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Field experiments on the spread of black currant reversion virus and its gall mite vector (*Phytoptus ribis* Nal.)

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SUMMARY

In two experiments the spread of reversion virus from a row of systemically infected black currant bushes heavily infested by the gall mite vector (*Phytoptus ribis* Nal.) was predominantly in the direction of the winds prevailing during the dispersal period. On each side of the sources there was a curvilinear decrease of galled buds and of virus infection as distance increased.

In another experiment a central source of mites and virus was surrounded by concentric hexagons comprising alternate rows of healthy and virus-infected bushes. At leaf-fall, galls were forty times more numerous on virus-infected than on healthy bushes; plants in the sector downwind developed the most galls and those upwind the least. On both healthy and virus-infected bushes in each sector, the incidence of galls decreased with increasing distance from the source. The gradients of infestation were steeper on healthy than on virus-infected bushes, especially in sectors upwind from the source. In some sectors the infestation gradients were distorted because many of the virus-infected bushes were so heavily infested that most of the buds became galled. The spread of virus to initially healthy plants decreased from 100 to 75% near the source, to zero at the periphery. More bushes became infected downwind from the source than upwind.

In each experiment more bushes developed galls than later produced symptoms of virus infection, the incidence of which was positively correlated with the number of galls recorded the previous winter.

INTRODUCTION

Black currant reversion virus, transmitted by the gall mite *Phytoptus ribis* Nal.,* causes the most serious disease of the black currant crop in Britain and some other European countries. Despite the prevalence of mites and reversion there is little detailed information on the pattern, distribution and manner of spread.

P. ribis can walk or leap short distances and is said to be distributed within bushes by rain or irrigation water. Distant spread may be by birds, insects or wind (Massee, 1928), although mites do not produce a thread that increases buoyancy. Aphids are now considered to be the most important insect carriers (Smith, 1960), yet the relative importance of the different methods of spread has not been investigated and

* Referred to as *Eriophyes ribis* (West.) Nal. in early publications and now sometimes considered to be *Cecidophyopsis ribis* (West.).

may vary with site and season. In recent experiments at East Malling no insect was sufficiently numerous during the dispersal period to explain the distribution of mites, and aphids were discounted (Thresh, 1965*a*, *b*). Spread was attributed to wind, which is considered to be mainly responsible for spreading an eriophyid in North America (Slykhuis, 1955), despite some association with aphids (Gibson & Painter, 1957).

P. ribis accumulates on the surface of galls during the dispersal period and under favourable conditions stands erect, balancing on the anal pad with legs waving in the air (Taylor, 1914). Mites then leap away and this has been interpreted as a response to passing insects (Warburton & Embleton, 1902). However, if wind is the main agent of dispersal the phenomenon may be an adaptation analogous to that of certain fungi for passing through the still boundary layer into the turbulent air stream (Gregory, 1961).

Lewis (1902), Lees (1920), Massee (1926) and Smith (1963) recorded the spread of mites to neighbouring bushes, and galls were more numerous in the leeward half of one experiment than to windward (Hatton, Amos & Tydeman, 1925). Similarly, reversion virus spread to neighbouring bushes (Swarbrick & Berry, 1937) and into plots growing to the east and west of a severely affected plantation (Amos & Hatton, 1928). Elsewhere it was impossible to distinguish between spread from outside sources and spread from foci of infection that were planted intentionally or unintentionally (Lees, 1924, 1925; Swarbrick & Berry, 1937; Spinks & Clothier, 1936). These difficulties were avoided in the present experiments to elucidate spread in the field and to facilitate a rational approach to control measures.

MATERIALS AND METHODS

In each experiment, 2-year-old 'trap' bushes (var. Wellington XXX) that had been pruned almost to ground level at planting were exposed to mites spreading from heavily infested sources. The latter were flowering bushes (var. Wellington XXX) about 4 ft. high, that had long been totally infected with reversion virus. There was at least 100 galls on each source. Each gall may contain up to 35,000 mites (Collingwood & Brock, 1959) that may disperse at the rate of 1000 an hour (Taylor, 1914). The trap bushes were originally free of mites, as they had been propagated from carefully selected cuttings in an isolated nursery sprayed five times with endrin in April, May and June. Samples of buds were examined for mites immediately after planting and were found to be uninfested.

