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# Population structure and responses to disturbance of the basidiomycete *Resinicium bicolor*

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**Summary.** *Resinicium bicolor* (Alb. & Schw. ex Fr.) Parm. [= *Odontia bicolor* (Alb. & Schw. ex Fr.) Bres.] is an outcrossing resupinate basidiomycete associated with root and butt rots of trees, but is itself only very weakly pathogenic. The distribution of genets among every spruce stump in a 70-year-old 1250 $m^2$ spruce stand was analysed using somatic incompatibility testing. *R. bicolor* was present on 40% of 8- to 10-year-old stumps. Nineteen genets were found occupying 32 stumps; yielding probabilities of colonisation following establishment by basidiospores of 0.20–0.24 and by mycelial extension or dispersal of 0.16–0.20. The probability of colonisation decreased with increasing distance from a point of establishment. *R. bicolor* responded to both enrichment and destructive disturbances by the formation of an extensive cord system which enabled it to colonise discontinuously distributed resources and to overgrow fungi adjacent to it in a single resource unit, including *Heterobasidion annosum*.

**Key words:** Population structure – Disturbance – *Resinicium bicolor* – *Heterobasidion annosum* – Biological control

The advent of population biology in the ecology of basidiomycetes came during the late 1970s when it was realised, and explicitly stated for the first time, that genetically different mycelia of the same species could co-exist as physiologically and spatially discrete individuals (Rayner and Todd 1982). The basis of fungal individualism is somatic incompatibility, a genetic system which allows the recognition and subsequent acceptance or rejection of 'self' and 'non-self', and it is the expression of somatic incompatibility which gives structure to populations. These systems appear to be polygenic and multiallelic in those species which have been examined (Boddy and Rayner 1988). Consequently, the probability that any two unrelated individuals will be homogenic for all, and hence compatible, is remote. Moreover, the large number of possible combinations means that two strains which are homogenic at the somatic incompatibility loci are almost certain to be genetically identical over the whole genome, i.e. they belong to the same genet. Somatic incompatibility is (usually) expressed by the formation of a macroscopically visible zone of antagonism where two genetically different mycelia meet. It occurs in both the field and the laboratory, thus providing a valuable tool for the analysis of population structure and dynamics. Its scope is, however, limited by breeding biology. For example, care must be taken when studying species that produce asexual spores or have an inbreeding bias (Boddy and Rayner 1988). It is therefore necessary to ascertain whether the species under study exhibits a sexual outcrossing system or not, in the case of basidiomycetes a homogenic incompatibility working between homokaryotic mycelia with the same mating allele.

The simplest analyses of population structure are based on arbitrarily selected samples and spatial scales of sampling (Chamuris and Falk 1987). More quantitative procedures have been used to analyse the spatial and size structure of populations of resource-unit restricted and non-restricted saprotrophs (Rayner and Todd 1982; Thompson and Rayner 1982; Thompson and Boddy 1983). Rather more studies of pathogenic wood-rotting fungi are available (Childs 1963; Korhonen 1978; Kile 1983; Thompson and Boddy 1983; Stenlid 1985). Spatial and size distributions provide important information on processes of growth and establishment. For example, Stenlid (1987) constructed a

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model describing the spread of genets of *Heterobasidion annosum* (Fr.) Bref. between spruce stumps and trees. Dickman and Cook (1989) used mycelial extension rates to analyse age structure in a population of *Phellinus weirii* (Murr.) Gilbertson, and found that many genets were more than 1000 years old. Using a different approach, based on the selection of sites of different ages and degrees of disturbance, Dahlberg and Stenlid (1990) analysed the spatial and size distributions of four populations of the Scots pine (*Pinus sylvestris* L.) mycorrhizal mutualist *Suillus bovinus* (L.) Kuntze and found that the median life expectancy of a genet was 35 years.

