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# Density and distance-to-adult effects of a canker disease of trees in a moist tropical forest

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**Abstract** We compared the spatial distribution of stem cankers on the canopy tree *Ocotea whitei* (Lauraceae) in a 20-ha plot on Barro Colorado Island, Panama, with spatial and temporal patterns of mortality in this host over the previous decade. The cankers occur both on adult and juvenile individuals, although juveniles are much more likely the adults to show symptoms. Disease incidence is host-density dependent, and both the presence of the disease and host mortality are more likely close to than far from a conspecific adult, which resulted in a net spatial shift of the juvenile population away from conspecific adults through time. Disease incidence is lower than expected among juveniles of *O. whitei* growing near to adults of the non-susceptible canopy tree *Beilschmiedia pendula*. The coincidence of spatial patterns of canker incidence and host mortality suggest a role for the disease in regulating host spatial distribution, in agreement with predictions of the Janzen-Connell hypothesis.

**Key words** *Ocotea whitei* · Lauraceae
Janzen-Connell hypothesis · Plant disease
Densitydependence

## Introduction

There is increasing evidence that diseases may play an important role in determining the community composition, demographics, genetic diversity, and spatial distribution of plants in natural ecosystems (Alexander 1992; Augspurger 1983b). One possible mechanisms underlying these effects was independently proposed by Janzen (1970) and Connell (1971). Their model states that when (1) adults and juveniles are susceptible to the same pests, (2) the pests attack host plants in a density-dependent manner, and (3) pest pressure is greater close to than far from a conspecific adult, then survival of offspring will be lower close to conspecific adults than farther away. Proportional survivorship of offspring increases with distance from the adult (due to decreased effect of pests), up to a point at which seed dispersal or edaphic conditions limit offspring establishment. The net result is decreased spatial aggregation of individual species, making space available to non-susceptible plant species. Although by itself this process probably cannot maintain the observed species diversity in tropical forests (Hubbell 1980), it is a widely cited mechanism by which biological diversity can be maintained or promoted.

Spatial patterns of recruitment and mortality consistent with the Janzen-Connell hypothesis have been identified for some tree species in natural communities (Clark and Clark 1984; Condit et al. 1992, 1994; Hubbell and Foster 1987; Hubbell et al. 1990; Sterner 1986), but there are few studies that specifically address whether the spatial distribution of plant disease conforms to the expectations of the model (Augspurger 1983a, b; 1984; Augspurger and Kelly 1984), or whether the spatial distribution of particular diseases are sufficient to explain observed patterns of mortality. Augspurger and Kelly (1984) show effects of both density and distance from adults, and an interaction between the two, in experimental studies of damping-off of seedlings in the tree species *Platypodium elegans* (Leguminosae) in moist tropical forest in Panama. However, they do not show that the adults are reservoirs of the pathogen, and they suggest that the denser shade near the adult tree may predispose the seedlings to disease. In the same study, only 6 of 16 tree species susceptible to damping-off were affected in a density-dependent manner. In a study by Connell et al. (1984), only 1 of 23 species in an Australian rain forest showed higher mortality of seedlings and saplings close to conspecific adults. A review by Burdon and Chilvers (1982) describes evidence for density-dependence of

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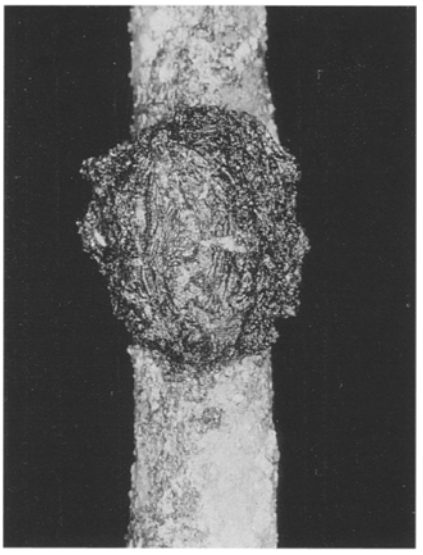

**Fig. 1** Canker on stem of *Ocotea whitei*

plant diseases in only 39 of 69 studies (57%) they extracted from the literature. They did not address the question of distance from a conspecific adult.

We need to link disease epidemiology with host demographic processes. An ideal opportunity for such a study resulted from observations of *Ocotea whitei* (Lauraceae) on the 50-ha permanent Forest Dynamics Project plot (FDP) in old-growth (seasonal tropical moist, semi-evergreen) forest on Barro Colorado Island, Panama (BCI; see Leigh et al. 1982 for detailed description of forest). The FDP, where all trees and shrubs (diameter≥1 cm at 1.3 m above the ground; hereafter dbh) have been mapped, measured, and identified, provides a unique opportunity for investigating the relationships between the spatial patterns of trees and their diseases in a natural community (see Condit et al. 1994 for detailed description). During the course of three periodic censuses (1982, 1985, and 1990), investigators noticed the *O. whitei* frequently had pathological cankers on their stems (Fig. 1) (D. Hamill and S. Hubbell, unpublished results). On the easternmost 20 ha of the FDP, where the current study was undertaken, *O. whitei* showed a 35% decrease in abundance between 1982 and 1990 (R. Condit, S.P. Hubbell and R.B. Foster, in prep). Recruitment of *O. whitei* into the smallest diameter class (dbh≥1 cm) was positively associated with proximity to conspecific adults between 1982 and 1985 (Condit et al. 1992), but 1–2 cm saplings growing beneath conspecific adults showed significantly poorer growth than those under adults of a different species (Hubbell et al. 1990). The observation that the cankers often effectively girdle a sapling suggests that this is symptomatic of a pathogen which is causing increased mortality in the host population. Identification of the causal agent of the cankers is under way.

