Monoculture versus mixture: interactions between susceptible and resistant trees in a mixed stand

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ABSTRACT

The use of diverse genotypes is an effective way of spreading risks. For this purpose, a mosaic of pure stands, each consisting of a single genotype, may be adequate under certain conditions. Mixed stands may offer a bonus if and in so far as an interaction between resistant and susceptible trees in a stand will reduce damage by pest, disease, wind, etc. A survey of such interactions and the mechanisms involved is given with regard to diseases, including *Fomes annosus*, *Nectria cinnabarina* and *Lophodermium pinastri*. Beneficial effects for the susceptible partners in the mixture as well as harmful effects for the partially resistant partners are noted. The net effect for the stand is dependent on many factors, including the damage threshold. Consequences for testing designs are mentioned.

INTRODUCTION

In the decisions to either plant or avoid stands of mixed genotypes, many considerations must play a role. Pure stands of a single genotype often may cost less to establish, tend and harvest, they may promise to produce more timber of a higher value, they seem to require less silvicultural expertise. There may be no alternative to a pure stand in cases where only one resistant or locally adapted genotype is available.

Monocultures are, however, widely believed to attract diseases and pests and to be more vulnerable than mixed stands, especially in the long term. Multiclonal varieties have been regarded as a means of deploying not-too-resistant clones (Schreiner, 1965). Further, mixed stands may have the advantage of offering a more varied scenery and, under certain conditions, of giving a higher production (Heybroek, 1978).

Monocultures have health hazards that come in 3 forms: first they may constitute a large, undivided risk, and it may be better to spread risks; second, the concentration of susceptible plants per se might increase the disease rates of the individuals, while the interaction between neighbours of different susceptibility might reduce those rates; third, monocultures might stimulate the evolution of new, more virulent or aggressive forms of the parasite. This paper deals briefly with the first aspect and concentrates on the second.

Mixing of different species that serve as alternate hosts to the same rust (or aphids, etc.) has profound but evident effects and will not be discussed here.

The severity of some diseases is considerably affected by the microclimate in the stand. Mixing of species may influence disease severity in either direction by influencing the microclimate. This effect will not be discussed either.

SPREADING THE RISKS

The notion is widely accepted that the exclusive use of a single genotype (e.g. clone) over a large area entails an enormous risk: if the clone fails for any reason, the failure could be total over the entire area, thus causing almost insurmountable problems for the management of the forest and for the industries depending on it. It seems more acceptable to have 10 clones, each on one tenth of the area: even if the chance of failure of any of these is 10 times as great (supposing that each has the same chance of failure as the earlier monopolist clone) the prospective damage is only one tenth and can be much better absorbed. It is the wisdom of not putting all eggs in one basket. It is the philosophy of insurance: many small risks are less serious than a single big risk that could radically destroy continuity. Spreading the risk is a good common sense precaution.

From this limited point of view, there is little advantage in individual mixtures: planting 10 blocks of 1000 ha with 1 clone each would spread the risk just as effectively as planting 10 000 ha with the mixture of the 10 clones.

The individual mixture may have an advantage, however, if compensation occurs: compensation being the process in which the neighbours fill the gap caused by a failing tree, thus increasing their own production and more or less compensating for the loss. This mechanism may be particularly effective if the failure occurs early in the stands' development and if initial spacing was narrow. On the other hand, if 2-5 clones fail, the mixed forest would become defective over the entire area. That loss is less easy to handle than if the failing clones had been planted in pure stands, which could be salvaged and replanted.

These considerations might apply particularly to poplar planted at final wide spacing, which reduces the effect of compensation, and grown in short rotations. The latter silvicultural trait is among those mentioned by Kleinschmit (1979) as reducing the need for mixing.

A relatively safe situation may exist even when monoclonal stands are used, provided the number of clones used per region is not small, provided the clones have varying backgrounds, and provided they are backed up by a wide array of experimental clones which are being kept under test for different sites and which form a reserve from which old clones can be replaced when failing for some reason (Heybroek, 1981).

THE EFFECT OF INTERACTIONS

This section deals with the question of how far the damage to a susceptible plant is decreased if it is surrounded by resistant instead of susceptible plants. It seems important to study the mechanisms involved.

Trees with different levels of resistance are found mixed in:

- stands consisting of different tree species, differing in resistance;
- stands consisting of a seedling population of 1 species with variation in resistance;
- stands consisting of clonal mixtures, varying in resistance;
- stands in which trees of 1 species of different ages are mixed, while susceptibility to the disease in question is limited to a narrow age-class.

This means that experience gained with traditional 'mixed stands' can be used to understand and perhaps to predict what will happen in a clonal mixture. However, in spite of the customary interest by foresters in the advantages and disadvantages of mixed stands, literature does not abound with well-documented examples of diseases that are much more serious in pure than in mixed stands. A case often cited, having the charm of the exotic, concerns *Hevea brasiliensis* (Willd.) Muell.: this species is said to be severely damaged by leaf disease if grown in pure stands in South America, but to be mainly healthy in the neighbouring virgin forest where it occurs singly between other species (Boyce, 1954). The search for examples is complicated by the fact that in the older literature, examples were collected and used mainly to prove or disprove the idea that diseases etc. are bound to be more serious in 'unnatural' stands than in 'natural' ones (Boyce, 1954; Peace, 1962, p. 18).

