Age Structure of Phoradendron juniperinum (Viscaceae), a Xylem-Tapping Mistletoe: Inferences from a Non-Destructive Morphological Index of Age

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AGE STRUCTURE OF PHORADENDRON JUNIPERINUM (VISCACEAE), A XYLEM-TAPPING MISTLETOE: INFERENCES FROM A NON-DESTRUCTIVE MORPHOLOGICAL INDEX OF AGE[1]

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ABSTRACT

We investigated the age-structure of the xylem-tapping mistletoe *Phoradendron juniperinum* in relation to characteristics of its host tree, *Juniperus osteosperma*. We first correlated branch structure in the mistletoe with age of the mistletoe infection as determined anatomically; this correlation provided a nondestructive, field method of obtaining age structure information. We then surveyed the mistletoe plants, applying our aging index, within a population of their host trees in southwestern Utah; the majority of mistletoe plants were 2–12 years old. This peak in abundance of mistletoe infections showed no correlation to total annual precipitation within or 1 year previous to the peaks, minimum winter temperature, or to warmer than average winter temperatures. However, there was a positive correlation ($r = 0.51$, $P < 0.06$) with the amount of summer precipitation. A log-linear analysis indicated that a greater than expected number of mistletoe infections occurred at 5–7 years of age and at approximately 3 m in height among all host trees. We suggest that this pattern resulted because this canopy position had greater leaf and branch areas and was visited most frequently by seed-dispersing birds. The log-linear analysis also revealed that fewer than expected mistletoe infections occurred at ages older than 10 years, yet our data indicate that plants can reach 20 years of age. The lack of infections >10 years of age was correlated to a period of below average precipitation, especially during the growing season, but not with cold winter temperatures, which in other studies had been suggested as a factor influencing mortality. We feel that drought may play an important role in influencing mistletoe mortality through its direct affect on host tree water status, but in addition we offer two alternative hypotheses to explain mistletoe longevity; the first is concerned with the relationship between carbon and nitrogen costs and maintaining large leaf areas in older plants, and the second addresses how increased hydraulic resistance in older and larger plants may be too costly for the plant, and stems are abscised.

POPULATIONS OF long-lived individuals commonly consist of members of different ages demonstrating different reproductive attributes, ecological characteristics, and/or physiological responses (Harper, 1977; Michod, 1979; Charlesworth, 1980; Seståk, 1985). Clearly then, for organisms with overlapping generations, understanding how the ages are distributed in space and time and in relation to aspects of their environment could play a critical role in evaluating important attributes of their biology.

Many aspects of the ecology and physiology of the perennial xylem-tapping mistletoe, *Phoradendron juniperinum*, have been reported to be age-dependent (Schulze and Ehleringer, 1984; Dawson, Ehleringer, and Marshall, 1990). However, formal indices of age were not established. Except in trees, obtaining age-structure information for long-lived plants can be problematic because age is either impossible to determine or must be estimated on the basis of plant size, which is almost always subject to error. As a consequence, little information exists on age-structure in nonarborescent perennial plant populations, and hence few correlations between age and ecological traits such as fecundity and/or physiological characteristics such as carbon economy have been established. Mistletoes provide an unusual opportunity to explore such pat-

terns in a nonarborescent perennial with a much longer generation time than those that have, in the past, provided the template for most of our best theoretical models of age-structure (Charlesworth, 1980).

Because a mistletoe's host largely defines its "environment," characteristics such as location within the host's canopy or the size of that canopy could influence establishment, growth, and reproduction, and hence the demography and age-structure of mistletoe populations. Here we report on a nondestructive index of age based on the branching structure of the mistletoe *Phoradendron juniperinum* and correlate it with an independent determination of age based on anatomical studies (Calvin, 1967). We applied this index to a population of mistletoes on *Juniperus osteosperma,* the Utah juniper, its principle host tree, to answer the following questions: 1) what is the age distribution of mistletoe plants? 2) does the size class of the host affect age-distribution patterns because different sized hosts represent different kinds of "environments"? and 3) does knowledge of the age of plants provide any insights into interesting correlates with other ecological characteristics of this species that may have otherwise been overlooked?