We investigated the incidence of cankers on both adults and juveniles of *Ocotea whitei,* and described the spatial distribution of the cankered juveniles greater than 1 cm dbh with respect to both susceptible conspecific adults, and to nonsusceptible heterospecific adults (as controls for microenvironmental factors). We then discuss demographic patterns of the host species that suggest that the canker disease may have played a significant role in determining the spatial distribution in this declining population.

## Methods

### Host species

*Ocotea whitei* Woodson [syn. *Nectandra whitei,* previously misidentified as *Ocotea skutchii* in Hubbell and Foster (1990) and Croat (1978)] are locally abundant in Central and South America. On BCI, they are strongly associated with ravines and moist slopes, such as those on the eastern and southern borders of the FDP. Trees flower in the beginning of the dry season, and single-seeded fruits ripen some 14–15 months later, with large crops in alternate cycles. The oily flesh of the fruits (4–6 cm long) is commonly eaten by large birds such as guans, which often drop the seeds in place (B. de Leon, *personal communication*). Dispersal of seeds away from the parent tree appears to be limited.

### Disease incidence

Presence or absence of cankers on the trunks and main branches of all *O. whitei* individuals (dbh≥1 cm) in the easternmost 20 ha of the FDP was determined during October and November 1991. Each individual was visually inspected for the presence or absence of cankers of the type illustrated in Fig. 1. Cankers formed on the trunks or braches, and ranged in size from less than 1 cm on small twigs to 20 cm or more on large trunks. The cankers consisted of erupting lesions in the bark, often accompanied by exuded resins that accumulate as dark, crumbly material. Internally, wood in the area of the lesions was discolored. Usually, when any cankers were present on an individual, several were encountered. Large individuals were inspected with binoculars, and although symptoms on the trunk and major branches could be determined accurately, it is possible that very tall individuals scored as healthy had cankers on braches in the dense high canopy. Although this may lead to an underestimate of infection among adults, most subsequent analyses do not depend on knowing the disease state of the adults, so the interpretations of results are unaffected. The related canopy tree *Beilschmiedia pendula* (Lauraceae) was used for certain analyses as a non-susceptible control; each individual in the 20-ha section was inspected in the same manner during November and December, confirming that this species is not susceptible to this canker disease, or at least is not symptomatic.

To determine if all size classes were equally likely to be symptomatic, $\chi^2$ analysis was used.

### Spatial distribution of disease

Joins-count statistics were used to determine whether canker incidence was spatially clumped within the already clumped distribution of *O. whitei.* Two individuals were "joined" if no other *O. whitei* individuals were located within the circle whose diameter had the two individuals at opposite ends (Fig. 2). Only pairs whose circle was contained entirely within plot boundaries were eligible to be joined. The number of joins of types healthy-healthy, cankered-cankered, and healthy-cankered was compared to the expected numbers of joins using the method described by Sokal and Oden (1978).

Distance to the nearest juvenile conspecific neighbor was used as a measure of host-plant density. The nearest-neighbor distance

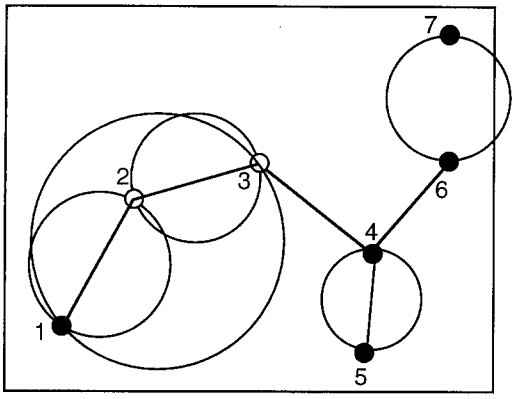


**Fig. 2** For joins-count analysis, trees are first classified as one of two types (i.e., cankered and healthy or dead and alive; here ○ or ●). A circle is then drawn for each pair of trees so that the trees are the ends of a diameter of the circle. If no other trees are found within the boundaries of the circle, the two trees are "joined" (1 to 2; 2 to 3). If a tree is found within the circle (tree 2 is within circle 1–3), or if part of a circle falls outside the plot boundary (circle 6–7), the trees are left unjoined. Counts of ○—○ (2–3), ●—● (4–5), ○—● (1–2), and total joins were compared to expected values as described in the text

for healthy and cankered juveniles were compared by *t*-test (differences between the means) and Kolmogorov-Smirnov test (differences between the distributions).