*Resinicium bicolor* (Alb. & Schw. ex Fr.) Parm. [= *Odontia bicolor* (Alb. & Schw. ex Fr.) Bres.] is a resupinate corticiaceous basidiomycete of cosmopolitan distribution. It occurs in the wood of many coniferous and deciduous tree species where its close association with decayed and discoloured wood in butt and root rots has led many workers to its description as a pathogen (Schönhar 1973; Domanski 1976; and others). Unfortunately, in most of these studies the presence of *R. bicolor* seems to have been equated with causation of the rot itself, mainly because the sampling procedures used meant that saprotrophic and necrotrophic behaviour could not be distinguished. In a more critical study, Hallaksela (1984) recorded *R. bicolor* in 2% of butt-rotted and wound-decayed spruce but, importantly, did not recover it once from the invasion front of any butt rot.

The little experimental evidence available suggests that *R. bicolor* is at most a very weak pathogen. Siepmann (1976, 1981a, b) recorded that *R. bicolor* grew through experimentally induced wounds into living tissue of spruce [*Picea abies* (L.) Karst.] and Douglas fir [*Pseudotsuga menziesii* (Mirb.) Franco] roots. Harrington et al. (1989) conducted pathogenicity tests on a range of wood-inhabiting fungi, including *R. bicolor* wherein colonised wood dowels were inserted into living roots of balsam fir [*Abies balsamea* (L.) Mill.] and red spruce (*Picea rubens* Sarg.). Only in balsam fir did *R. bicolor* cause significantly more discolouration than in the controls. Also, it grew into root tissue, but the rate of colonisation, at 2 cm in 13 months, compares poorly with the rates of recognised pathogens such as *H. annosum*, which can invade spruce roots at 30 cm $yr^{-1}$ (Stenlid 1985).

More recently, workers have begun to study *R. bicolor* in a strictly saprotrophic context. Holdenrieder (1984) examined its distribution within stumps, Schönhar (1988) found it in 70% of second rotation thinning stumps of spruce and Shaw (1989) found it on 22% and 27% of experimentally generated stumps of western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] and Sitka spruce [*Picea sitchensis* (Bong.) Carr.]. All authors noted a strong reciprocal relationship between the distributions of *R. bicolor* and *H. annosum* and speculated on possible biological control of the latter by the former.

*R. bicolor* has a unifactorial (bipolar) mating system (Siepmann 1971) indicating an outcrossing mating strategy. Here, we report initial observations on the population structure of *R. bicolor* and its responses to disturbance.

## Materials and methods

### *Field sampling*

Nine spruce stands in central Sweden were examined qualitatively for the presence of *R. bicolor* and other wood-inhabiting fungi, and 62 stumps were excavated. Living roots growing close to stumps inhabited by *R. bicolor* were examined closely. Wood samples were taken from stumps, incubated in moist chambers at 21–23° C for 7–14 days, and outgrowing cords isolated onto Hagem agar (Stenlid 1985) supplemented with 5 ppm Benlate. Another stand, of 70-year-old spruce at Rånäs (18° 10′ E, 59° 50′ N), was selected for further study. The position of every tree and stump in an arbitrarily selected 25 × 50 m sub-site was mapped. All 80 spruce stumps from the previous thinning 8–10 years before sampling were inspected for the presence of mycelial cords and subcortical mycelial mats similar to those known to be produced by *R. bicolor*. Samples were collected and examined at × 400 magnification using transmitted light for the presence of large, hyaline asterocystidia, which are characteristic of the species (Nobles 1964). Cords and mycelial mats with asterocystidia were gently removed from their substratum and placed onto 2% Malt Extract Agar (MEA) containing 5 ppm Benlate. After incubation for 1–5 days at 21–23° C outgrowing mycelium was inspected for the presence of clamp connections and, if present, subcultured onto 2% MEA and incubated as before. Subcultures were checked for the presence of asterocystidia after 7–14 days growth. A total of 32 isolates was obtained.