The disease process can be divided in 2 phases, and in both neighbours can play a role. In the first phase, the individual host-tree must be reached by the parasite, and in the second, the parasite must multiply or spread on or in the host until the damage-treshold is reached.

Reaching the host

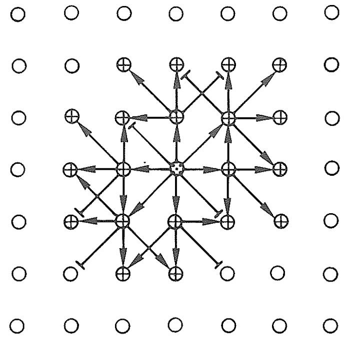
In the first phase, in which the host is reached by the parasite, 3 groups of cases can be distinguished.

1. In one group of cases, the host needs to be reached only once: once the

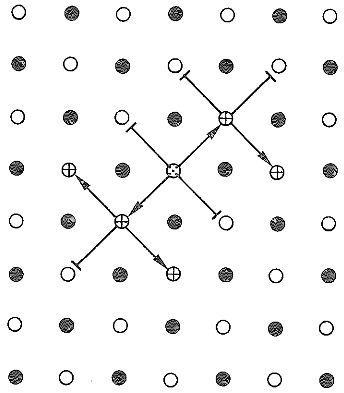
parasite has reached the tree, it can survive and spread in it or on it. This applies for example to perennial cankers, wood inhabiting fungi, etc.

The presence of resistant neighbour trees can have a delaying effect, which may or may not be of practical use, as illustrated in the following examples:

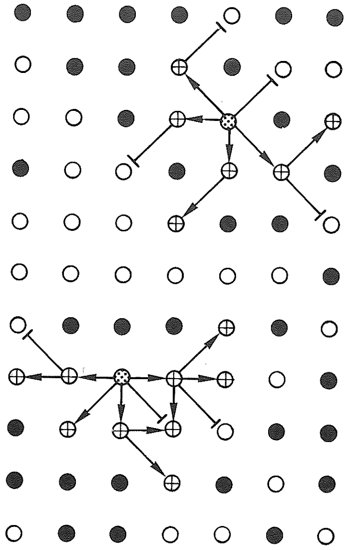
- The chestnut blight spread quickly through most of the area of *Castanea dentata* (Marsh.) Borkh., scarcely differentiating between pure and mixed stands. Some outlying stands or individuals escaped at first, but even isolated trees, planted in the Midwest of the United States, far outside the natural area of the species, were finally reached and succumbed.
- The perennial canker of beech, caused by *Nectria ditissima* Tul., was a rarity in the original mixed coppice-with-standards in north-eastern France. It increased to epidemic levels after these forests were converted to pure even-aged beech woods (Perrin & Vernier, 1979). Apparently, under the old regime, the presence of many non-hosts allowed even susceptible beeches to escape infection.
- Several tree diseases spread through live root grafts; for some, even mechanical root contact is sufficient (Epstein, 1978). Among them are oak wilt, Dutch elm disease and *Fomes* root rot. It seems plausible that planting tree species susceptible to these diseases in mixtures with resistant individuals, of the same or of other species, will greatly reduce this type of spread of the disease. Indeed it has been shown that both oak wilt (Epstein, 1978) and *Fomes* root rot (Rennerfelt, 1947) are much less severe in mixed than in pure stands. From the models in Fig. 1a-c it appears, that the use of 50 % resistant trees is enough to virtually stop the spread from one focus, provided transmission occurs between neighbours only. Roots may, however, extend much further than the crown of the tree, making root contacts possible among trees that are not direct neighbours (Stiell, 1970; Eis, 1978). If root contacts occur between diagonal neighbours in 50 % of the cases, reduction in infection is still considerable (Fig. 1): in the same time required to infect 20 trees in the pure stand, only 5 trees would be infected in the 50 % resistant stand. In the models of Fig. 1, systematic mixing was more effective than random mixing. The protective effect will clearly diminish as the root systems range wider, and tends to disappear when the initial infection is higher, that is, when the number of foci increases. There is also an age-effect as the relative range of the root system changes with age (Eis, 1978) and as mixtures of different species tend to be more difficult to maintain with increasing age. Perhaps the possibility of reducing the incidence of these diseases through mixed plantings should be explored further. It may be difficult to find non-hosts that can be mixed in without silvicultural problems, but even the admixture of partially resistant hosts, that is trees through which spread is slower, might give a worthwhile reduction of disease in the stand.



a. Spread in a homogeneously susceptible stand. 20 transmissions.



b. Spread in a stand with 50%, evenly distributed, resistant plants. 5 transmissions.



c. Spread in a stand with 50%, randomly distributed resistant plants. In two examples 6 and 9 transmissions are realized.