To test for effects of distance from conspecific adults and host density on the incidence of disease, each individual was assigned to the nearest adult-sized (dbh≥30 cm) *O. whitei*. We counted the number of individuals, within 1-m distance intervals from the nearest adult, that were alive in the 1990 census, and either (1) cankered in 1991, (2) healthy in 1991, or (3) dead in 1991. The cumulative proportion of the total number of individuals in each group (e.g., proportion of cankered individuals at all distances that were within distance $x$ of an adult) was determined. A Monte Carlo simulation (1000 runs) was used to determine whether the observed cumulative distributions for cankered, healthy, and dead individuals were significantly different ($P \leq 0.05$) from the distribution of all individuals alive in 1990. Testing was done at 1-m distance intervals. The analysis was performed on all juveniles (1 cm≤dbh<30 cm) and separately on small (1 cm≤dbh<4 cm), medium (4 cm≤dbh<8 cm), and large (8 cm≤dbh<30 cm) juveniles. Because adults that have recently died could have had effects (during the years before their death) on nearby juveniles, all individuals that were larger than 30 cm dbh in 1982, 1985, or 1990 were included as adults, even if they had died by 1991. Each juvenile was counted only one time. Any individual nearer to a plot boundary than to an adult was excluded from the analysis. All individuals more than 60 m from a conspecific adult were counted as members of one distance interval.

To partition the confounded effects of distance from adult and density of juveniles, the effect of distance from conspecific adults on disease incidence was analyzed separately for juveniles near to (<3 m) and far from (≥3 m) their nearest conspecific juvenile (high and low density, respectively) using a Monte Carlo simulation as described above. A cutoff nearest-neighbor distance of 3 m was selected to divide the juvenile population roughly in half.

To test whether the effects of distance from an adult was species-specific or whether any large tree would produce the same effects, the analysis described in the previous paragraphs was repeated for the distribution of juvenile *O. whitei* individuals around adults of *Beilschmiedia pendula* (Lauraceae). *Beilschmiedia* was chosen because it is in the same family as *O. whitei* but is apparently not susceptible to the disease, has similar fruits, and because the two species have similar spatial distributions in the 20-ha site. Both species are most common on a moist slope on the eastern and southern borders of the plot (Fig. 3). To compare the minimum distances to adult *O. whitei* and *B. pendula,* only juveniles that were closer to an adult of each species than to a plot boundary were included.

## Host demographics

In order to determine whether the spatial and temporal demographic patterns of *O. whitei* suggest that disease may play a role in population regulation, we analyzed several aspects of the 1982, 1985, and 1990 Forest Dynamics Project census data, as well as the 1991 disease census data. We tabulated population size, recruitment, and mortality for each census. Annual mortality was calculated for each intercensus interval using a "compound interest" model. The model for 1-year time units is $I=I_0(k+1)^t$, where $I_0$ is the number of stems at the beginning of the intercensus interval, $I$ is the number of survivors at the end of the interval, $k$ is the population growth rate per year, and $t$ is the number of years in the interval (Campbell and Madden 1990). Percentage mortality per year then equals $(-k \times 100)$. These calculations assume constant

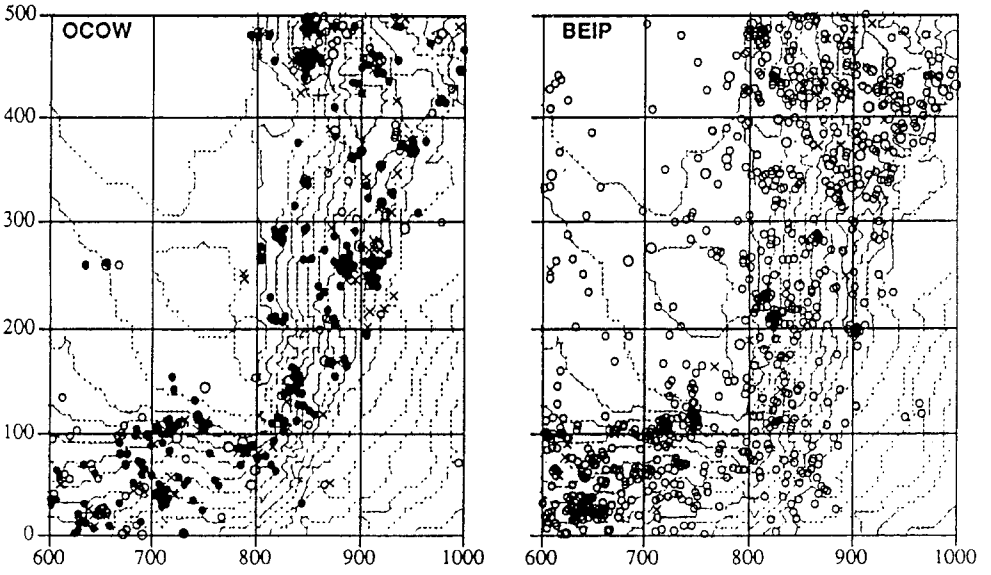


**Fig. 3** Maps of distributions of *Ocotea whitei (OCOW)* and *Beilschmiedia pendula (BEIP)* in the easternmost 20 ha of the Forest Dynamics Project plot on Barro Colorado Island. *Axis labels* represent distance north *(vertical axis)* and east *(horizontal axis)* in meters from the south-west corner of the 50-ha plot. *Contour lines* are 2-m intervals, ranging from 155 m in the NW corner to 121 m in the SE corner. *Open symbols* are healthy individuals, *closed symbols* cankered individuals, and ×s for dead individuals in 1991

mortality rates across years within an intercensus interval, although it is possible that mortality was much higher in certain years within an interval than in others (i.e. mortality was very high during the 1982–1983 drought: Leigh et al. 1990).