Experimental sites

The preliminary experiments were about 40 yd. apart and orientated similarly, at sites having the same aspect as standard meteorological equipment (including a Dines anemometer) situated 400 yd. to the east. The hexagon experiment was 600 yd. west of the previous ones and in a less exposed situation. All infested bushes were removed from around each experiment and possible sources of contamination were at least $\frac{1}{4}$ mile away.

Experimental design

Preliminary experiments (*planted March* 1962 *and March* 1963). In the first experiment forty healthy bushes were planted $2\frac{1}{2}$ ft. apart in each of five rows 6 ft. apart.

A source bush was planted in the centre of each row to form a line running from east to west.

In the second experiment eight rows were 6 ft. apart with a source bush in the centre of each row and twenty-five healthy bushes on each side. Bushes were 2 ft. apart in the centre of the plot and 4 ft. apart at the ends, where little spread was expected.

Hexagon experiment (planted January 1964). This experiment was designed to elucidate the spread of mites and virus in relation to wind direction and it was made very sensitive by including bushes already infected with reversion virus, which are highly vulnerable to mite infestation (Thresh, 1964). A circular plot would have been appropriate, with a single source of mites placed centrally and with healthy and

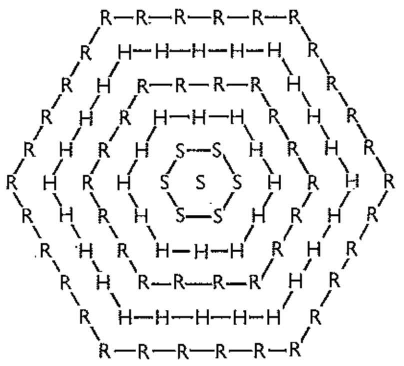

Fig. 1. The arrangement of the bushes in the centre of the hexagon experiment. S = source of mites and virus, H = healthy trap bush, R = reverted trap bush.

virus-infected bushes exposed alternately along radii. As such an arrangement was impracticable, S. C. Pearce and D. H. Rees suggested that the bushes should be planted in staggered lines, to form a series of concentric hexagonal rows (Fig. 1). Seven bushes formed the central hexagonal source, while the surrounding seventeen hexagonal rows were planted alternately with healthy and reverted trap bushes. The bushes and rows were 2 ft. apart in the central twelve hexagonal rows and 4 ft. apart in the outer five (Fig. 1).

Observations

The period of mite dispersal was determined annually in experiments to be described elsewhere. Successive batches of plotted plants were exposed at weekly intervals alongside heavily infested sources and dispersal occurred mainly through the blossom period when the prevailing wind was from the south-west.

Mites spread from the sources to the early growth of the adjacent bushes and shoots infested at the apex developed severely malformed leaves. These were conspicuous by mid-July, when records were made.

By leaf-fall, axillary and apical buds which had become infested with mites developed into rounded galls, which were counted. The position of each gall was noted as the number of nodes from ground level.

Symptoms of virus infection were conspicuous from the outset on all the source bushes and on the infected bushes exposed in the hexagon experiment. Bushes becoming infected during the experiments were diagnosed by examining the blossom as flowering began and by fortnightly inspections of the leaves. All primary spread was detected by such detailed recording during the second year of each experiment and it was unnecessary to retain the bushes for a third year, although this was done in the preliminary experiments.