Legend:

● resistant plant
○ susceptible plant
——► spread of disease
——┤ unsuccessful attempt at spreading
⊕ infected plant
◌ focus

Figure 1. Spread of disease through root contacts; assuming that all direct neighbourships lead to transmission, but only 50% of the diagonal neighbourships; over a time period sufficient for two diagonal transmissions.

2. In a second group of cases, diseases that require an annual reinfection from outside, the poplar rusts *Melampsora medusae* Thuem. and *M. larici-populina* Kleb. can be taken as examples. In these, the fungus often has to come from far. A mixture of susceptible poplars with some non-hosts might at best cause a minor delay in the first infection and the onset of the build-up of the epidemic. This effect may be even non-existent if the whole stand is infected at the same time by a cloud of spores. (The effect of mixing on the build-up of the epidemic is discussed in the next section.)

3. Between these 2 groups, *Nectria cinnabarina* (Tode) Fries provides an intermediate case. Pathogenic strains of this fungus form annual cankers that continue to sporulate for 1 or 2 years. For a successful infection, wounds must be present at the right time of the year and under the right weather conditions. Genetic resistance occurs. If genotype, condition and environment of the host are favourable for disease development, a single tree can reinfect itself year after year; if not, the tree will lose the parasite for few or many years until a new colonization occurs. Then, a larger closed population of host trees is needed to maintain a local population of the pathogenic strain of the fungus. A single such tree, surrounded by non-hosts, might remain free of infection for many years as the fungus did not happen to reach it at the right moment.

For this intermediate category, in which a tree may shed or lose the parasite for some time until the next recolonization, parallels can be found in the island-theory of MacArthur & Wilson (1976). These authors, comparing the numbers of animal species present of islands of different size and at different distances from the mainland, conclude that the chance for extinction of a species on an island increases as the island is smaller and as the possibility for recolonization decreases where other islands or the mainland are more remote. Chances for extinction also depend on the size of the population: all populations fluctuate in size over the years, a small population can easily disappear completely in such a fluctuation. Now, the groups of host-trees may be regarded as ecological islands in a 'sea' of non-hosts; local extinction of the parasite on the group of host trees might in critical cases depend on the size of the group, and on the distance from the 'mainland', the source of reinfection. It further depends on the intensity of attack on the host or the amount of parasite present on the single tree: the 'population size'.

Returning to *Nectria cinnabarina*, it can be expected that at low levels of disease, a mixed stand of host and non-host trees may lead to better health of the hosts. Matters are complicated, however, by the fact that pathogenic strains can survive for some time as saprophytes. Local extinction of *N. cinnabarina* is pursued artificially by the nurseryman who practices sanitation rigorously. Once the nursery is 'clean', many susceptible moments will not lead to infection because of the absence of the parasite.

In forestry practice, this mechanism of local extinction of and delayed recolonization by the parasite seems of limited value, as it may require the reduction of the proportion or number of host trees to a level that is not interesting economically.

The build-up of a parasite population

Once the parasite has found the host tree, generally a build-up of its population is needed before the disease can reach the damage treshold. Here again, resistant neighbours may have an effect on the outcome of the process.

The classical and successful example is the multiline in oats, as described by Browning & Frey (1969). It consists of a mixture of several separate host-parasite combinations, in which host A is compatible with parasite race 1, and B with 2, etc., but not A with 2, nor B with 1, etc. Thus the spores of 1 generated on A and landing on neighbour B, will be ineffective and lost for the epidemic on A, and vice versa. Thus the build-up of the population of parasite 1 on the component A will be based on a severely diluted spore cloud, so that the build-up is delayed considerably.

The concept cannot be simply copied for all host-parasite combinations. Success depends on whether a reduction in the density of the spore cloud will be sufficient to delay the build-up of the population, and whether this delay will be sufficient to reduce the damage to the host. Then, size is important: the individual cereal plant is small, long and narrow, so that spores produced on it have a fair chance of landing on neighbouring plants. In comparison, the crown of a single tree provides a large volume of leaves with the same genotype. In the crown, a small epidemic could develop independently, unaffected by the presence or absence of a resistant neighbour tree.

The multiline is developed to employ vertical resistance. In forest trees, however, within 1 species, mainly some degree of partial, horizontal resistance can be found. A priori, mixing such trees does not look promising. More effect might be expected from mixing highly divergent genotypes: hosts and non-hosts, different species.

Certainly, not any mixing of trees with different levels of resistance will be beneficial. Although it might be hoped that the presence of the more resistant would somehow protect the less resistant plants, the reverse may happen as well: the less resistant plants may act as disease spreaders, overcoming the resistance of the more resistant partners. An example of the latter possibility is given by Maslow (1970, page 62):

"White elm (*U. laevis*) suffered in the prefecture Rostov, Ukraine, much less from Dutch elm disease than field elm (*U. carpinifolia*), at least in the earlier years of the epidemic. In plantings of the first and second growth class, where up to 100 % of the trees [of field elm, see page 61] got infected, no more than 7 % of the white elms died.

