what characteristics were possibly involved in the females oviposition behaviour, bark samples were obtained immediately an ovipositor was withdrawn from a log. The drill type was noted and after freezing and thawing the osmotic pressure of expressed sap determined. High osmotic values were obtained where single drills were found and low values, or low moisture contents, in regions where treble and higher multiples were made. Double drills were made at intermediate values. A gradient of increasing osmotic pressure occurs from the lower to the upper regions of trees and the conditioning effect of females on healthy trees resulted in a rapid decline in the general osmotic pressure of the trees. Naturally attacked trees have been found to have lower values at the time of attack than unattacked trees of similar class.

2. Resistance

The resistance of individual trees to Sirex attack involves counteracting the effect of the mucosecretion and the establishment of *Amylostereum* sp.. Studies by the Forest Research Institute indicate that, for a given dosage of muco-sectretion, tree mortality is enhanced by the presence of the fungus.

Generally three types of resistance mechanism may operate. First, resin may flood oviposition drills. Secondly, the fungus may be isolated behind a barrier of polyphenols. The progressive stages of polyphenol formation were reported by Coutts & Dolezal (1966). Thirdly, a critical mechanism must operate within the tree to restore translocation and mediate respiration.

Finally, the efficiency of the above mechanisms may be affected by the genetic constitution of the host tree in terms of resin characteristics and vigour.

Physiological Aspects of Host Tree Favourability for the Woodwasp

severely suppressed nvironmental stress nce suggests that a d growth processes than from healthy natic oxidation or

ithin the tree. The inhoem whereas in he latter case, the and unacceptable em is sufficient to ain root and stem nctional, and the

the restoration of ee death.

our by drilling with is may be rejected

dom, although the c properties of the

at all sites. The icates that the site ndition a tree.

ck progresses the properties of the stemmed, mature er multiples in the sensing of a tree's ved in the females withdrawn from a of expressed sap low values, or low irills were made at wer to the upper a rapid decline in nd to have lower

the effect of the Research Institute to presence of the

resin may flood solyphenols. The 1966). Thirdly, a respiration.

netic constitution

Conclusion

The woodwasp, Sirex noctilio is attracted to physiologically stressed trees by an attractant which is released from the stem when the supply of soluble solids is limiting. The female insect, having been guided to the tree, assesses the stem with its ovipositor. Oviposition behaviour is modified by the properties of the phloem and in the initial stages of an attack fewer eggs are deposited. The muco-secretion inoculated into the tree during attack reinforces the initial stress condition and favours the recruitment of more females and greater debilitation.

Resistance is associated with the more vigorous tree and involves both physical and chemical mechanisms. Although the efficiency of these mechanisms would be modified by a tree's genetic make-up, it does appear that sound silvicultural practice in terms of site and spacing will counteract the destructive potential of Sirex, by favouring individual tree vigour.

References

Coutts, M.P. 1968. Rapid physiological change in *Pinus radiata* following attack by *Sirex noctilio* and its associated fungus, *Amylostereum* sp.. *Aust. J. Sci.* 30: 275-276.

Coutts, M.P. and J.E. Dolezal, 1966. Polyphenols and resin in the resistance mechanism of *Pinus radiata* attacked by the woodwasp, *Sirex noctilio*, and its associated fungus. Forestry and Timber Bureau Leaflet 101, 19 pp.

Dr J.L. Madden, CSIRO Division of Entomology, Tasmanian Regional Laboratory, Hobart, Tasmania.

Proc. ecol. Soc. Aust. 3: 147-149.