RESULTS

Preliminary experiments on spread from line sources

Little spread of mites occurred in 1962 and only nine of the 200 bushes developed shoots with mite-affected leaves. Eight of the affected bushes were in the north-east quadrant, suggesting that spread had been mainly in the direction of the south-west

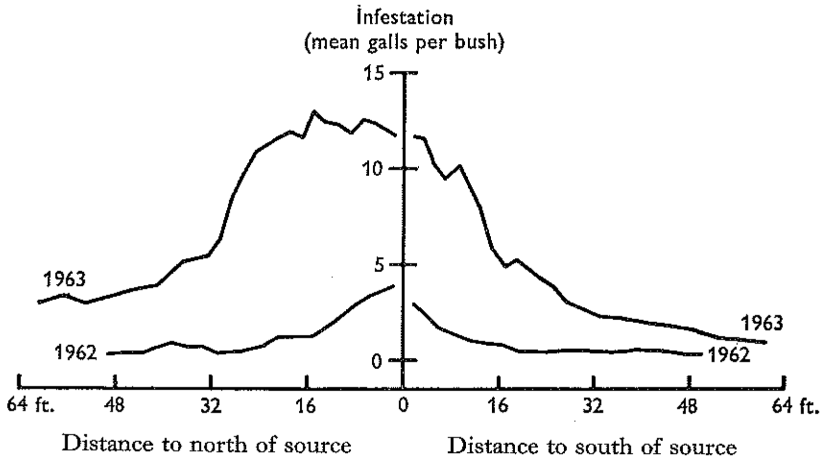

Fig. 2. The spread of mites to healthy bushes exposed to the north and south of line sources in the preliminary experiments.

winds prevailing during the dispersal period. There was a similar trend in the 1963 experiment, when mites spread extensively and fifty-four of the 400 bushes developed shoots with mite-affected leaves.

Far fewer galls developed in 1962 than in 1963, when galls were as numerous at the periphery as they were on bushes alongside the sources in 1962 (Fig. 2). Nevertheless, even the most heavily infested bushes had less than 25% of the buds infested and the gradients of infestation would have been little changed if more buds had been available for colonization (Gregory, 1948). Galls were largely restricted to the lower half of each affected shoot and as in previous experiments (Thresh, 1965*c*) the peak of infestation occurred 5–10 nodes from the base.

In both experiments galls were concentrated in the north-east quadrant. The infestation decreased curvilinearly with increasing distance to the north and south of the sources in 1962 and to the south in 1963 (Fig. 2). A peak of infestation occurred 10–14 ft. to the north of the sources in 1963, followed by a rapid decrease with distance. Similar distributions with a peak downwind from the source have been recorded for fungal spores, when deposition from an elevated source was influenced by winds blowing consistently from one direction (Schrödter, 1960; Sreeramulu & Ramalingam, 1961). This occurred in 1963, but not in 1962, when winds from the north-east were almost as frequent as those from the south-west.

The spread of virus was not apparent until the second year of each experiment. Even then the leaf symptoms were often inconspicuous and restricted. Only about half the infected bushes had previously produced the glabrous flower buds typical of reversion disease and invariably these were restricted to a few nodes of each affected shoot.

Nineteen bushes became infected by spread in 1962, when symptoms were restricted to few shoots and to only one of each bush affected at blossom. More infected bushes occurred in the north-east quadrant of the plot than elsewhere and sixteen were within 20 ft. of the source, compared with only three 20–50 ft. away.

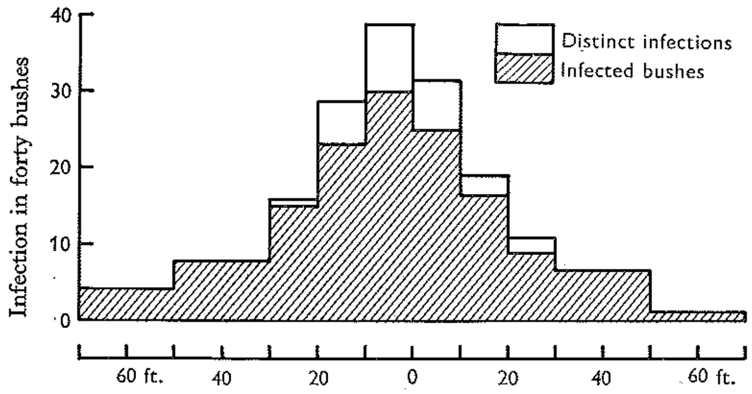

Fig. 3. The spread of virus to healthy bushes exposed to the north and south of a line source in 1963.