MATERIALS AND METHODS—*Study populations*—Samples of the host tree, *Juniperus osteosperma* (Torr.) Little, the Utah juniper, that were parasitized by the xylem-tapping mistletoe, *Phoradendron juniperinum* Gray (nomenclature follows Welsh et al., 1987), were collected in three widely separated populations in Oregon and Utah. The southernmost population was located in the southwestern corner of Utah near the boundary of Coral Pink Sand Dunes State Reserve (latitude 37°3'N, longitude 112°45'W, 1,855 m elevation), approximately 7 km from the Arizona state line. The second population in Utah was located in Skull Valley (latitude 40°21'N, longitude 112°36'W, 1,740 m elevation), approximately 100 km west of Salt Lake City. The northern- and westernmost population was collected near the city limits of Bend, Oregon (latitude 44°03'N, longitude 121°18'W, 612 m elevation; sampled by Dr. Clyde Calvin).

Host and parasite anatomical studies—I) *Anatomical background:* Srivastava and Esau (1961) established that the age of a mistletoe infection could be determined anatomically. The tissues of the endophytic system of *Phoradendron* form structures termed the cortical haustoria, which are longitudinally oriented strands in the host bark, and "sinkers," which

are radially oriented extensions into the host xylem (Calvin, 1967). The age of any sinker can be determined from the number of annual growth rings traversed in the host wood. Thus, the longest sinker is the oldest and provides a way to age each infection (Srivastava and Esau, 1961; Fig. 2). The sinker does not grow intrusively within the host xylem, but once it has penetrated the host phloem it establishes a meristematic region at the junction of the host plant vascular cambium and the host xylem. Subsequent growth of the sinker occurs in synchrony with the meristematic activity of the host vascular cambium, and the sinker eventually is embedded in the host xylem. This occurs without embolizing xylem tracheids or otherwise damaging the host wood, allowing the parasite xylem and host xylem to become linked and form a continuous xylem flow pathway between host and parasite (Calvin, 1967).

II) *Anatomical methods:* Subsequent to the morphological analyses (see below), a total of 136 specimens, each consisting of a juniper branch segment and its attached mistletoe stem, were prepared for light microscopy (79 from Coral Pink Sand Dunes, 43 from Skull Valley, and 14 from Bend, OR). Each specimen was trimmed of excess foliage, immersed in 60% ethanol, and subjected to a mild vacuum to promote thorough wetting of the tissues. After a minimum of 48 hr in ethanol, the specimens were mounted in a sliding microtome (American Optical, model 860, Buffalo, NY) and sectioned at 20-μm intervals. Transverse sections were obtained from the basal portion of each mistletoe stem and from two locations on each juniper branch segment: 1) at the junction between the branch and its mistletoe stem; and 2) at points 1–1.5 cm, both proximally and distally, from the junction. Two hundred sections from each of these locations were prepared and from these it was usually possible to examine between 95 and 125 undamaged sections. In some specimens it was difficult to obtain this many undamaged sections; however, in these cases a minimum of 25 sections were examined from each juniper branch location. The sections were stained in 1% ethanolic safranin O and observed by light microscopy at ×100. Photomicrographs were obtained with a Zeiss Photomicroscope II (Oberkochen, West Germany).