The condition of white elm was dependent on the abundance of spore infection and of stem damaging insects, the latter being dependent on the presence of field elm in the immediate neighbourhood of white elm: *in all stands where white elm occurred in mixture with the severely diseased field elm, dying of white elm was of much higher significance, in cases even nearly total.*" (Italics by H.M.H.)

LOPHODERMIUM PINASTRI

Some idea of what can happen when hosts with varying degrees of partial resistance are mixed can be gained from data on needle cast caused by *Lophodermium pinastri* (Schrad. ex Hook.) Chev., collected in the Dutch programme on genetic improvement of Scots pine (Squillace et al., 1972, 1975; Kriek & Bikker, 1973).

In one experiment, 14 Dutch provenances were compared with 4 German provenances under severe disease-conditions. The experiment contained 3 replicate blocks: each single plot consisted of 5 rows, each of 60 plants; spacing 1.50 m between rows and 1.20 m in rows. In each block, provenances were randomized. Four and eight years after planting, mortality and growth were assessed. The provenances clearly separated into 2 groups: after 8 years, the German provenances suffered an average mortality of 45.5 %; the Dutch provenances varied slightly around an average of 20.1 %. Mortality could be primarily attributed to needle cast, though *Armillaria mellea* (Vahl.) Quél., present throughout the area, accelerated the dying of weakened trees.

Plots of the 'resistant' provenances,when situated next to a plot of the 'susceptible' provenances (Fig. 2) showed a slightly significant higher mortality. The influence of the susceptible plots was not evident beyond the width of one neighbour plot, that is 10.5 m. Unfortunately, the limited number of susceptible provenances did not allow assessment of the reverse effect, that is, a possible lower disease rating in susceptible plots bordered by resistant plots.

Fig. 2 is based on assessments by Kriek & Bikker (1973), following the method that Squillace et al. (1972) had used with earlier data. For each plot of a resistant Dutch provenance, the deviation of its disease rating from the average provenance rating was plotted against its distance from a susceptible German plot. This showed that on average, a plot of a resistant provenance had a 6.5 % higher disease rating than the provenance average if it was adjacent to a susceptible plot. The more remote plots, necessarily, had a slightly lower disease rating than the provenance average.

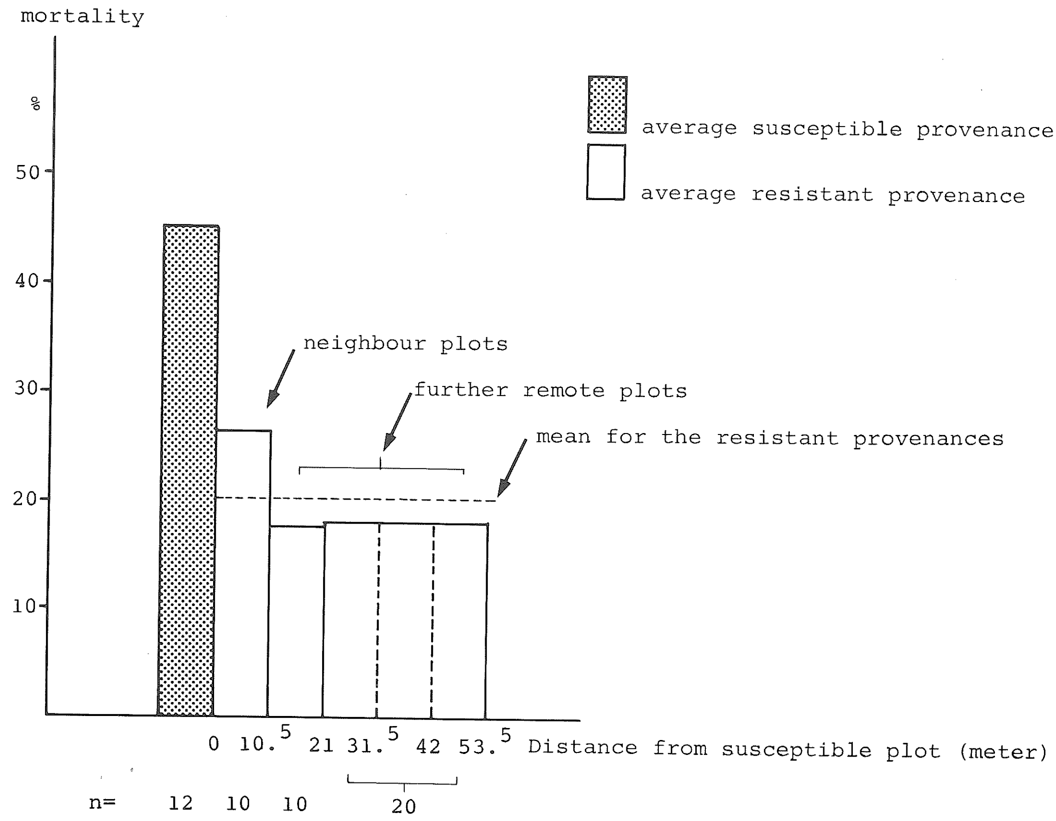


Figure 2. Disease ratings after attack by *Lophodermium pinastri* in plots of relatively resistant provenances of Scots pine, in dependence on their distance from the nearest plot of a susceptible provenance (based on data in Kriek & Bikker, 1973).