Virus spread in 1963 was much greater than in 1962, although again the number of infected bushes was less than the number previously recorded with galls. Infection was concentrated in the north-east sector and decreased with increasing distance from the source (Fig. 3). Spread was so intense that some bushes near the source must have been infected more than once, as they developed glabrous flower buds on several different shoots. Other bushes developed leaf symptoms on branches remote from those with affected blossom; such 'multiple infection' decreased with increasing distance from the source and did not occur beyond 30 ft. (Fig. 3).

Spread from central hexagonal source

The slight infestation of the *healthy* bushes was similar to that recorded in 1962 and only four shoots bore mite-affected leaves. A total of 545 galls was found after leaf-fall, and 216 of the 462 bushes were infested, with an average of only 1·2 galls per bush.

The *reverted* bushes were highly vulnerable to mites; about half their shoots developed malformed leaves and 23,281 galls were found after leaf-fall. Only four bushes escaped infestation and there was an average of 50·6 galls per bush. The forty-fold difference between the numbers of galls on healthy and reverted bushes was even greater than elsewhere (Thresh, 1964), due to climatic differences and to the small plots used previously, when there were so many sources of mites that there was much multiple infestation of the reverted bushes.

Differences in the degree of multiple infestation also explain why the ratio between galls on reverted and healthy bushes in the hexagon experiment was at a maximum in the least heavily infested sectors and in the peripheral rows.

The distribution of galls between sectors was very similar for the healthy and reverted bushes (Fig. 4). Most galls occurred in the sector 30–90° north of the source,

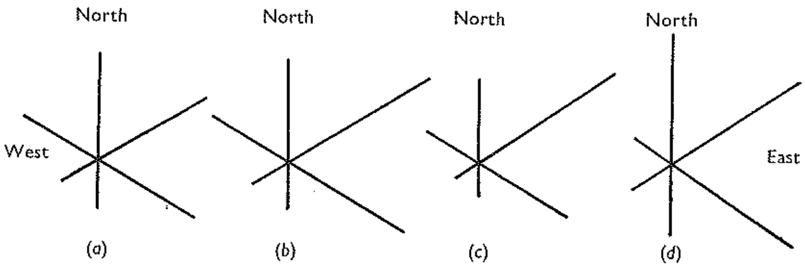

Fig. 4. The spread of mites and virus into each sector surrounding the hexagonal source. In each diagram the lines are proportional in length to the number of galls or virus-infected bushes.

with fewest in the 210–270° sector. This suggests an influence of the prevailing winds. However, many galls were found to the north-west and south-east and their distribution was not closely correlated with the duration of wind from each direction. The correlation coefficients were not increased by considering only winds above 5 m.p.h. (Smith, 1960) or those occurring in dry, warm conditions favouring dispersal (Taylor, 1914; Smith, 1960). This suggests that dispersal was influenced by additional factors, of which air turbulence caused by the buildings and trees to the west and south may have been important.

In each sector of the hexagon experiment and on both healthy and reverted bushes, infestation decreased with increasing distance from the source (Figs. 5 and 6). For the healthy bushes the relationships were curvilinear; the gradients being steepest near the source and steeper upwind than downwind.

Each reverted bush had about 150 buds and near the source so many buds became infested that the majority must have been invaded by more mites than is necessary to cause gall-formation. Consequently infestation gradients were curvilinear in the least infested sectors of the experiment and almost linear elsewhere, because of multiple infestation (Fig. 5). Downwind from the source, but not in other sectors, the maximum infestation occurred 8–10 ft. away from the source.