For each specimen, the maximum number of juniper growth rings traversed by the mistletoe "sinker" was determined (Fig. 2). This number was considered equal to the age of the mistletoe infection (see Calvin [1967] for further anatomical and methodological details). False growth rings in the juniper could easily
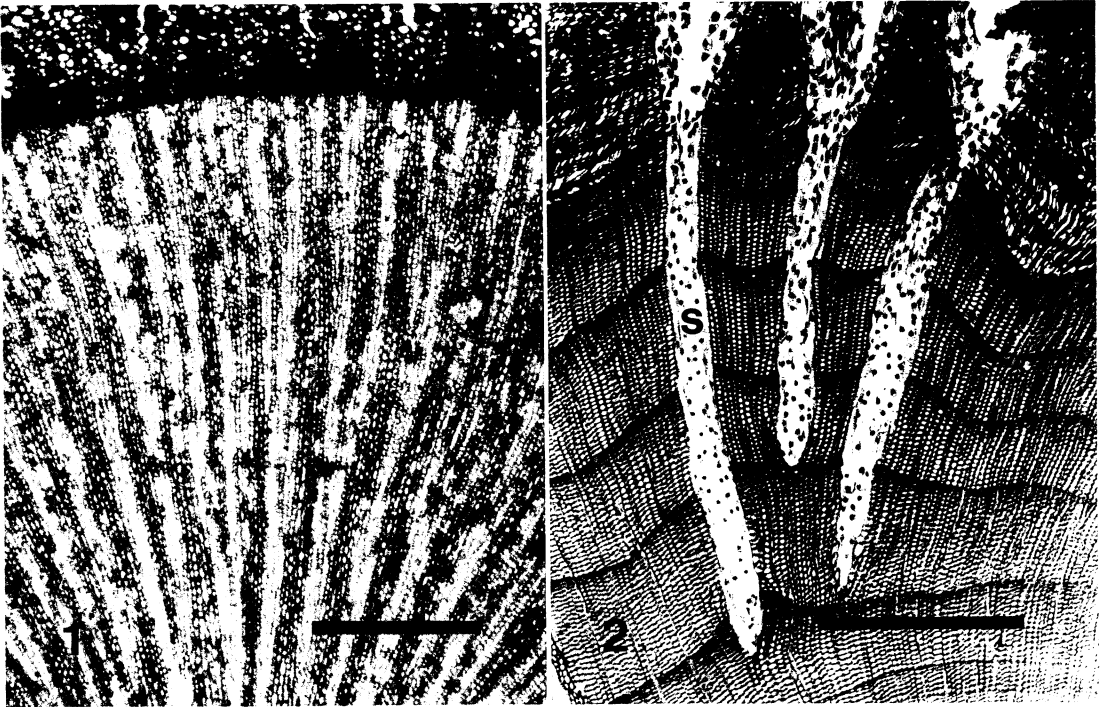
Fig. 1, 2.   **1.** Transverse section through the basal portion of a stem of *Phoradendron juniperinum*. Note the lack of distinguishable growth rings. Bar = 500 μm. **2.** Transverse section of a *Juniperus osteosperma* branch, taken approximately 1 cm from the junction between the branch and a mistletoe stem. Note that endophytic "sinkers" (s) can vary in the depth (= age) which they are embedded in the juniper branch. Only the sinker that traversed the greatest number of juniper growth rings was used to age the mistletoe infection. Bar = 500 μm.

be distinguished and were not included in the determination of age.

Mistletoe morphological studies—Prior to determining the age of each mistletoe infection using the destructive anatomical methods outlined above, four possible estimates of plant age based on different morphological traits of the stems were made for each sample. The objective was to obtain the best possible nondestructive morphological index of age based on the highest correlation between one of four stem-morphological traits and the known age of each infection as independently determined from anatomical studies. The four measures of stem morphology evaluated were: 1) the total number of nodes on the longest stem; 2) the total number of nodes at which lateral branches arose on the longest stem; 3) the total number of branches on the longest stem where a visible (0.5–1.0 mm) change in diameter occurred regardless of whether the junction where these branches arose was bifurcate, trifurcate, or greater; and 4) the number of bifurcate branching events (Fig. 3). A bifurcate branching event is much like a branch order that was originally