It was possible to study both effects, however, in a large scale half-sib test of 294 Dutch plus trees of Scots pine. Needle cast was assessed 7 years after establishment of the test, using a scale of 1 through 7, based on the presence of needle spots and on loss of foliage. The highest rating represented dead trees. The test consisted of six 7 × 7 lattice squares, each containing 4 replicates. One of the lattice squares, containing 49 families, was analyzed in detail for needle cast occurrence. Interaction between resistant and susceptible families was evident when the ratings of the 4 corner trees of the 4 × 4 tree plots were compared with those of the 4 inner trees. The inner trees were always surrounded by their own kind; the corner trees, however, by trees of other families. It was found that corner trees of resistant plots had higher average disease ratings than the inner trees, as they were mostly surrounded by trees of more susceptible other families; the reverse was true for the susceptible plots, while there

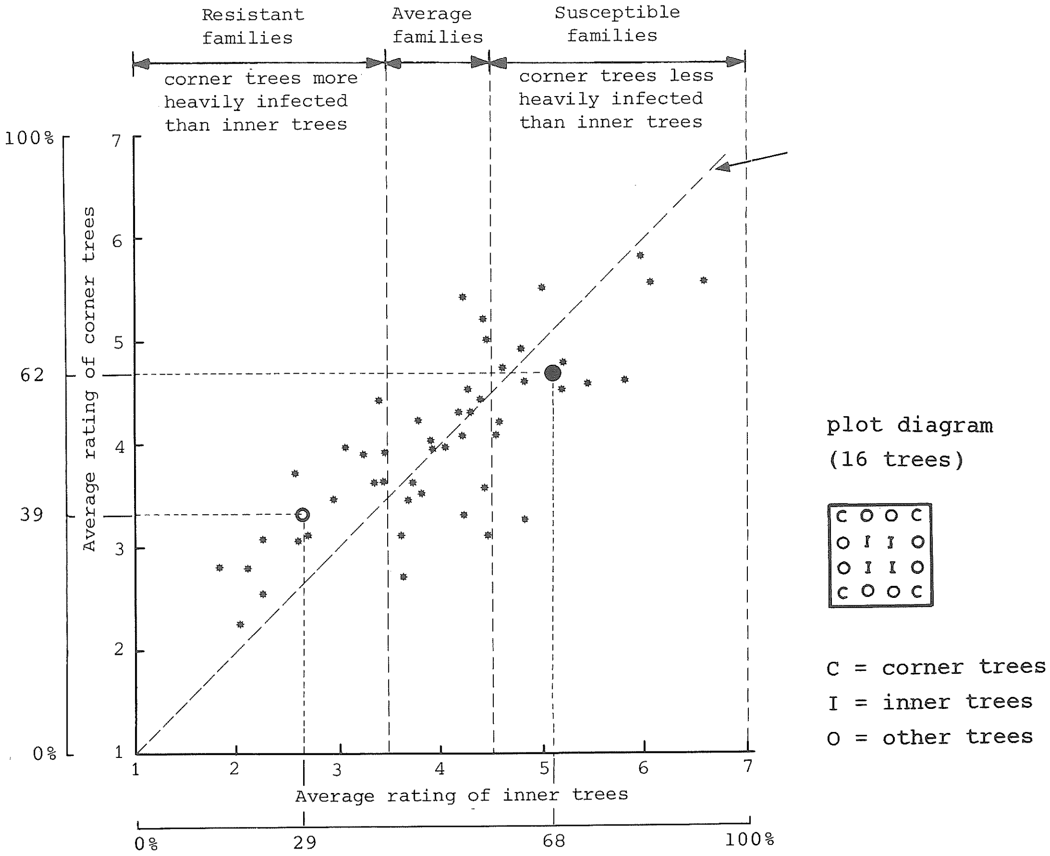


Figure 3. Average disease ratings (*Lophodermium pinastri* on *Pinus silvestris*) of 'corner trees' over 'inner trees' (see plot diagram) of the 4 plots of each of the 49 half-sib families in Experiment 2 of the progeny trial. The field ratings: 1 = healthy, 7 = dead, are converted to 0-100%. RL: hypothetical slope (= 1) if the differences between inner and corner trees were independent of resistance of families. o = median score for the (relatively) 'resistant families', ● = median score for the 'susceptible families'. In the former group, the inner trees are less diseased, in the latter group, they are more diseased than the corner trees. After Squillace et al., 1972.

was no difference between corner- and inner trees in the average families (Fig. 3).