Two stumps from the Rånäs site, which were known to be colonised by *R. bicolor* were excavated. Cords and subcortical mycelial mats were checked for the presence of asterocystidia and, if positive, mapped, isolated, checked again, and paired as above. Twenty isolates were obtained from stump 1, and 27 from stump 2. After sampling, stump 1 was sectioned at approximately 20 cm intervals and discs approximately 2 cm thick removed. These were incubated at 6° C for 42 days and then examined using incident light at × 40 magnification for the presence of *Heterobasidion annosum*. The distribution of *R. bicolor* was determined on the basis of the presence or absence of asterocystidia in samples of mycelium.

### *Tests of somatic incompatibility*

All possible pairings of cultures were tested using the following procedure. Inocula were cut from the leading edge of a 7–14 day old colony using a 3 mm diameter cork borer and placed onto 2% MEA plates in a pentagonal arrangement with one inoculum at the centre, i.e. six inocula per plate, with approximately 2 cm spacing between inocula (Fig. 1). Plates were incubated for 6–8 weeks at 21–23° C in the dark and scored for the presence of incompatibility on the basis of comparisons with control pairings. Pairings which were putatively compatible or which could not be assigned definitely were then repeated using the spatial arrangement of Dickman and Cook (1989) in which four inocula, two from each strain, are placed at the corners of a square in the centre of a plate, with approximately 2 cm between inocula (Fig. 1). Control and test pairings can be compared on the same plate with this arrangement. It was not used throughout the study due to the workload involved, which is approximately 10 times greater than that of the first method.

### *Mating tests*

Single spore isolations were made from one fruit body collected from a thinning stump of spruce. A basidiospore suspension was plated onto 2% MEA and incubated at 21–23° C overnight. Well-separated germlings were localized under × 100 magnification and their positions were marked using a dummy objective fitted with a metal tube with a diameter slightly less than the field of view. They were then picked off under × 20 magnification using a fine needle and cultured on MEA. Homokaryons were paired by placing 3 mm

**Fig. 1.** The expression of somatic incompatibility and compatibility in *Resinicium bicolor*. Six strains have been inoculated onto the upper plate and two inocula each of two strains onto the lower plates. In the top plate the lower four strains are compatible, and the upper two incompatible. The two strains in the lower right plate are incompatible, and those in the lower left plate compatible. The four inoculum arrangement gave the more reliable data. Zones of antagonism are *arrowed*

diameter inocula cut from 7 day old colonies 1–2 cm apart on MEA plates, and incubated as above. The pairings were examined periodically, both macro- and microscopically, for changes in the morphology and the emergence of secondary mycelium with clamp connections.

### *Growth in soil*

Growth in soil was analysed using a technique developed by Dowson et al. (1989). A sandy soil similar to the one at Rånäs was collected from a recently clear-felled spruce stand at Sätuna (17° 40′ E 60° 10′ N). The litter and humus layers were removed from five randomly selected sites and the underlying soil removed to a depth of 20 cm, sieved through a 5 mm mesh in order to remove large particulate organic material and preserve crumb structure and stored at −13° C until required. Living spruce branches 10–17 mm diameter were collected from the Rånäs site. Algae and lichens were removed using a wire brush and the branches were cut into 40 mm lengths and stored at −13° C until required. Wood lengths were sterilised by autoclaving three times at 24 h intervals for 30 min at 121° C. Two strains of *R. bicolor* were multiply inoculated onto 100 ml 2% MEA in 500 ml conical flasks and incubated at 21–23° C until an even mycelial mat had developed (approx. 14 days). Sterile wood cylinders were added and incubated until well colonised (approx. 50 days). One colonised wood cylinder was added to a space cleared in the centre of a soilfilled 24 × 24 cm bioassay tray (Nunc) and a non-sterile wood length (the 'bait'), or a similarly sized piece of silicone rubber tubing (the control) placed 40 mm away orientated in parallel with the colonised wood length. Soil trays were incubated at 15° C. Sterile water was sprayed onto the soil surface at intervals in order to maintain water content at 16%, which is close to the field capacity of the soil used. Mycelial extension towards and away from the bait was examined at regular intervals by inspecting the underside of the tray.