used by geomorphologists studying stream drainage patterns (Horton, 1945). However, it differs in that here we assume that the number of branches form a constant geometric progression with bifurcation number. For *P. juniperinum*, bifurcation ratios are relatively constant from one bifurcation event to another and therefore result in a relatively constant bifurcation ratio for the system, whether branch diameter changes or not (Niklas, 1978). This pattern is not seen in all plants, however, as discussed by Steingraeber and Waller (1986). Only one new branching order is added each year in *P. juniperinum*. Thus, a branching junction is assumed to represent the location where the next age class of branch originates, but need not be a product of higher-order branches from all directions as is required for ordering stream drainages. Flowering occurred on the current year's stem growth, while fruiting occurred on the second-year's stem growth. Sexual maturity of plants does not occur, however, until year 3 to 5. The position of lateral branches in some instances where damage had occurred were determined by the presence of an easily recognized branch "scar." Method 4 assumes
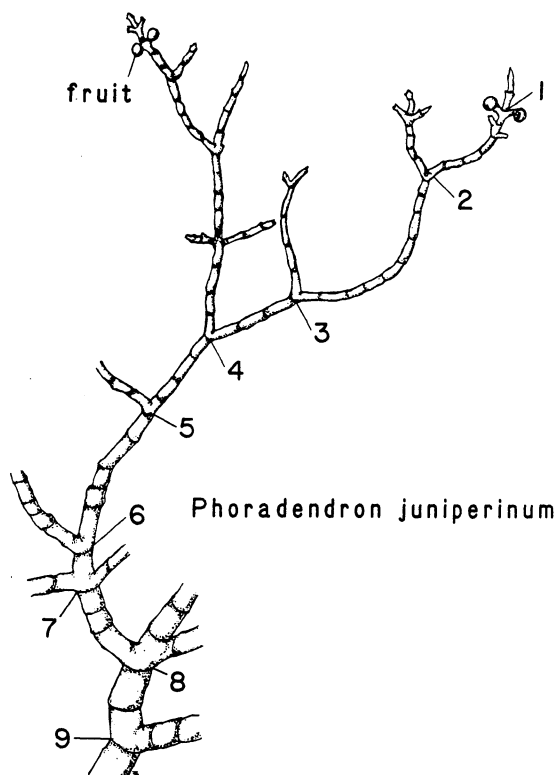
Fig. 3. Diagram of the mistletoe branch structure in *Phoradendron juniperinum*. The numbers at each branch-point indicate the next branch segment of different age. The branch biomass distal to the point where each number arises (= the next branch of a different age) represents tissue of that age. Fruit pedicels occur on 2-year-old branch segments. Flowers are produced from current year's stem growth. The plant illustrated is 10 years old.

that the branching event can be recognized by bifurcate stem junctions although some mistletoes found growing in shaded parts of the host tree had trifurcate branch junctions.

At trifurcate branch junctions, only those junctions that maintained the constant bifurcation ratio were screened as acceptable next branch-orders and counted. This method proved adequate because it provided the best correlation with age as determined anatomically (see below). In *P. juniperinum*, if one quickly scanned among numerous individuals, the current year's growth often appeared to have a "laterally branched" appearance at the times of the year after flowering and just prior to the winter season. These apparent "branches" were floral pedicels, not lateral branches, and were not counted as such. Individuals were most reliably aged in the autumn, after the majority of stem growth had taken place. All age determinations were done on plants that showed no obvious signs of die-back. We feel

that in plants that have died-back or resprouted, the age of an infection cannot yet be determined with confidence because the oldest mistletoe stems may have died and abscised. If resprouting has occurred, the current age of any mistletoe stem will not reflect the true age of the infection but only the age of the newly added standing biomass. Such individuals formed a small fraction (<9%) of the population we surveyed.