To determine whether individuals that died were drawn randomly from among those that died between 1982 and 1991, or whether there was evidence for spatial foci of mortality, we used the joins-count statistics described above. The overall population was first defined as all the individuals that died during 1982–1991. For each intercensus interval (1982–1985, 1985–1990, 1990–1991), individuals were placed in one of two classes: (1) died in the current interval or (2) died in another interval. For each interval, joins of current-current, other-other, and current-other individuals were compared to expected values. We also investigated spatial shifts in the distribution of juveniles with respect to nearest conspecific adults by tabulating the number of individuals in 2-m distance intervals around nearest adults for the 1982 and 1991 populations.

We analyzed the data separately (1) including only those individuals tagged in 1982, and (2) including new recruits in 1985 and 1990. This permitted us to determine whether the expected shift away from adults (predicted by the Janzen-Connell model) took place for an uneven-aged cohort (1982), and whether any such mortality was offset by higher recruitment near to conspecific adults than far away. We used the Kolmogorov-Smirnov test to compare spatial distributions.

Regression analyses, Kolmogorov-Smirnov tests, *t*-tests, and data tabulation were performed using StatisticaMac (StatSoft 1991). All other analyses were performed using programs written in THINK Pascal (Symantec 1991) and run on a Macintosh IIci.

## Results

Cankers were found on all sizes of *O. whitei,* but were significantly more common on smaller individuals than on larger ones ($\chi^2$=137.15, $P\leq0.001$, $df$=4) (Table 1). We did not determine whether small individuals were actually more often infected with the disease agent or were just more likely to express symptoms once infected, than were large individuals. However, a minimum of 72% of the 442 living individuals were diseased in October–November 1991.

*O. whitei* is spatially aggregated on the plot (see Fig. 3), and diseased individuals were spatially aggregated within that distribution. We used joins-count statistics to compare the frequencies of cankered-to-cankered tree joins, healthy-to-healthy tree joins, and cankered-to-healthy tree joins to those expected under the assumption of random distribution of cankered individuals throughout the population. There were significantly more cankered-cankered and healthy-healthy joins and significantly fewer healthy-cankered joins than expected in the null model ($P\leq0.01$ for all). This indicates that there is significant clumping of diseased individuals within the host distribution (Table 2).

Canker incidence was dependent on the density of the host plants. Using distance to the nearest conspecific neighbor as a measure of host density, we found that cankered juveniles were significantly closer to their nearest conspecific juvenile (mean=4.5 m; SD=5.1; $n$=285) than were healthy juveniles (mean=6.2 m; SD=5.7; $n$=65), as determined both by $t$-test for different means ($t$=2.366; $P\leq0.05$) and Kolmogorov-Smirnov test for different distributions (max. – and + differences –0.016 and 0.239; $P\leq0.01$). This suggests a positive density-dependent effect of hosts on disease incidence, consistent with the prediction of the Janzen-Connell model.

Third, we asked how distance from a conspecific adult (dbh≥30 cm) was related to incidence of cankers by examining the cumulative distribution of healthy and cankered juveniles in October-November 1991 and juveniles that had died between the 1990 and 1991 censuses, compared to the distributions expected based on individuals alive in the 1990 census. There were significantly more deaths than expected ($P\leq0.05$, 1000 runs of a Monte Carlo simulation) at most distances closer than 20 m from an adult and significantly fewer than expected at several distances greater than 30 m (Fig. 4). Additionally, there were significantly fewer than expected healthy juveniles within most distances from 16 to 41 m from an adult (Fig. 4). Half of all healthy juveniles are at distances beyond 22 m, while fewer than 30% of all individuals are beyond this distance. Half of all juveniles are found within 13 m of a conspecific adult, while 50% of dead juveniles are within only 10 m. Juveniles growing near to adults are more likely to die than those at greater distances, and individuals growing far from adults are more likely to remain canker-free.

Similar results were obtained when the analysis was performed only with juveniles in the smallest size class (1 cm≤dbh<4 cm), except that there were also significantly more cankered individuals than expected within 2 m of an adult and at all distances beyond 20 m (Fig. 5). Only 48% of all healthy individuals in this size class are found within 23 m of an adult, whereas 78% of all individuals are within that same distance. Analysis using on-

**Table 1** Health status of *Ocotea whitei* alive in 1991 census by diameter size class

| Diameter (cm) | Cankered | Healthy | %Cankered |
|---|---|---|---|
| 1–4 | 185 | 19 | 90.7 |
| 4–8 | 88 | 19 | 82.2 |
| 8–16 | 34 | 35 | 49.3 |
| 16–30 | 2 | 16 | 11.1 |
| 30 and over | 12 | 32 | 27.3 |
| Total | 321 | 121 | 72.6 |

**Table 2** Joins-count statistics for spatial distribution of cankers of *O. whitei*

| Join type | Observed | | Expected | Variance | *P*-value |
|---|---|---|---|---|---|
| Healthy-healthy | 76 | > | 53.3 | 35.9 | 0.01 |
| Cankered-cankered | 429 | > | 377.3 | 83.4 | 0.01 |
| Cankered-healthy | 211 | < | 285.3 | 134.0 | 0.01 |