If the resistant families of Fig. 3 as a group are contrasted with the susceptible families as a group, the data of Fig. 3 can conveniently be represented in a diagram like Fig. 4. In this 'mixogram', disease ratings (ordinate) can be given for a resistant host in pure stand (left-hand

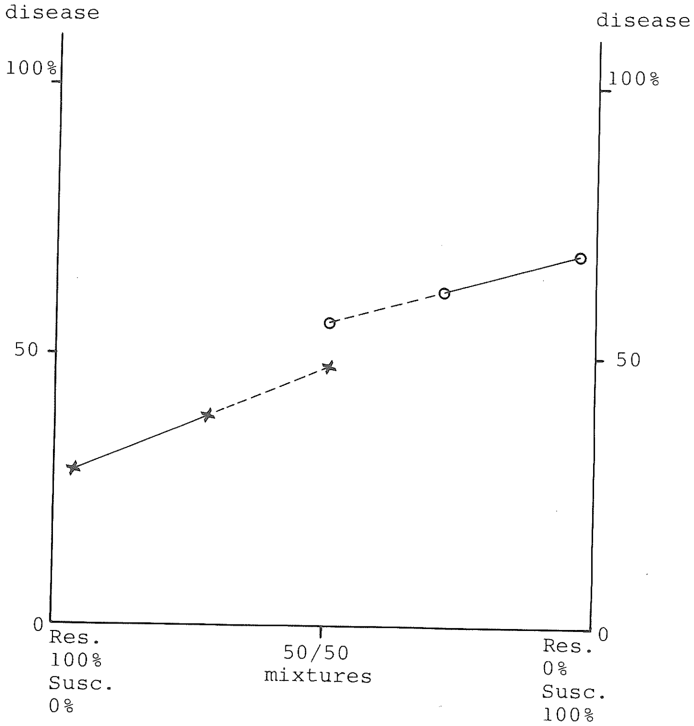


Figure 4. Disease rating (*Lophodermium pinastri*) for a group of resistant families (×) and susceptible families (o) of Scots pine grown in mixtures of different proportions (--- extrapolations).

side), for a susceptible host in pure stand (right-hand side) and for each of them grown in mixture in any proportion. The line for the resistant family group shows that the inner trees, which represent a more pure stand situation, are less diseased than the corner trees which represent a more mixed stand situation. The actual position of the line in the graph, and thus its slope, is dependent on some assumptions about the reach of this neighbour effect: even the inner trees may be affected to a certain extent by plots of different susceptibility in the periphery.

Fig. 4 is derived from Fig. 3 as follows. In Fig. 3 in both the relatively resistant and susceptible group, the median score was drawn. Then the median disease rating of the corner tree and of the inner tree of either group could be read on the ordinate and abscissa respectively. These were converted into percentage (1 = 0 %, 7 = 100 %), giving the values on the ordinate in Fig. 4.

Some assumptions had to be made in order to assign to the corner trees and inner trees certain values on the abscissa. It was assumed that the influence of a neighbour tree is proportional to the square root of its distance from the tree in question. This means that, if the surrounding trees are regarded as standing in concentric rings around the tree in question, the influence of rings farther out decreases quickly in spite of the fact that they contain more trees. The ratio of the influence of the first 3 rings (of 4, 4 and 12 trees) to that of the following 3 rings (of 16, 20 and 24 trees) is 9 to 4. This proportion is even increased if not only distance, but also interception or a filtering effect is considered to reduce the influence. It could be assumed, rather arbitrarily, that interception is 0 % for the first ring (direct neighbour), 20 % for the second ring, 40 % for the third, 60 % for the fourth, 80 % for the fifth, 90 % for the sixth. By doing so, the ratio of the influence of the first 3 rings to that of the following 3 rings is 7.4 to 1.1. Rings further out play a minute role. Under these assumptions, a tree surrounded by no more than 3 rings of its own kind, would still score $7.4/(7.4 + 1.1) \times 100\ \% = 87\ \%$ on the abscissa.

The half-sib test contained families of all levels of susceptibility, not just two. A corner tree, e.g. in a resistant plot, has in its first ring of 4 neighbours 2 of its own kind, and 2 'others' of 2 different families. These are samples of the entire population: 'resistant', 'average' and 'susceptible' families. In a simplifying approximation the 'others' are regarded as consisting of 50 % 'resistants' and 50 % 'susceptibles'. The situation is then reduced to a mixture between 'resistants' and 'susceptibles', or 'own kind' and 'the different kind'. The composition of the various rings of neighbours can thus be identified as to 'own' and 'foreign'; this is multiplied by the 'weight' or the relative influence of the ring, and values of the different rings added. Using higher interception-factors than in the above example (0 %, 50 %, 80 %, 90 %), the result is that corner trees would be influenced 72 % by their own kind and 28 % by the opposite kind, while for the inner trees the relation would be 97 % versus 3 %.