Population surveys—To assess the population age-structure of mistletoes on their hosts in the Coral Pink Sand Dunes population, infected host trees were surveyed for the number, age (using the index established below), and position of all mistletoes. For each mistletoe, its age, height within its host tree, and the host tree size class were recorded. Host trees were grouped into three broadly separated size classes based on the circumference of the main trunk at its base. Size classes were: 45–60 cm, 75–90 cm, and >105 cm. Eighty-six percent of all trees sampled fell within these size classes. Ten trees were randomly chosen from each size class. Tree-size class divisions based on tree diameter at breast-height were not applicable in *J. osteosperma* because many trees had more than one trunk at their base. Height within the trees was divided into 1-m increments from the ground surface.

Analyses—The population survey data were analyzed using a multiway contingency analysis (Feinberg, 1970) to test the association of age with mistletoe abundance, host tree size class, and height within the tree. The analysis was based on a log likelihood ratio chi-square statistic (G value) and tests the interaction of age with any one or combination of the other variables by comparing the goodness of fit between observed and expected cell values when expected values are calculated from models including and then excluding the interaction of interest. For the present study, the full model from which expected values were obtained was age (A) × height within the host tree (H) × host tree size class (SC)[=A × H × SC]. The two-way models were A × H, A × SC, and H × SC and were tested against the full model using the procedure stated above. A recent review by Vepsäläinen, Savolainen, and Penttinen (1988) provides a discussion of this analysis, how the models are applied to obtain the expected values, and where its use with ecological data is appropriate.

RESULTS—*Anatomical studies*—Age of a mistletoe infection could not be determined by

counting annual growth rings from the mistletoe stem itself because clear "rings" could not be distinguished (Fig. 1). As previously suggested (Srivastava and Esau, 1961; Calvin, 1966, 1967), the age of each mistletoe infection was determined by counting the number of annual growth rings of the host branch traversed by the longest (oldest) endophytic "sinker" (Fig. 2). This anatomical aging method has also been found acceptable for the dwarf mistletoe, *Arceuthobium* (Scharpf and Parmeter, 1966). Ninety-three percent of the sections taken from the zones 1–1.5 cm away from the junction of the mistletoe stem with the juniper branch had sinkers that could be reliably aged. Sections taken from directly beneath the junction could be used only 6% of the time; tissues from this region were highly deformed and "sinkers" were obscured by a proliferation of other endophytic tissues. In samples where age estimates from both regions could be determined, there was agreement between the samples 92% of the time. In the 8% where ages from the two regions did not agree, samples that were taken from directly beneath the stem/branch junction were 1–2 yr older than those taken 1–1.5 cm away from the junction.

Morphological studies — Four morphological indices of age were evaluated. The total number of nodes on the longest stem (index #1) was nonsignificantly correlated with mistletoe age determined anatomically (y = −0.684 + −0.207x, r^2 = 0.13, P = 0.61, populations did not differ). A similar nonsignificant correlation was found for the total number of nodes at which lateral branches (or branch scars) arose on the longest stem (index #2; y = 0.841 + 0.246x, r^2 = 0.19, P = 0.53, populations did not differ). The third morphological index showed an improved and significant correlation with age of the mistletoe determined anatomically over the first two indices: Skull Valley population — y = −0.026 + 0.316x, r^2 = 0.56, P = 0.05; Coral Pink Sand Dunes population — y = 0.194 + 0.352x, r^2 = 0.45, P = 0.05; the Bend population was not analyzed because the samples were lost after their use in the analyses of indices 1, 2, and 4). However, a regression slope in the range of 0.31–0.35 suggested that there was not a one-to-one correspondence between age determined from the sinker depth and age determined from the branching index. Although the correlation was moderately strong, because the slope of the regression was less than one, method 3 would likely yield underestimates of age (see below).

The fourth morphological index of age (the number of bifurcate branching events on the longest stem; Fig. 3) was most highly correlated with age as determined by the number of annual growth rings of the host traversed by the mistletoe "sinkers" (Fig. 4). If there was complete agreement between the sinker depth and the number of bifurcate branching events, the slope of the linear regression would be equal to one (1), and the intercept would pass through the origin. For none of the three populations surveyed were the slopes of the regression significantly different from one nor was there significant variation among populations in the observed slopes (Student's t-test, P = 0.01; Fig. 4). Moreover, the y-intercept did not deviate significantly from zero (Fig. 4) and no significant differences were observed among the three populations (Fig. 4), demonstrating a robustness to the index such that it could be applied across a wide range of populations. Although intersexual differences in the branching pattern were observed in the dwarf mistletoe genus *Arceuthobium* (Kuijt, 1970), no such differences were detected in *P. juniperinum*.