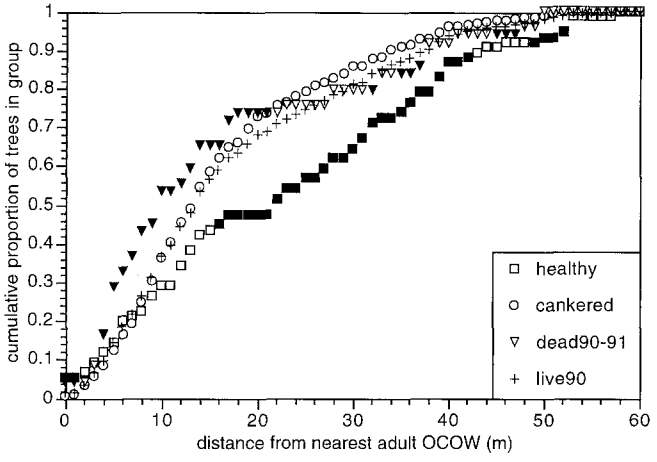


**Fig. 4** Cumulative proportion of juveniles (1 cm≤dbh<30 cm) of *Ocotea whitei* around adults of *O. whitei* with respect to health status of juvenile in 1991 census. *Symbols* indicate cumulative proportions at 1-m intervals. *Closed symbols* are significantly different from distribution of all trees alive in 1990, based on 1000 runs of a Monte Carlo simulation ($P \leq 0.05$)

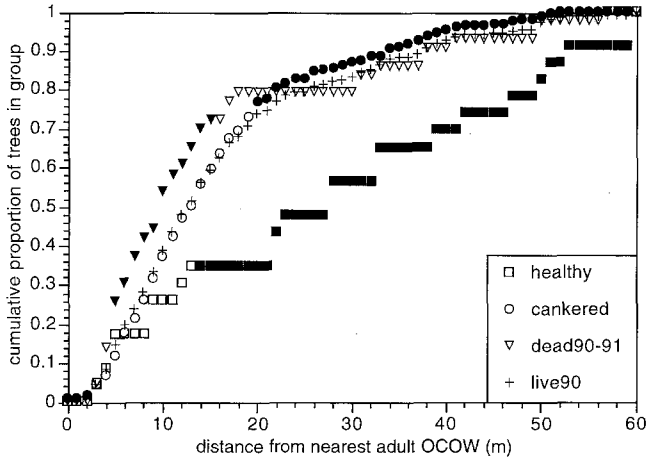


**Fig. 5** Cumulative proportion of juveniles of *Ocotea whitei* in the smallest size class (1 cm≤dbh<4 cm) around adults of *O. whitei* with respect to health status of juvenile in 1991 census. *Symbols* indicate cumulative proportions at 1-m intervals. *Closed symbols* are significantly different from distribution of all trees alive in 1990, based on 1000 runs of a Monte Carlo simulation ($P \leq 0.05$)

ly mid-sized juveniles (4 cm≤dbh<8 cm) showed significantly more cumulative numbers of cankered individuals and fewer healthy individuals at most distances between 37 and 58 m from the nearest *O. whitei* ($P \leq 0.05$, data not shown), but no significant relationship between distance and mortality. Large juveniles (8 cm≤dbh<30 cm) showed no significant relationship between distance from a conspecific adult and health status (data not shown). These results indicate that the relationship between distance from a conspecific adult and health status of juvenile *O. whitei* is strongest for the smallest individuals, but includes juveniles in the 4–8 cm size-class as well.

The effects of distance from conspecific adults and density of juveniles are confounded, with higher densities of juveniles close to adults than farther away. In order to test whether the effect of distance from adults was an artifact of the higher density of juveniles near to adults, we performed the analysis for the effect of distance from conspecific adults separately on individuals whose nearest juvenile *O. whitei* neighbor (in 1990) was less than 3 m away (high density; $n$=247), or equal to or greater than 3 m away (low density; $n$=212). The results from both analyses (Fig. 6) are very similar to that for all juveniles (Fig. 4), except that cankered individuals for low density trees and dead (1990–1991) individuals for high-density trees were not significantly different from expected. Juveniles growing farther from adults of *O. whitei* are more likely to remain healthy than those close to adults, regardless of the density of juveniles.