A size-factor is also apparent here: when the stand is fully grown, each plot of 16 trees will be replaced by 1 large tree, which will thus be situated at the 50-50 point on the abscissa of the mixogram. Although this tree could still be influenced by its neighbours, the entire situation of disease, susceptibility, spore flight and stand climate would be different, which would probably reduce the effect.

It is thus clear that a 'neighbour effect' does exist. From these data, it can even be predicted that in the more resistant families a further decrease in disease rating can be obtained by planting the tree in an individual mixture with a non-host, as was reported by Fischer (1957).

CONSEQUENCES FOR TESTING DESIGNS

A closer inspection of Fig. 4, and a tentative extrapolation of the lines shows several points of interest. Apparently, when grown in an individual 50:50 mixture, the differences in disease ratings between the resistant and susceptible families would even be smaller than now. On the other hand, when grown in pure stands, the resistant families would be less diseased, and the susceptible families more diseased than the average obtained in this test field. In a test field such as the one under consideration, the resistance of the relatively resistant families tends to be underestimated, and this effect will be greater when the plots are smaller. This bias is well-known in agricultural plant breeding (Parlevliet, 1975, 1979).

Squillace et al. (1972) discuss the merits of different test designs. As they found the disease may have a partially unexplained 'patchy' pattern, they would like randomized individual tree plots with many replications and wide spacing. Alternatively, to reduce interactions between families, they suggest rather large square plots (4 × 4 trees and more), in which only the interior trees are measured. Intermediate blocks would be undesirable. Isolation rows of a relatively resistant family between plots could also reduce interactions between families.

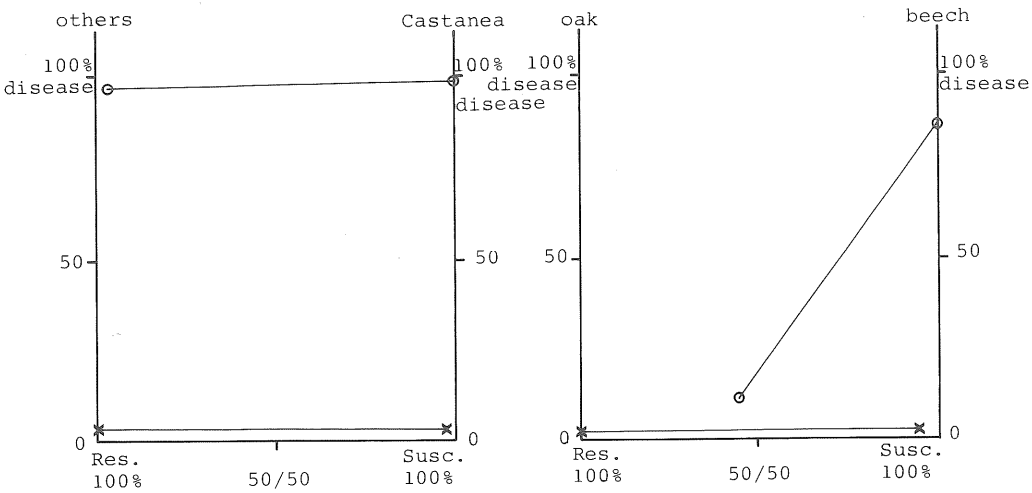
A similar but reverse effect is recognized in the testing for growth rate in forest tree breeding, as differences in growth rate between clones or families tend to be overestimated when plots are small.

The use of mixograms

In Fig. 4 it can be seen that the negative influence of the mixture on the resistant partner is similar to the beneficial influence on the susceptible partner. How would this change if a more resistant partner would be involved? Such plants would be less affected by the spores produced by the susceptible plants, their line in the graph would drop and become more horizontal. At the same time, as the resistant trees would contribute less to the spore cloud, the line of the susceptible group would tend to descend more steeply. The parallellism in Fig. 4 would be lost, the new graph would approach that of a mixture between a host and a non-host. On the other hand, if the susceptibility of the susceptible partner was increased, its line in the graph would rise and tend to become more horizontal as mixing with resistant material would tend to have less effect.

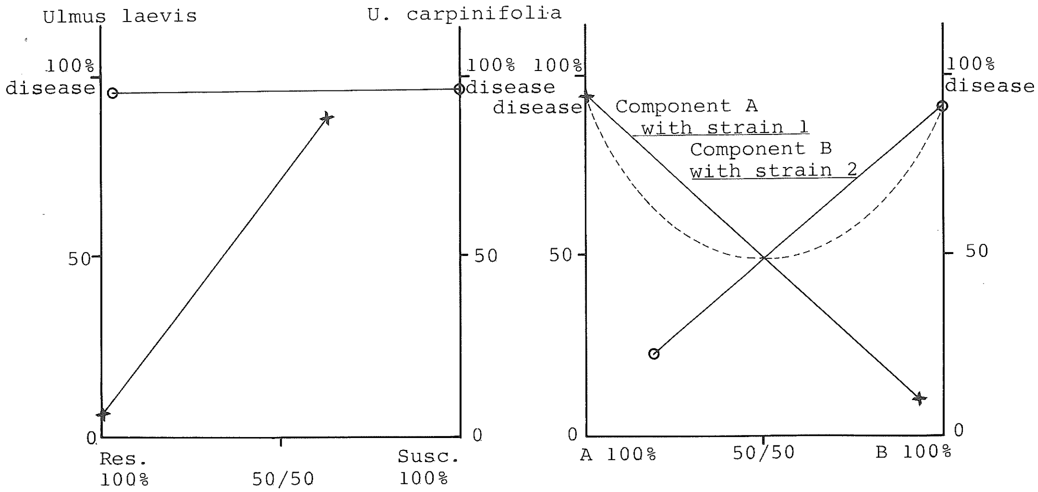
Thus the 'mixogram' may be a useful tool for visualizing the effects of mixing genotypes. Mixograms were tentatively sketched for some of the examples of host-disease combinations given above (Fig. 5). Note that in the case of the multiline, the pathogens for the 2 hosts are different.