Population surveys — Using the aging index established above (Fig. 4) our surveys of the Coral Pink Sand Dune population showed that across all host tree size classes and canopy heights the greatest number of mistletoe infections were between 2 and 12 years of age (Fig. 5). Peak abundances were not correlated with total annual precipitation in either the same year or the year when establishment would have taken place (r = 0.42, P < 0.08, N = 11); the year previous to each peak (Climatic Records from the National Oceanic and Atmospheric Administration, Annual Summary, 1969–present, vols. 71–present and the Bureau of Land Management Weather Station Records, Kanab, UT). Further, there was no correlation of mistletoe abundance with minimum winter temperature (r = 0.11, P < 0.20, N = 11) and warmer than average winter temperatures (r = 0.08, P < 0.50, N = 7), a result previously reported. If the data for the number of mistletoe infections during these peak years is correlated with summer precipitation (June–September) there was a positive correlation (r = 0.52, P < 0.06, N = 11). This correlation suggests that a relationship exists between the greatest number of surviving recruits and a host that is growing in a year (or site) of favorable water status. In addition, the sharp decline in the number of mistletoes older than 10 years of age did not show a correlation to cold winter temperatures as previously suggested (Wagener, 1957; Lightle, Weins, and Hawksworth, 1964; Spooner, 1983). However,
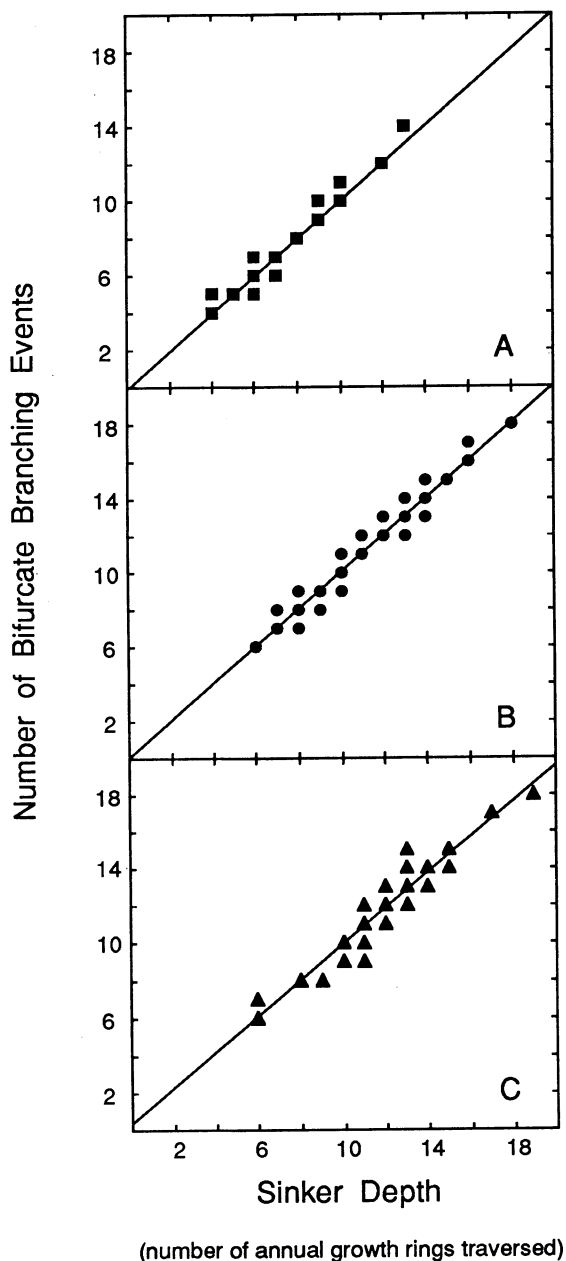
Fig. 4. The correlation between age, as determined from the number of bifurcate branching events, and age, as determined from maximum sinker depth. The three panels represent the correlation from three populations near Bend, Oregon (A); Skull Valley, north-central Utah (B); and near the Coral Pink Sand Dunes State Reserve, southwestern Utah (C). No significant differences (Student's t-test) in the linear regression were observed between populations. The slopes do not differ significantly from 1.0, nor do the y-intercepts differ significantly from 0.
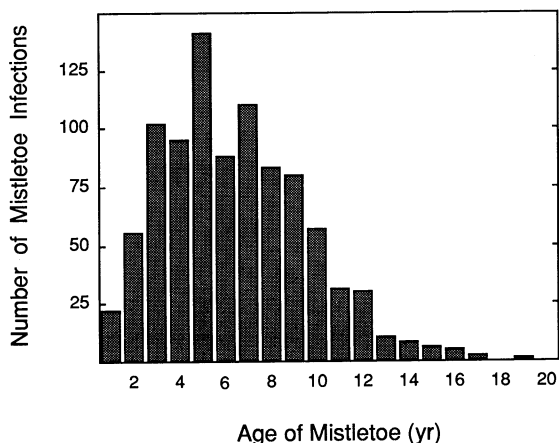

