Dispersal of the beech scale (Cryptococcus fagi Baer.) in relation to the development of beech bark disease[1]

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Cryptococcus fagi Baer., the primary pathogen in beech bark disease, disperses passively on air currents to find new hosts. There are steep aerial density gradients of dispersing larvae from individual infested trees, from which they disperse a mean distance of 10.3 m in a mean windspeed of 0.75 m per second. Greatest aerial densities occur at a height of 1 to 3 m but a few larvae are carried by up-currents above the canopy and so have a greater potential range of dispersal.

The efficiency of deposition of larvae is inversely proportional to tree diameter. The size of the adult population that developed on trees close to a heavily infested „source" tree was not proportional to the number of larvae deposited on them, suggesting heterogeneity in susceptibility of the trees to attack.

Beech bark disease is present in most of Britain's beech *(Fagus sylvatica)* forests killing a small but unquantified number of trees annually. It is endemic rather than epidemic. The trees affected are of limited importance commercially but the forests are in areas of natural beauty and have considerable amenity value.

The disease is caused by an infestation of the scale insect *Cryptococcus fagi* Baer. on the bole of the tree, followed by an attack of the ascomycete fungus *Nectria sp.* which causes bark death (Ehrlich, 1934; Parker, 1974). The ability of the pathogens to spread within and to some extent between forests has important management implications. This paper summarises some aspects of the dispersal of the primary pathogen *C. fagi*.

DISPERSAL

Larvae of some scale insects, like fungal spores and some lepidopteran larvae, are dispersed passively on air currents. Their dispersal is independent of flight behaviour and in consequence is easier to estimate and interpret. Larvae of *C. fagi* disperse mainly during August, September and October. Relatively few eggs become airborne, suggesting that activity of larvae plays some part in take-off. In studying dispersal of *C. fagi* our objectives were firstly to examine the distance/density relationship of larvae dispersing from a source and measure the vertical density profile of airborne larvae and secondly, to determine the factors affecting deposition of larvae on trees. We then attempted to relate these aspects of dispersal to the epidemiology of the disease.

The fall-off in aerial density of larvae with distance from an infested „source" tree within the forest was determined from suction traps placed downwind of the source and the data fitted to the regression equation $L_n y = a + b \sqrt{x}$ where y = density of larvae and x = distance from source. Curves of this shape with a sharp fall-off in density near the source and a long tail, have median distances dispersed (distance travelled by 50% of larvae) less than the mean distance (FREEMAN, 1977). The distances dispersed were estimated by the method of HAWKES (1972). In a mean windspeed of 0.75 ms^{-1} the median distance dispersed was 7.1 m, and the mean distance 10.3 m. The average spacing between trees in an unthinned crop is 1–2 m and therefore this limited dispersal is adequate for local spread within the forest.

As a result of turbulence and convective movements under the canopy (OLIVER, 1975) some larvae once airborne are carried upwards. The vertical aerial density profile of larvae within beech stands shows that greatest densities occur at 1 to 3 m from the ground, with a rapid fall-off in density above this. However, some larvae penetrated above the top of the canopy (12 m in height) and were trapped at 18 m, the highest point sampled. They represented a small percentage of the larvae trapped but in the faster moving air above the canopy they could be dispersed over longer distances which would depend on wind speed and the pattern of air movement over the canopy.

Dispersal of the larvae, therefore, appears to take place by two routes, one as a steep gradient in numbers of airborne larvae from local sources under the canopy enlarging foci of infestation, the other a shallow gradient above the canopy allowing potential long range dispersal and the formation of new foci of infestation. This seems analogous to gradients of dispersal suggested for some fungal pathogens eg *Phytophthora infestans* (MONT.) DE BARY (VAN DER PLANK, 1975).

DISTRIBUTION AND DISPERSAL WITHIN THE FOREST

Most dispersing larvae fall to the ground without landing on a host tree. There is no host-finding component in their dispersal and host selection presumably occurs after deposition on the tree trunk. In a comparison of the deposition of larvae on trees of different diameter, it was found to be more efficient on trees of smaller diameter, as expected by analogy with deposition of fungal spores (GREGORY, 1961); in addition, most larvae were deposited on the lower part of the bole.

Larvae were also experimentally trapped on trees which surrounded a heavily infested source tree. The size of the adult population on the trees around the source was determined and the population removed prior to trapping. The density of deposition on the trees decreased rapidly with distance from the source, as expected from the aerial density gradient of dispersing larvae. This simple distance/density relationship was modified to a small extent by the effect of tree diameter. In addition, it was found that the size of the previous adult population on individual trees was not proportional to the density of larvae deposited on them; trees adjacent to the source tree were not the most heavily infested.

This relationship between infested and uninfested trees has been noted in some early accounts of the disease (BOODLE & DALIMORE, 1911; RHUMBLER, 1914). The present results show that this is not a result of escape from attack but suggests heterogeneity in the population in susceptibility. The importance of the

host plant in the development of infestations is further suggested from the few trees in our sample area that were heavily attacked on the bottom part of the bole, the part on which most larvae were deposited.

CONCLUSIONS

Larvae of *C. fagi* disperse passively and the low windspeeds within a forest limit the distances dispersed so that gradients of aerial density from individual infested trees are steep. This dispersal probably enlarges foci of infestation. A small percentage of dispersing larvae are carried above the canopy and are capable of a longer range of dispersal, dependent on the windspeed and pattern of air movement over the canopy. This gives rise to shallow density gradients, allowing the formation of new foci of infestation some distance from the source.

Many trees within the forest remain at least temporarily uninfested, not as a result of escape from attack but probably due to differences in susceptibility. This limits the extent to which the disease is aggregated within the forest and probably also affects its rate of spread. It may be possible to exploit these aspects of disease development and by appropriate management, reduce the impact of this disease in our beech forests.

ACKNOWLEDGEMENT

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