A mixogram by itself, giving only biological information, cannot tell whether a certain mixture is advantageous or not. This will depend not only on the economic or other value of the partners in the mixture, but also on the level of the damage treshold (Fig. 6). If the damage threshold is high, at A, the 50:50 mixture is very advantageous as the disease rating of the susceptible host is reduced to below that level. If the damage threshold is



Chestnut blight on *Castanea dentata* (o) and other tree species (×) in the eastern American forest. Lines nearly horizontal: hardly any interaction.

Nectria ditissima in NE France (after Perrin). Susceptible beech (o) is heavily affected in pure stands, little if mixed with resistant oak (×).



Dutch elm disease in Ukraine (after Maslov). If susceptible *U. carpinifolia* (o) is admixed in stands of 'resistant' *U. laevis* (×), the latter is badly affected.

Simplified multiline with two 'lines' (with their pathogens). The dotted line would give the average disease rating of the mixed stand at different compositions.

Figure 5. Sketches of 'mixograms' of four different host-host-parasite combinations.

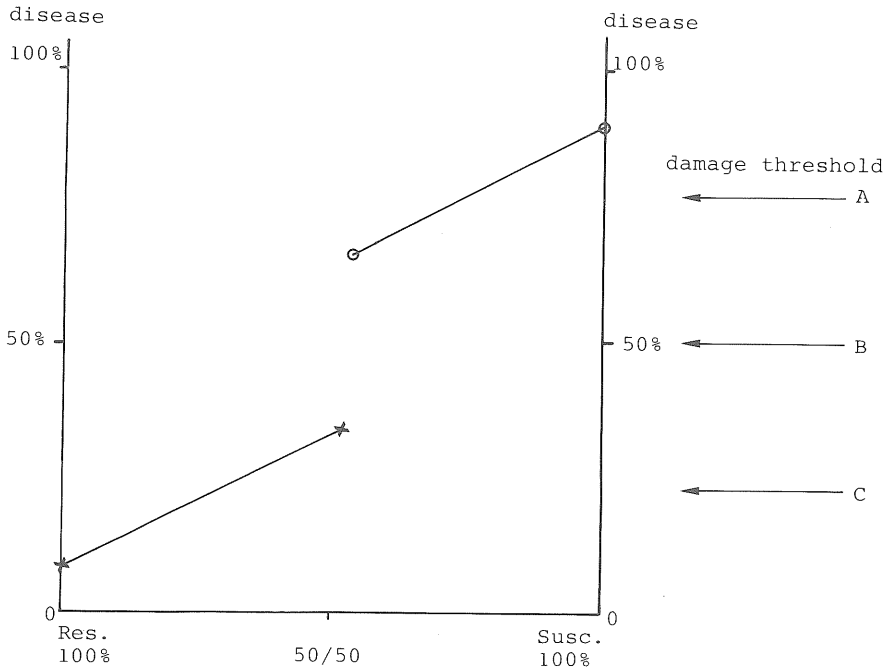


Figure 6. The effect of different levels of the damage threshold on the economic acceptability of mixtures of hosts with partial resistances. See text.

intermediate at B, mixing is of little use as the resistant partner remains good, the susceptible poor. If the damage threshold is low at C, the mixture is unadvisable as damage can only be avoided by growing the resistant partner in a pure stand.

CONCLUSIONS

1. In discussing the health hazards of pure stands, arguments stressing the danger of the undivided risk should be kept separate from those stressing that disease incidence must be higher in pure stands.
2. Broad generalizations on the effect of mixing of genotypes on the health of a stand or its components are dangerous. The effect may be different for each disease, site, host or case. Mixing may even be detrimental.
3. The mixing of a host with a non-host, which often means mixing different species, may have more effect than mixing hosts with partial or horizontal resistance, but it may entail greater silvicultural problems.
4. Mixing should be done consciously, after a study of disease and host has allowed the prediction that mixing is advantageous. Blind mixing will only in rare cases lead to useful reduction of disease incidence.

5. Mixing of genotypes is a poor substitute for breeding for resistance in forest trees.

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