Fig. 5. Frequency age-distribution of 660 mistletoe infections growing on 30 host trees from a population surveyed near the Coral Pink Sand Dunes State Reserve, southwestern Utah.

fewer mistletoes are seen in all age classes following years of low summer rainfall. For example, not only were 1976 and 1977 years of lower than normal precipitation, but very little of that precipitation came as summer rain. This lack of precipitation corresponds to the marked decline in all mistletoes > 10 years of age (Fig. 5).

The age-specific distributions as a function of host tree size class were significantly different ($G = 20.27$, $P = 0.05$; Fig. 6). Smaller host trees had fewer mistletoe infections than larger trees as well as a peak in the age distribution at 7 years of age (Fig. 6A). Mid-sized host trees had the greatest number of younger mistletoe infections and three peaks in the age distribution at 4, 5, and 7 years of age (Fig. 6B). The largest host trees had the greatest number of infections and a larger proportion of 3- and 5-year-old mistletoes than any other host tree size class (Fig. 6C). In addition, small host trees had significantly fewer ($G = 23.67$, $P = 0.05$) than the expected number of infections in their upper canopies but a significantly greater number of infections in their lower canopies (Fig. 7A), while mid-sized (Fig. 7B) and larger host trees (Fig. 7C) had very close to the expected number of infections at all canopy heights.