### *Statistical analyses*

The point of establishment of an individual genet was defined as the centremost stump within the clump of stumps occupied by it. Where a genet occupied just one stump, then that stump was defined as the point of establishment. The distribution of points of establishment was compared with the distribution of the remaining stumps using a coefficient of segregation (method of Pielou 1961, described in Greig-Smith 1983). This technique utilises nearest-neighbour relationships in that four classes of nearest neighbour can be distinguished; points of establishment and other stumps may have as their nearest neighbour either a point of establishment or another stump, and the number of individuals falling into each class can be tested for departures from random expectations using a contingency table.

In order to determine the proportion of stumps colonised at distances away from a point of establishment, concentric circles, as recommended by Hengeveld (1989), were drawn at intervals on the distribution map and the number of stumps colonised by the same genet as in the point of establishment, and the remainder, determined for each distance.

## Results

Tests of nine sibling homokaryons from one fruit body gave a 1:1 ratio of compatible and incompatible pairings, thus confirming the finding of Siepmann (1971) of a unifactorial mating system in *R. bicolor*. Clamp connections were not formed by homokaryons, but were observed in all pairings where a demarcation zone did not form. The so-formed heterokaryons yielded somatically incompatible reactions when paired with each other.

Initial screening at nine locations demonstrated that *R. bicolor* is one of the most frequent colonisers of spruce stumps in central Sweden. Other frequently encountered species of cord-forming fungi were *Armillaria borealis* Marxmüller and Korhonen, *Coniophora arida* (Fr.) Karst. and *Hypholoma capnoides* (Fr.) Kumm. Pathogenic behaviour towards spruce roots was observed once, where a root had grown through decaying wood colonised by *R. bicolor*. The fungus had colonised (intracellularly) the outer layers of cortical cells which had become separated from the inner layers by newly-laid periderm beyond which colonisation did not occur.

*R. bicolor* was recovered from 32 8- to 10-year-old stumps (40%) at Rånäs. Zones of antagonism produced during somatic incompatibility testing ranged from very weak, consisting of mycelial accumulations and some discolouration, to strong, where both pigment and droplets of liquid were produced (Fig. 1). Only two pairings out of the total of 496 (excluding controls) could not be assigned as either compatible or incompatible, and were excluded from further analysis. The spatial distribution map (Fig. 2) shows that the population at the sample site consisted of 19 genets. Sixteen occupied one stump each and the remainder occupied 3, 5 and 8 stumps, with maximal radii of 5.3, 23.0 and 7.4 m respectively. Analysis of the spatial distribution of points of establishment gave a coefficient of segregation of −0.20, indicating some clumping of points of establishment within the population of stumps, but this value was not significant (chi-square = 1.57 with 1 *df*, $P > 0.05$). The proportion of stumps colonised by a genet with increasing distance away from its point of establishment fell curvilinearly from 0.10 at 2 m to 0.00 at 38 m (Fig. 3).

Of the two stumps at Rånäs which were investigated thoroughly (see Materials and methods), stump 1 was