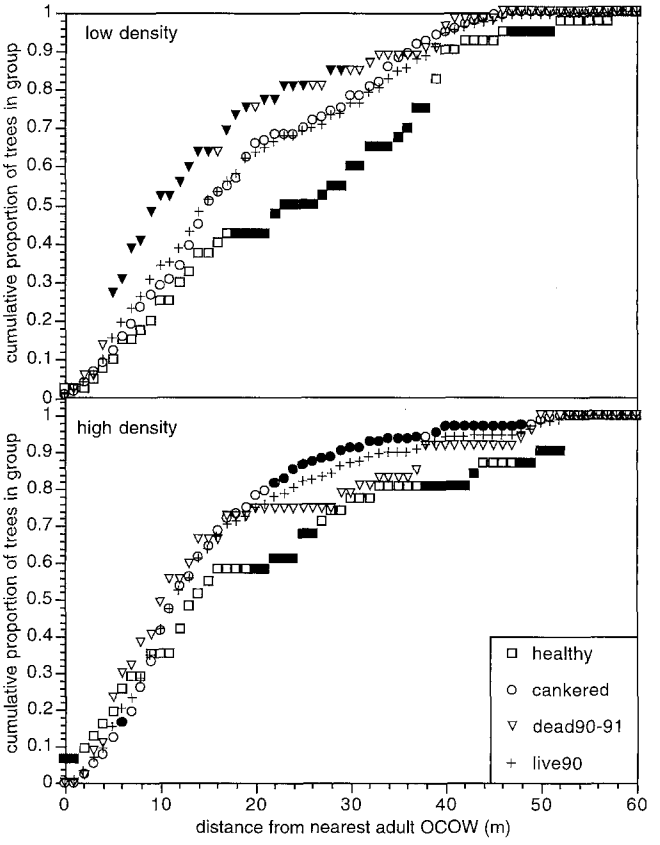


**Fig. 6** Cumulative proportion of juveniles (1 cm≤dbh<30 cm) of *Ocotea whitei* around adults of *O. whitei* with respect to health status of juvenile in 1991 census. Analyses performed separately for individuals growing at high density (distance to nearest conspecific juvenile <3 m; $n$=247) and low density (distance≥3 m; $n$=212) in 1990. Individuals closer to a border than to an adult or juvenile were excluded. *Symbols* indicate cumulative proportions at 1-m intervals. *Closed symbols* are significantly different from distribution of all trees in density class alive in 1990, based on 1000 runs of a Monte Carlo simulation ($P \leq 0.05$)

To test whether proximity to an adult of a non-susceptible species could affect the health status of *O. whitei* juveniles through effects on microclimate of other non-species-specific effects, we performed the same analysis on the cumulative proportions of small juveniles (1 cm≤dbh<4 cm) of *O. whitei* around the non-susceptible

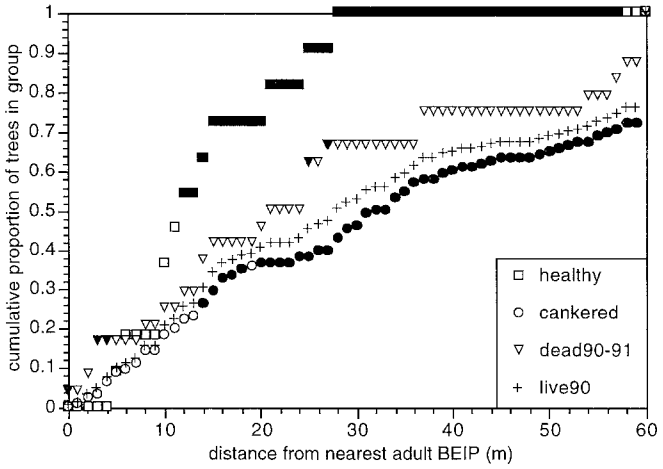


**Fig. 7** Cumulative proportion of juveniles of *Ocotea whitei* in the smallest size class (1 cm≤dbh<4 cm) around adults of *Beilschmiedia pendula* with respect to health status of juvenile in 1991 census. *Symbols* indicate cumulative proportions at 1-m intervals. *Closed symbols* are significantly different from distribution of all trees alive in 1990, based on Monte Carlo simulation ($P \leq 0.05$)

*Beilschmiedia pendula*. *O. whitei* and *B. pendula* have similar spatial distributions (Fig. 3). Results of this analysis were the opposite of the previous results; significantly more healthy *O. whitei* were found close to adults of *B. pendula* (between 12 and 57 m) than expected ($P \leq 0.05$; Fig. 7). In fact, all healthy *O. white* in this size class were found within 28 m of an adult *B. pendula*, although only half of individuals of all size classes were within this distance. Additionally, there were fewer than expected cankered juveniles around adult *B. pendula* (at 14–59 m, except 19 m). The increased probability of disease among *O. whitei* juveniles near conspecific adults is thus not likely to be a result merely of proximity to a large tree, but may be related specifically to distance from an adult *O. whitei*.

It is possible that the lower incidence of disease among juvenile *O. whitei* growing close to an adult *B. pendula* is a casual result of an underlying spatial distribution whereby individuals that grow near an adult *B. pendula* necessarily are far from an adult *O. whitei*. To test this, for the 197 *O. whitei* (1 cm≤dbh<4 cm) that are closer both to an adult *B. pendula* and to an adult *O. whitei* than to a plot border, the numbers of individuals closer or farther than 14 m from adults of each species were subjected to $\chi^2$ analysis. The cutoff distance of 14 m was chosen as the distance at which there were both significantly more healthy individuals and fewer cankered individuals than expected around *B. pendula* (Fig. 7). There was no significant relationship between distance to the nearest adults of *O. whitei* and *B. pendula* for the juveniles of all health groups combined *O. whitei* ($\chi^2 = 2.7942$; $P = 0.0915$), nor for healthy, cankered, and dead individuals separately ($P > 0.1$ in all tests). This indicates that the decreased probability of disease among individuals near adults of *B. pendula* is not a simple function of greater distance from adult of *O. whitei*.

**Table 4** Percentage mortality of *O. whitei* trees in each size class on a per-year basis for each intercensus interval

| Dbh | Intercensus interval | | |
|---|---|---|---|
| (cm) | 1982–85 | 1985–90 | 1990–91 |
| 1–4 | 12.4 | 9.0 | 29.9 |
| 4–8 | 4.1 | 2.9 | 13.7 |
| 8–16 | 4.5 | 3.0 | 1.4 |
| 16–30 | 4.1 | 2.6 | 5.3 |
| 30+ | 3.0 | 1.4 | 2.2 |
| Total | 9.9 | 6.4 | 19.5 |

## Host demographics

The population of *O. whitei* in the 20-ha plot has been rapidly declining at least since the 1982 census (Tables 3 and 4). Deaths far exceed recruitment into the lower size classes (Table 3), and estimated annual mortality rates range to almost 30% per year for the 1–4 cm dbh juveniles, and 1.4–3.0% for adults. These estimates suggest a mean mortality rate for all individuals larger than 1 cm dbh of about 9% per year over the 9-year period.

