PHYSIOLOGICAL SUPPRESSION IN PINUS RADIATA AND ITS SUSCEPTIBILITY TO SIREX

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Summary

On the grounds of indications obtained with histochemical staining reactions for tree enzymes and of observations related to susceptibility to Sirex, it is suggested that optimum development of Sirex larvae is reached in those trees which, due to some physiological debility in performing normal processes, tend towards constantly increased fatty acid metabolism. The wide range of internal conversions of reserve materials can therefore explain the variations in Sirex susceptibility at different levels of infections by the symbiont.

Introduction

During investigations into the susceptibility of certain types of P. radiata trees to the Sirex woodwasp and its fungal symbiont in southern Tasmania, an attempt was made to detect any marked physiological differences between representative trees by determining the relative intensity of some of the tree enzymic reactions, especially those associated with photosynthetic and respiratory activities. When conducting other experiments in this field, it was observed repeatedly that, in selecting trees for Sirex resistance, it can be misleading to use vigour of the green crown as the only criterion. This is particularly so in young regrowth stands.

Experimental outline

In the preliminary tests reported in this paper, only bud and shoot tissues were used in order to preserve those trees which proved to possess good inherent qualities. The tests were done on trees representing the following characteristics :-

1. Resinous, vigorous trees with good annual increment and vigorous buds;

2. Trees with dark green crowns, growing normally and with approximately average resin yield;

3. Suppressed trees, still with relatively good crowns, but bearing weak and non-vigorous buds, similar to those suffering from previous Chermes attack.

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It is known from other experiments that trees from which resin flows freely can successfully resist *Sirex* attack, although an effect is shown in later years by some deterioration of their wood due to the formation of wood lesions, stained dark brown by resin which fills the oviposition tunnels. Such trees and those with intermediate characteristics are unlikely to be affected by *Sirex* except under conditions where the insect population density is high and where suitable breeding material in the form of fully susceptible trees is limited. These trees can be regarded as survival hosts.

Buds were cut with their respective branchlets from the lower and middle levels of the crown and stored in a refrigerator for short periods before treatment. Sectioning was done to a 60 μ thickness on a sliding microtome equipped with a freezing stage. This allowed the sections to be handled without breaking during transfer from one staining solution to another.

Stained sections were mounted in glycerine and observed under a stereo-microscope at forty-five times magnification. Detailed descriptions of the histochemical staining methods for enzymes are outside the scope of this short paper and those interested are referred to Vanden Born (1963), Nemec (1962), or Pearse (1953, 1954). Only those tests which gave relevant results are discussed below.

Results

No differences were detected visually in the intensity of staining between buds from different parts of the crown.

The bud sections from suppressed trees, stained for one of the respiratory enzymes - succinic acid dehydrogenase - gave, as an indirect result, a purplish colouration of lipid inclusions which were reacting with the INT reagent. The test for neutral lipids did not stain the pith of the trees of the first two groups, but all sections from suppressed trees stained dark blue.

In contrast to oxygen-rich carbohydrates, fats are oxygen-starved and are also hydrophobic. Turgor pressures in the cambial region were estimated at well over 200% of saturation ~~pressure~~ for the first two groups, and around 160% for the suppressed trees. Trees in the latter category are regarded as fully susceptible to *Sirex*. On a tree experimentally ring-barked at the butt, an effect similar to *Chermes* sucking was produced, manifest after some time in the form of unthrifty growth with weak buds. This tree also yielded a higher fat content.

No differences were found between the three groups in the relative activities of phosphatases, phosphorylases and the amount of tannins produced. In the peroxidase activity test, less differential staining of tissue was apparent in the suppressed group.

Dominants, mostly resistant to Sirex attack, are characterised by stronger staining for phenol oxidases which are localised in the chloroplasts.

Discussion

The varied range of experiments conducted to date tends to indicate that Sirex resistance is due to a complex combination of physiological factors. Susceptibility seems to depend on the tree's physiological condition at the time of attack and is probably an expression of the tree genotype, modified by a wide range of phenotypic characteristics induced by environmental conditions. Favourable silvicultural treatment is one such factor. Unfavourable influences on the other hand may be site deterioration, climatic factors, wounding of the cambium, an imbalance between the crown and root systems through defoliation by insects or fungi, or lowering of the overall vigour by sap removal or concentration (e.g., damage by drought, fire or sucking insects). Influences such as these can induce a change in the physiological make-up of the tree. A sustained change at an early age is probably responsible for the suppression of trees in the stand. Some suppressed trees can be relatively resinous and when their growth rate is slow and their wood consequently dense, they are unattractive to Sirex. Vigorous dominants were found to produce consistently high levels of resin and phenolic compounds (Coutts, 1965), which also render them unattractive to the insect.

Authors, cited by Mutton (1962) and others, have commented on the increase in the fatty acid content -

(a) in logs after felling and storage (Kahila, 1957; Mutton, 1958);

(b) in trees during the winter months (Hilditch, 1951; Arrhenius, 1942); or

(c) in the resin upon wounding (Anderson, 1955).

We can also safely assume that when conversion of fats to carbohydrates is inhibited by damage to living cambial cells, an accumulation of fatty acids can occur in the butt and root tissues, if their upward flow is blocked. Our many observations in Tasmania indicate that the larger Sirex larvae are usually found in basal parts of the logs, in tree butts, or tunnelling towards the roots in trees which were suppressed as a result of the environmental conditions outlined above.

It is not fully understood to what extent changes in the tree's metabolic processes in the fatty acid cycle are heritable and dominant. It is suggested that sustained periods of fat production are a more common feature of an unbalanced coniferous metabolism than has been hitherto thought, and can be manifest in a moribund tendency if the tree if forced to maintain this trend for prolonged periods.

The formation of fatty acid starts in plants at the point of acetate incorporation into the varied products of metabolism (Mudd and McManus, 1965). So far, very little is known on fat metabolism of pines and still less of its suggested relationship with a suppressed condition. This aspect is being investigated further in a study of the inter-relationship between the Sirex symbiotic fungus and its host.

Conclusion

An increase in the fat content and its irreversibility under yet unspecified circumstances is considered responsible for suppression in pines which provides a condition conducive to successful establishment of the symbiont and development of Sirex larvae. These conditions are obviously quite complex, although a working hypothesis for future steps in the investigations can be postulated as follows :-

The symbiotic fungus introduced at oviposition is "starved" in trees of low carbohydrate content, finding it necessary to produce its exogenous enzymes in quantity. Nevertheless, a fat-rich, low-oxygen substrate may be more suitable for the Sirex larva. The toxicity of the fungal oxidases is at a high level in such trees and may be enhanced by a hypersensitive reaction of the host towards the phenols (induced by the fungal attack), since these are foreign to the fat-biased tree metabolism. Such a relationship is near enough to being paradoxical. In the trees of intermediate susceptibility, where only a small proportion of the carbohydrate is converted to fats, the fungus is able to remain viable, but with a proportional lowering of its lethal effect through lessened production of the oxidative enzymes. The effect will depend on the rate of infection, although the possible influence of a fungal inhibitor should not be ignored.

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