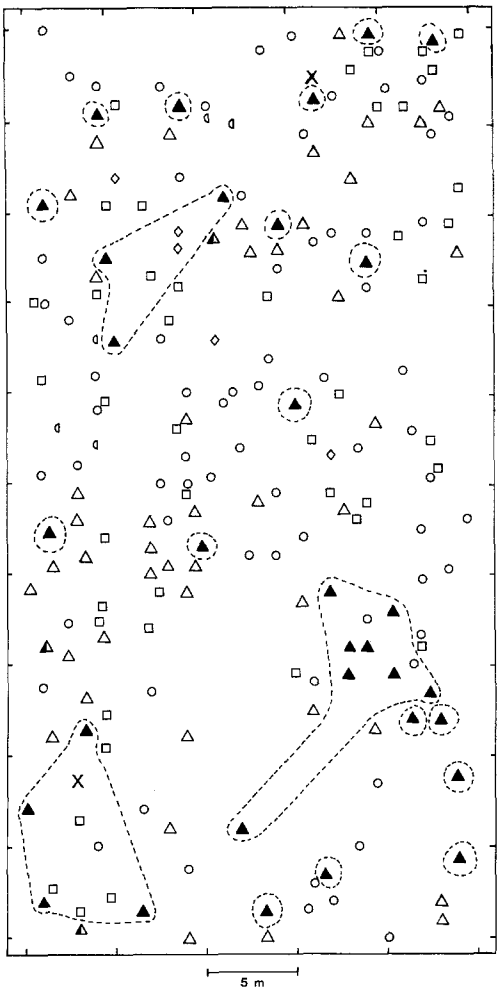


**Fig. 2.** The spatial and size distribution of *R. bicolor* in a spruce stand. *Triangles*, spruce stumps from the last thinning 8–10 years ago; *closed* – *R. bicolor* present, *open* – *R. bicolor* absent, *half open* – stump still alive. *Circles*, spruce stumps over 10 years old. *Squares*, Scots pine stumps. *Diamonds*, birch (*Betula* sp.) stumps. The stump marked with a × contained *R. bicolor* which was compatible with the group of four in the lower left hand corner (also marked with a ×). The *dashed lines* encircle groups of stumps occupied by the same genet of *R. bicolor*

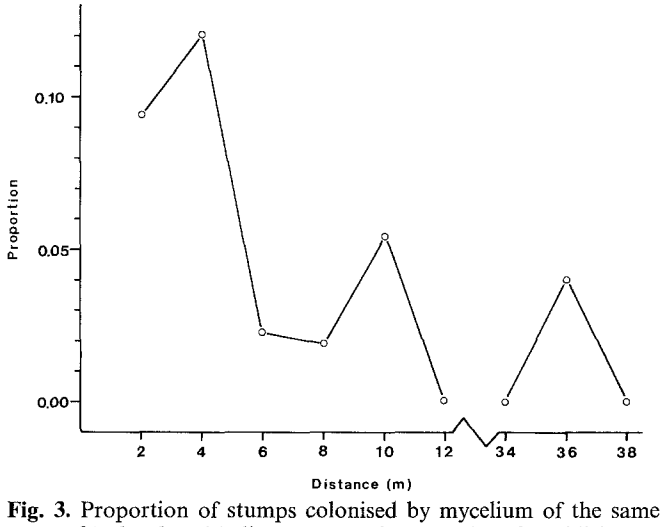


**Fig. 3.** Proportion of stumps colonised by mycelium of the same genet of *R. bicolor* with distance away from a point of establishment

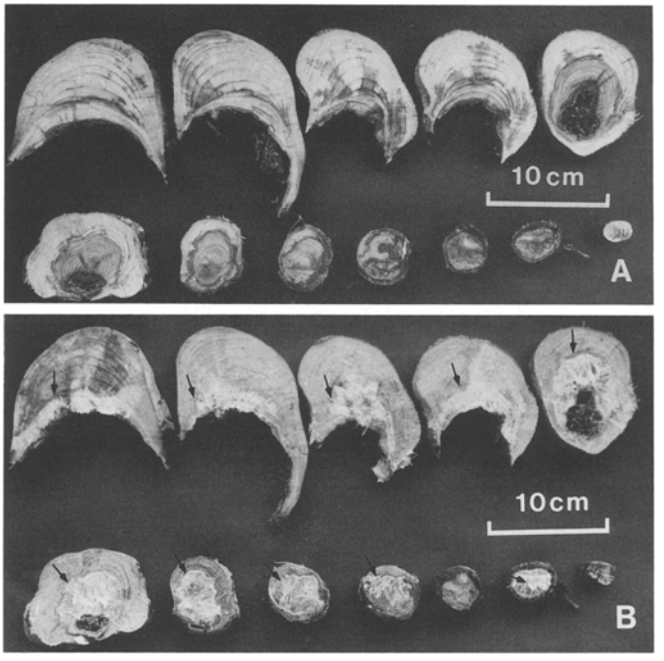


**Fig. 4 A, B.** Sections cut at intervals from a 2.20 m long root containing *R. bicolor* **A** before and **B** after incubation at + 6° C for 42 days. *R. bicolor* cords have extended into areas colonised by other fungi including *Heterobasidion annosum*