Joins-count statistics suggest that the spatial pattern of the mortality may be changing over time. In the 1982–1985 intercensus period, mortality was significantly clumped compared to all the deaths for 1982–1991. Table 5 shows significantly more like-type joins and fewer cross-type joins than expected. This suggests spa-

**Table 3** Intercensus population changes for *Ocotea whitei* in the 20-ha plot. Shown are the number of stems alive in each size class (diameter at 1.3 m) at the beginning of the intercensus period, the number of individuals that died or died back to smaller than the minimum size class, and the number of new stems recruited at the end of the interval. New recruits were not recorded in 1991

| | 1982–1985 | | | 1985–1990 | | | 1990–1991 | |
|---|---|---|---|---|---|---|---|---|
| Dbh (cm) | Live | Deaths | Recruits | Live | Deaths | Recruits | Live | Deaths |
| 1–4 | 613 | 201 | 77 | 436 | 163 | 49 | 291 | 87 |
| 4–8 | 120 | 14 | 0 | 132 | 18 | 2 | 124 | 17 |
| 8–16 | 39 | 5 | 0 | 56 | 8 | 0 | 70 | 1 |
| 16–30 | 25 | 3 | 0 | 24 | 3 | 0 | 19 | 1 |
| 30+ | 46 | 4 | 0 | 45 | 3 | 0 | 45 | 1 |
| Total | 843 | 227 | 77 | 693 | 195 | 51 | 549 | 107 |

**Table 5** Joins-count statistics for spatial distribution of mortality of *O. whitei* across three intercensus intervals. Joins are for trees that during the current intercensus interval vs. trees that died in another census interval

| Join type | Observed | | Expected | Variance | P-value |
|---|---|---|---|---|---|
| 1982–1985 | | | | | |
| Current-current | 187 | > | 166.4 | 73.0 | 0.05 |
| Other-other | 278 | > | 240.1 | 83.5 | 0.01 |
| Current-other | 343 | < | 401.5 | 198.8 | 0.01 |
| 1985–1990 | | | | | |
| Current-current | 141 | | 131.8 | 64.8 | ns |
| Other-other | 296 | | 286.1 | 86.1 | ns |
| Current-other | 371 | | 390.1 | 190.8 | ns |
| 1990–1991 | | | | | |
| Current-current | 18 | | 15.9 | 12.8 | ns |
| Other-other | 580 | < | 595.9 | 53.1 | 0.05 |
| Current-other | 210 | | 196.2 | 75.9 | ns |

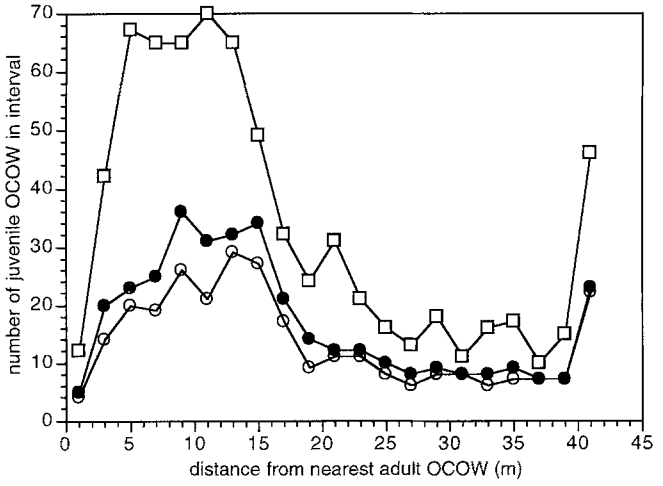


**Fig. 8** Number of juveniles (1 cm≤dbh<30 cm) of *Ocotea whitei* in 2-m distance intervals around adults of *O. whitei*. *Open squares* are all individuals in the 1982 census; *open circles* are those individuals tagged in 1982 that survived until the 1991 census; *closed circles* are all individuals alive in 1991, including 1985 and 1990 recruits

tial foci of mortality were present at that time. In the 1985–1990 intercensus, no such clumping was found, and mortality appears to be randomly distributed within the overall population. However, for 1990–1991, there were significantly fewer other-other joins than expected ($P \leq 0.05$), suggesting the appearance of hyperdispersion of mortality throughout the test population. This pattern of aggregated mortality passing through time toward hyperdispersed mortality is consistent with expected results if mortality was originally concentrated in foci such as those caused by many diseases, but as the disease spreads to include most or all of the population and individuals in the original foci die, mortality becomes random or even hyperdispersed.

One prediction of the Janzen-Connell hypothesis is that the mean minimum distance between adults and a cohort of juveniles should increase through time, as disproportionately more individuals die near to adults than farther away. Figure 8 shows that the uneven-aged cohort of juveniles tagged in 1982 shows just this type of shift away from adult *O. whitei* between 1982 and 1991. Including recruits in the 1985 and 1990 census does not compensate for this effect (Fig. 8).