Fewer bushes became infected with reversion virus than previously developed galls. In each sector, infection was zero at the periphery and increased curvilinearly to become almost total adjacent to the source, where there was multiple infection (Fig. 6). As with galls, more bushes were infected to the north and east of the source than to the south and west.

The hexagonal rows of fully reverted trap bushes were removed in January 1965

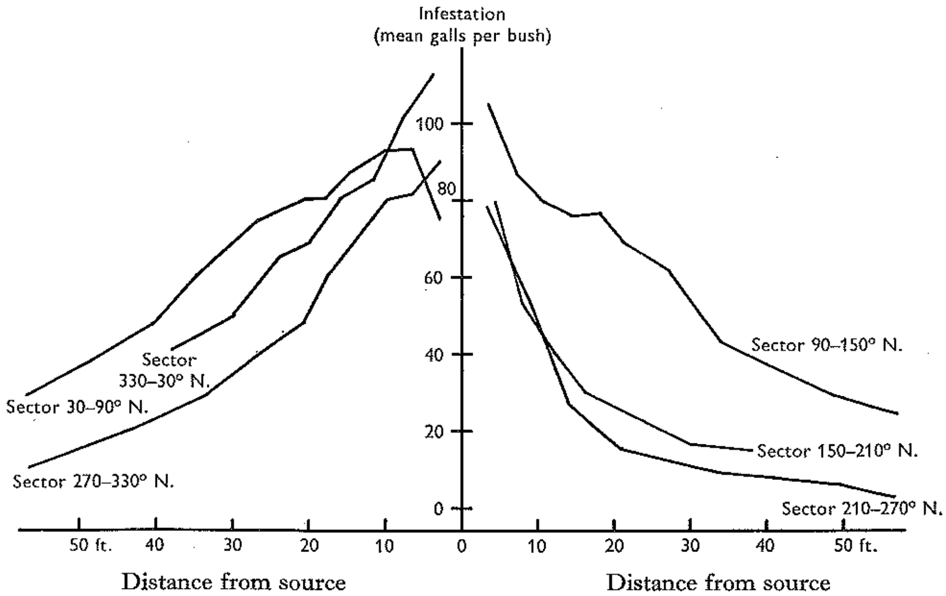

Fig. 5. The spread of mites to the reverted bushes exposed in each sector surrounding the hexagonal source.

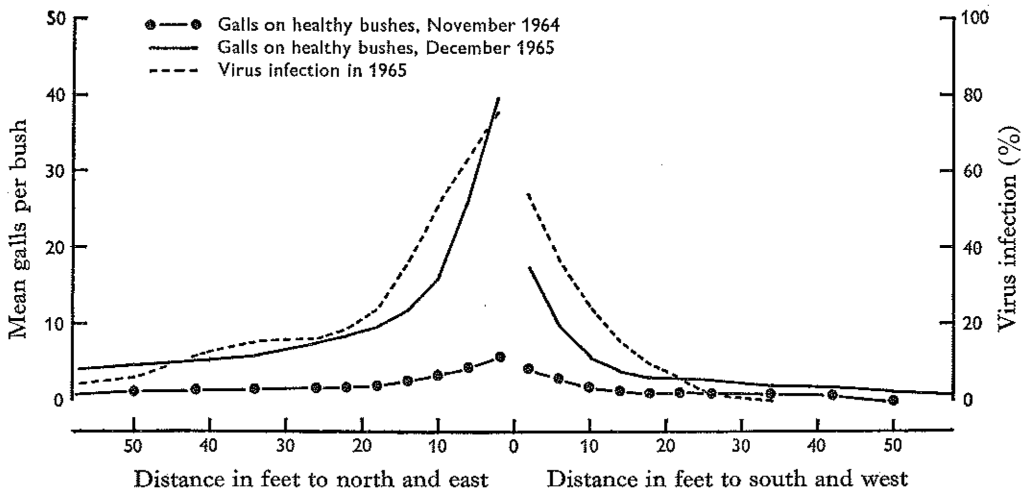

Fig. 6. The spread of mites and virus to the healthy bushes surrounding the hexagonal source.