colonised, and rotted, by *H. annosum*. It contained *R. bicolor* in one root only. Cords of *R. bicolor* were present throughout the friable *H. annosum*-rotted wood of the root. The less degraded wood contained two genets, one in the proximal 30 cm and the other in the distal 1.80 m. Both individuals occupied a high proportion of the cross-sectional area of the root, but this proportion decreased distally in a pattern reciprocal to that of *H. annosum*. On incubated discs, cords of *R. bicolor* were formed at the margins of its domain and extended across areas uncolonised by it to cover the developing mycelium of other fungi, including *Verticillium* sp., *Cephalosporium* sp. and *H. annosum* (Fig. 4). *R. bicolor* produced very little aerial mycelium from other parts of its domain. All roots of stump 2 at Rånäs (see Materials and methods), and the root collar, contained the same, single, genet of *R. bicolor* and no *H. annosum*.

Mycelial cords of *R. bicolor* extended freely from the inoculum wood in both the control (no bait added) and treatment (bait added) trays (Fig. 5). In the controls, cords ceased to grow once they had reached the edge of the tray. Thereafter, smaller cords regressed and disappeared while thicker cords either became enlarged or did not change. In the trays where a spruce bait was provided, cords which came into contact with the bait ceased to extend, and colonised the bait by the production of diffuse mycelium. Cords which did not touch the bait continued to grow. Subsequently, cords extended from the newly colonised bait in the direction away from the centre of the tray. Cord extension from the original, central, inoculum was progressively reduced so that after 104 days cords from the bait comprised the only active extension front. New cords from the bait extended