## Discussion

The canker disease of *Ocotea whitei* shows all the characteristics necesary to affect the host population in accordance with the Janzen-Connell hypothesis (Connell 1971; Janzen 1970). The cankers occur both on adults and juveniles, although juveniles are much more likely than adults to show symptoms, the probability of an individual being cankered is significantly higher on juveniles growing at high host density than low, and both the presence of the disease and host mortality are more likely close to than far from a conspecific adult, resulting in a net spatial shift of the juvenile population away from conspecific adults through time.

Both effects of juvenile density and distance from nearest conspecific adult are evident in this host-pathogen system. Distance-from-adult effects on tree health are present at both high and low densities, although perhaps there is an increased effect on mortality at low densities and a stronger effect on canker incidence at high densities. These results may indicate that both adult-juvenile and juvenile-juvenile pathogen transmission are important in the spread of the disease. Further study on the identity and mode of transmission of the causal agent are required to elucidate this point.

The effect of distance from an adult seems more likely to be related specifically to adult of *O. whitei*, than to environmental effects of being near a large tree. Juveniles of *O. whitei* growing near adults of the con-familial but apparently non-susceptible *Beilschmiedia pendula* were more likely to be healthy than expected. Although this 'safe-haven' effect around *B. pendula* could be an analytical artifact caused by the physical difficulties of an individual being physically near to adults of both *Ocotea* and *Beilschmiedia,* there was no significant relationship between distances to the nearest adult of these two species, suggesting this is not the case. It is possible that the *Beilschmiedia* adults or their immediate environment present some cue to induce resistance mechanisms in *O. whitei* that are otherwise not active. There is evidence in the literature for communication among individuals of *Ocotea tenera* that results in modified sexual expression (Wheelwright and Bruneau 1992). Inter-plant chemical communication systems are known that induce disease resistance both within and across species (Baldwin and Schultz 1983; Farmer and Ryan 1990). It is also possible that there is something about the neighborhood of *Beilschmiedia* adults that is a deterrent to the pathogen itself or to its vectors. Experimental studies are required to clarify the role of *Beilschmiedia* adults, if any, in disease incidence in *O. whitei*.

The spatial clumping of disease incidence may be due to limited pathogen dispersal (and thus clumping of the disease), or alternatively may indicate a significant clumping of healthy individuals, due to shared resistance of spatially aggregated, closely related individuals or escape from disease due to microenvironmental variation.

Condit et al. (1992) show that *O. whitei* had a higher than expected recruitment rate into the 1–8 cm dbh size class within 20 m of conspecific adults, which they interpreted as not supporting the Janzen-Connell model. However, our results may indicate that for this species disease pressure among juveniles up to 8 cm dbh near to conspecific adults may be sufficient to produce the expected Janzen-Connell patterns of survival.

Because disease incidence data is not available prior to the 1991 census, it is not possible to determine whether the cankers are the cause of the very rapid decline of this species. Disease incidence, and growth and mortality rates of healthy and cankered individuals will be followed for several years to better understand the effect of this disease on host survival and growth. However, the similarity in spatial patterns of mortality and disease, and the severity of the cankers in the present population, suggest that this disease is a good candidate for a major population regulator. A spatial-temporal computer model for the role of the disease in the host population dynamics (G.S. Gilbert, in prep.) supports this view.

The identity of the canker-causing organism and species-specificity of the canker disease are yet to be determined. Cankers of very similar appearance have been found on individuals of most other lauraceous species in the plot (all much rarer species than *O. whitei*), but at much lower frequencies (G.S. Gilbert, *unpublished data*). Because of the scarcity of healthy juveniles and a near absence of fruit set in the last 2 years, we have not been able to complete definitive testing to show what organism(s) is the cause of cankers on *O. whitei*. However, an isolate of the fungal genus *Phialophora,* which has been frequently isolated from cankers, was the only fungus of five candidates to induce cankers when inoculated into *Phoebe cinnamomifolia* (Lauraceae) (G.S. Gilbert, *personal observation*). *P. cinnamomifolia* is affected by cankers of the *Ocotea* type on the 50-ha plot. Work is continuing to determine whether the various species of Lauraceae share a common pathogen, and to determine definitively the causal agent of the cankers on *O. whitei*.

It is not known whether the disease is endemic to the population or was introduced to the island and is now in an epidemic phase. Two other non-contiguous populations of *O. whitei* on Barro Colorado Island, each about 1 km from Forest Dynamics Plot, also showed similar canker frequencies (G.S. Gilbert, *personal observation*). This suggests that the disease was not brought to the plot during its establishment, and that the high incidence of the disease is not likely to be an artifact of the human activity on the plot.

Many forest declines are triggered by predisposing stress factors such as extremes of moisture and temperature (Houston 1984). Barro Colorado Island experienced an exceptionally wet year in 1981 (4467 mm) followed by an El Niño-related drought (1967 mm rain). The average rainfall on the island is approximately 2600 mm, but annual rainfall has been steadily decreasing for the past 50 years (Windsor 1990). It is possible that the extreme wet or dry years in the early 1980s, or the sequence of the two, increased the susceptibility of the *O. whitei* population to what had been a endemic disease. Rare environmental events such as droughts may have long-lasting effects on perennial populations through biological mediators such as pathogens.

Regardless of the origin of the disease or the existence of predisposing environmental factors, the canker disease of *O. whitei* appears to be capable of regulating the spatial distribution of the host trees in old-growth rainforest, consistent with the Janzen-Connell model.

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