to facilitate the growth and inspection of the previously healthy bushes. More than 2000 galls remained on the original sources and there were 545 galls on the initially healthy bushes. These were left unpruned and in 1965 the number of buds available for colonization increased sixfold compared with 1964. There was a corresponding increase in the number of galls and 3029 were found after leaf-fall. The increase in the infestation was similar in each sector and in each hexagonal row, so that the levels of the infestation gradients were affected and not their form (Fig. 6). This is consistent with the weather conditions during dispersal in 1965, which were similar to those of 1964 in being wet and mild with consistent south-west winds.

Bushes that developed reversion symptoms in 1965 tended to have the most galls when examined after leaf-fall, but these bushes also had the most galls when still symptomless in 1964 and the first appearance of symptoms was not associated with greatly increased susceptibility to mites. Other unpublished experiments have confirmed that the resistance of healthy bushes to mites decreases over several years as virus infection becomes systemic. Recently infected bushes are unimportant foci for further spread and mites have such difficulty in surviving on them that the infestation may die out, especially when acaricides are used. This emphasizes the importance of removing infected bushes before they are completely invaded by virus if spread is to be controlled effectively. Where prompt roguing lapses, bushes frequently become heavily infested with mites that menace all other bushes in the vicinity.

The association between galls and reversion virus

The number of mites reaching healthy bushes during the dispersal period was very much greater than the number that survived and caused galls (Thresh, 1965*d*) and the number of bushes with galls exceeded the number that became virus-infected. This is explicable if mites can feed and transmit virus only on reaching immature tissues inside buds. Such an explanation is consistent with the frequent appearance of virus symptoms on shoots developing near galls and with the correlation between the incidence of virus and the distribution of galls (Fig. 7). Moreover, acaricides that seem to act primarily on mites after they have invaded buds are less effective in preventing the spread of virus than materials forming toxic surface deposits (Thresh, 1965*a*, *b*).

All bushes with more than forty galls became virus-infected and the probability of infection decreased with decreasing numbers of galls. As in previous experiments (Smith, 1963; Thresh, 1965*b*) a small proportion of the bushes without galls developed virus symptoms. The significance of these infections is uncertain; galls may have been overlooked on such bushes, particularly if the affected buds were few, small or harboured a predator (Thresh, 1965*c*). Alternatively, the mites may have died after introducing virus, possibly because they were males or unfertilized females.

Healthy bushes are so resistant to mites that they develop few galls and each gall probably results from invasion by only a few mites (Thresh, 1965*d*), yet the number of virus-infected bushes in the three experiments was 25, 58 and 32% of the number with galls. Consequently, infection efficiency (*sensu* Gregory, 1961) was high in relation to the proportion of mites that became established, but low in relation to the total number dispersing. This suggests that the main factor limiting virus spread was the inability of mites to reach susceptible sites, and not because they failed to carry virus or because virus did not persist. The problem may be resolved when new varieties of black currant have been derived from black currant × gooseberry hybrids that are immune to mites yet susceptible to virus by graft-inoculation. Such varieties will show field immunity to virus if mites are unable to reach susceptible sites.

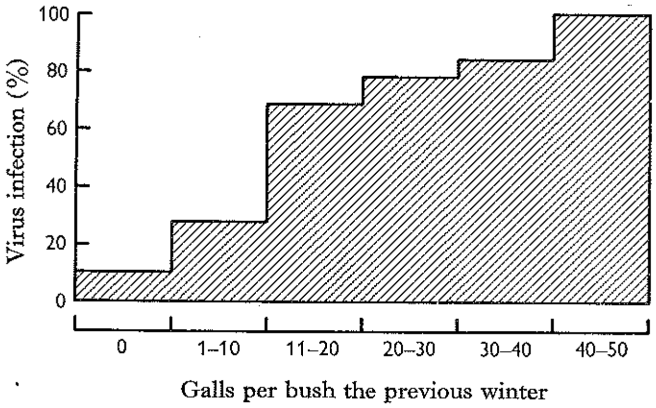

Fig. 7. The incidence of virus in relation to the mite infestation recorded the previous winter. Combined data for all experiments.