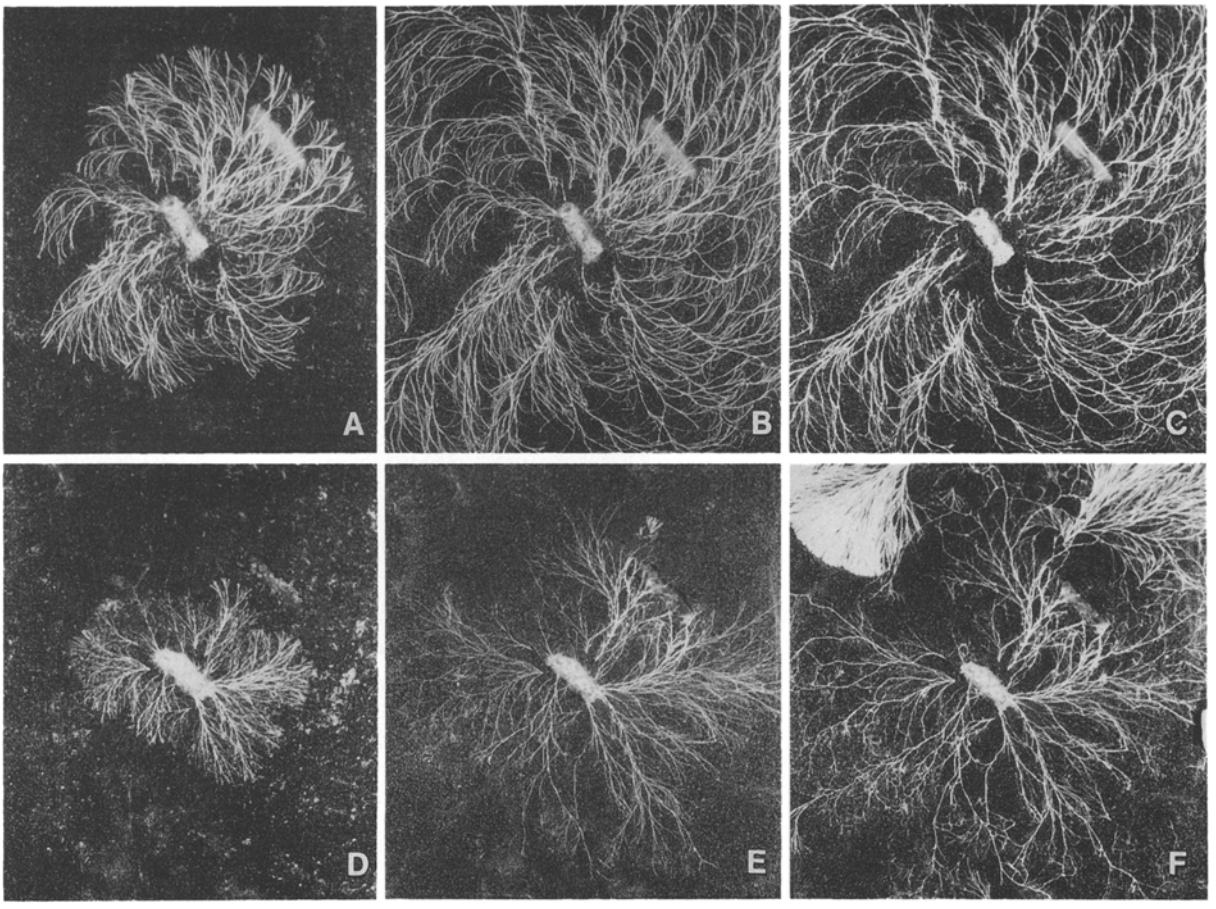


**Fig. 5 A–F.** Outgrowth of *Resinicium bicolor* cords from spruce wood through soil. **A, B, C** – control tray, with plastic tubing: **D, E, F** – treatment tray with spruce wood bait added. **A, D** taken at +28 days, **B, E** at +56 days, and **C, F** at +102 days

through areas already covered by cords from the central inoculum. Mean linear extension rate of cords during the first stages of outgrowth (with 95% confidence interval, $n=11$) was 2.45 ($\pm 0.31$) mm day$^{-1}$.

## Discussion

The study of population structure in fungi suffers from one major problem; whereas the physical limits of plants are usually apparent immediately, those of most fungi are hidden, and cannot be identified without extremely intensive sampling programmes. One solution, and the one adopted here, is to examine a defined set of resources for the presence of the species under study. Unfortunately, other resources which are excluded from the definition may also be occupied. For example, *R. bicolor* was observed on several fallen branches within the sample site indicating that either the density of individuals (number per unit area), or estimates of their size, or both, are wrong. The calculated size of individuals also depends upon resource density, distribution and the intensity of sampling. Problems associated with resource density and distribution are partially avoided if only the most distant points from which compatible isolates were recovered are used to calculate the maximal radius. Techniques that are used to calculate the space occupied by a plant, such as Voronoi polygons (Hutchings and Slade 1988) cannot be used.

In the present study, pattern analysis indicated that the establishment of genets at colonisation microsites are subject to random, stochastic events. The composition of communities in individual resource units is often extremely variable (Swift 1976), exhibiting low constancy of species. Such observations gave rise to the concepts of component and unit communities (Swift 1976; Lussenhop 1981). The spatial distribution data presented here provide a simple explanation, that of the involvement of random events in the establishment of individuals, for the lack of predictability in the development of many fungal communities and the low constancy of species within them.

Spatial maps and size distributions of individuals have been determined in populations of several species of *Armillaria* (Hood and Sandberg 1989; Kile 1986, and references therein), *H. annosum* (Stenlid 1985, 1987), *Tricholomopsis platyphylla* (Pers.: Fr.) Sing. (Thompson and Rayner 1982), *Phanerochaete velutina* (Pers.) Parmasto (Thompson and Boddy 1983), *Suillus bovinus* (Dahlberg and Stenlid 1990), *Phellinus weirii* (Dickman and Cook 1989) and now *R. bicolor*. All are strikingly similar. In general, the picture is one of a larger number

of small individuals, and a smaller number of large individuals. The relative proportions of small and large individuals is commonly interpreted as representing differences in establishment by basidiospores or by the mycelial extension of already-established individuals, both of which reflect site history. However, some distributions may be species specific; for example, *A. luteobubalina* tends to consist of fewer, larger, individuals whereas *A. hinnulea* has larger numbers of small individuals (Kile 1986).