DISCUSSION

Experimental technique

Systemic diseases of woody perennials tend to spread more slowly than those of herbaceous plants. Reversion is exceptional and the rapid spread in these experiments was typical of the rate at which black currant plantations deteriorate if they are near potent sources of infection. Nevertheless, there must have been enormous mortality of mites during dispersal. Annually there were 5–20 million mites in galls on the sources, yet the number of galls recorded on healthy bushes at the end of each season did not exceed 3029. Infestation efficiency was much higher on the reverted bushes exposed in the hexagon experiment.

The trap-bushes were inefficient in collecting mites, partly because they had been pruned at planting and little regeneration had occurred when dispersal commenced. Unpruned bushes at Long Ashton became infested more heavily than pruned bushes (Smith, 1963), but pruning is necessary to ensure satisfactory growth under the relatively dry conditions at East Malling. Ideally, bushes should be established a year before they are required and then left unpruned to present a large catchment area to mites and a favourable micro-climate.

The experimental designs had certain limitations and in each experiment mites spread to the periphery and presumably beyond. The experiments with line sources involved an equal number of 'trap' bushes at each distance from the source, but as the sources were not completely surrounded by bushes it was impossible to establish precisely any correlation between wind direction and dispersal. The hexagon design was an improvement, although different numbers of bushes were exposed at each distance and the bushes in each hexagonal row were not a uniform distance from the centre. Of even greater significance was the difference in susceptibility of the healthy and reverted bushes to mites. The sensitivity of the reverted bushes was invaluable in following the spread of mites at extreme distances from the source, where the healthy bushes seldom became infested. By comparison, the healthy bushes gave reliable infestation gradients near the source, where the reverted bushes became almost totally infested.

The assay of dispersal more effectively than is possible with bushes depends upon the development of suitable mechanical traps capable of sampling large volumes of air. Eriophyids are too small to be caught in automatic suction traps used for insects and too large to be caught efficiently in spore traps. Sticky plates (Staples & Allington, 1959) and a suction apparatus (Smith, 1960) have limitations, but rotorods may have possibilities. Clearly there is scope for the development of new techniques if the gradients of infestation reported here are to be compared with gradients in the deposition of mites and if infestation and infection efficiencies are to be determined accurately.

Practical implications

The experiments gave clear gradients of mite-infestation and the gradients of virus-infection were similar, but distinct. There are many similar curvilinear relationships that can be expressed by simple parameters determined by the amount of spread and the rate at which this decreases with distance (Gregory & Read, 1949). Spread is influenced by the size and arrangement of the source, by topography and climate and by the health, variety and size of the bushes exposed. Extrapolation of the curves indicates that spread decreases to zero only at great distances from the source, especially if this is large. Consequently, on present knowledge there is no fixed distance beyond which it may be considered absolutely safe to establish new black currant plantations or nurseries.

Bushes for certification must be isolated by 50 yd. in Scotland and 100 yd. in England. These arbitrary requirements usually decrease infection to a low level, although considerable spread sometimes occurs over greater distances from heavily infested plantations, where the number of galls may exceed 200,000 per acre. Moreover, an eriophyid mite of cereals occurred on sticky slides exposed 150 ft. above ground and $1\frac{1}{2}$–2 miles from the nearest known source (Miller, 1955). *P. ribis* may also be blown far, but the spread of both species is limited by their vulnerability to starvation and desiccation (Smith, 1960) and virus may not persist long in starving mites. Until these factors are investigated the maximum possible isolation should be given to all new plantings, which should be upwind rather than downwind of known infestations. There may be advantages in making plantations larger and fewer, provided that healthy young bushes are not established alongside diseased stocks. Extreme isolation should be given to bushes destined for propagation, particularly those of specially selected stocks.

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