In *R. bicolor*, the presence of 19 genets in 32 stumps indicates that colonisation occurs via both the immigration, formation and establishment of genets new to the site and by their subsequent mycelial extension. If it is assumed that the variation in size is due to age, as seems likely, then the proportion of stumps from the last thinning which were colonised by basidiospores is $16/80 = 0.2$. The remainder, also $16/80 = 0.2$, were colonised via mycelial extension of earlier-established, older individuals. The implication is that old mycelia form perennating cord systems in the soil, litter layer or old stumps which only colonise enrichment disturbances (fresh stumps) when they are provided; i.e. primary resource capture is mediated by mycelial extension.

A second explanation assumes that all individuals are the same age and were recruited as one cohort at the time of thinning. Thus, the proportion of stumps colonised by basidiospores is $19/80 = 0.24$, and by mycelium $(32–19)/80 = 0.16$. The extremely skewed size distribution could have arisen as a result of (1) different linear extension rates, (2) non-linear growth rates or (3) competition in which only a few individuals 'win', to become large and most 'lose', to remain small (Hutchings 1986). The extension of cords in the laboratory was 2.5 mm $day^{-1}$, indicating that it takes several years to move between tree stumps. Thus, when an individual arrives at a stump it will already have been colonised by other individuals of the same or different species, and must colonise the stump by secondary resource capture through combative mechanisms such as hyphal interference.

*R. bicolor* responded to both destructive and enrichment disturbance by rapid outgrowth from its resource base to colonise its surroundings. In root 1, it and *H. annosum* appeared to be in either deadlock or a very slow replacement reaction. Following stress alleviation through destructive disturbance (sawing the root into pieces) it appeared to gain an advantage and proceeded to replace fungi, including *H. annosum*, adjacent to it. This has been observed many times in related work on the colonisation of urea-treated spruce stumps by *H. annosum* (P. Brantberg, personal communications, and unpublished personal observations), in which discs are cut from stumps and incubated. In soil, *R. bicolor* extended throughout its disturbed environment to colonise an enrichment disturbance (a spruce bait) and form a system of perennating cords. Thus it would appear that the age/disturbance model is the more appropriate. However, the degree to which secondary resource capture shapes the population structure of *R. bicolor* needs further investigation.

The relatively high frequency of *R. bicolor* on stumps indicates that this species may be a major component of the decomposer community of spruce forest. Other workers (see Introduction) have also found similar, relatively high frequencies in both stumps and dead trees. *R. bicolor* would thus seem to offer three potential routes for the biological control of root and butt rot pathogens such as *H. annosum*. One is the primary capture of resource by the arrival and establishment of spores on enrichment disturbances such as fresh cut stumps, a second the arrival of cords at damaged, dying stumps (thinning or otherwise) and a third the secondary capture of resource by replacement reactions, most probably at destructive disturbances but possibly also in undisturbed environments. However, B. Greig (personal communications reported in Shaw 1989) has found that *R. bicolor* is not an effective competitor of *H. annosum* in esteblishing on stump surfaces. Our finding that half of the stumps colonised by *R. bicolor* were colonised by mycelium indicates that this second mode of dispersal should be considered when *R. bicolor* and other cord-forming fungi are considered as possible biological control agents. Recently, a (cord-forming) species of *Hypholoma* has been observed to replace a pathogenic species of *Armillaria* (Pearce and Malajczuk 1990). Management practices which enhance the inoculum of saprotrophic, cord-forming, wood-inhabiting fungi in forests may indirectly result in reductions in the incidence of butt and root rot. In general, the analysis of size distributions offers the opportunity for rewarding insights into population structure and dynamics, particularly for sites where accurate details of stand history are available.

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