The log-linear analysis indicated a significant association between the age of a mistletoe infection and the height of that plant in the host tree ($G = 20.16$, $P = 0.05$; Fig. 8). Across all host tree size classes there were fewer 1- to 3-year-old mistletoe infections than expected. This result may be influenced by the fact that these plants are much harder to see due to their
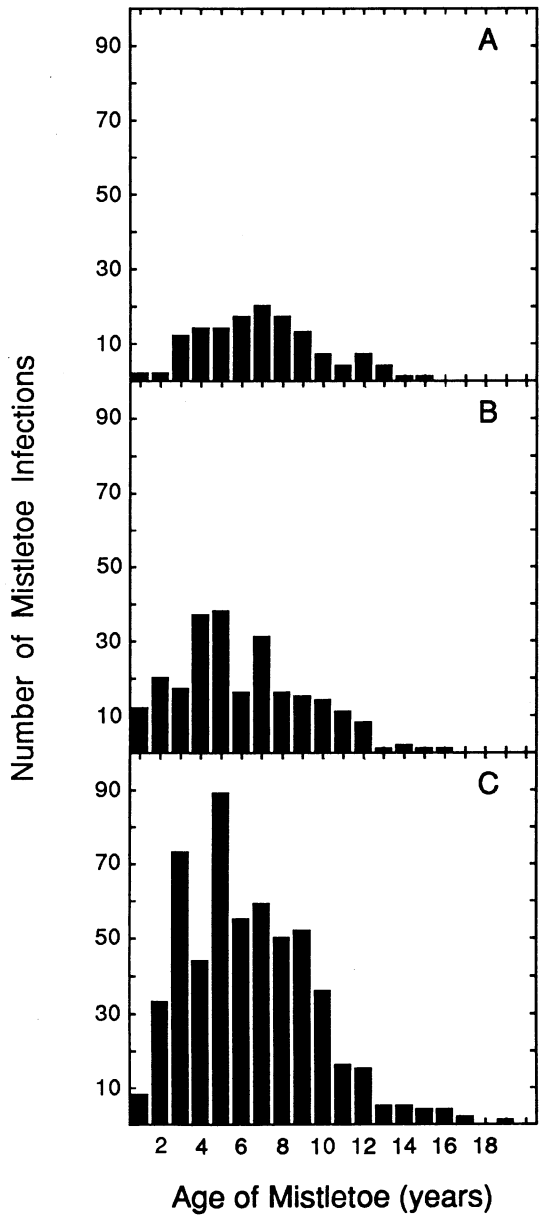
Fig. 6. Age-distribution of mistletoe infections growing on host trees of different sizes. The size classes of host trees were (A) 45–60 cm, (B) 70–95 cm, and (C) >105 cm circumference at base. Eighty-six percent of all host trees in the sample population fell within these size classes.
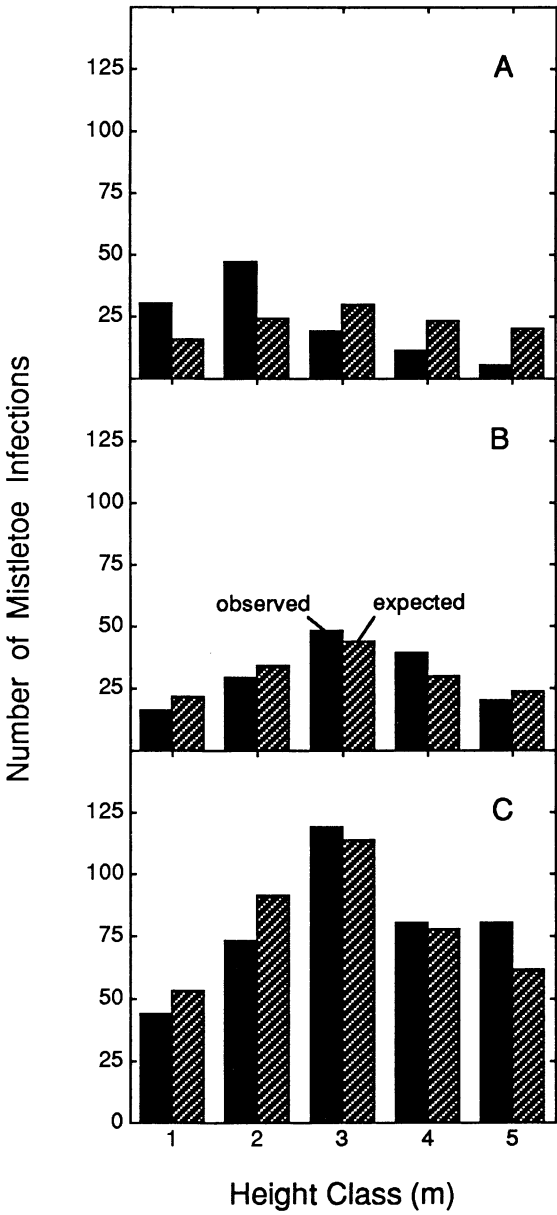
Fig. 7. The observed (solid bars) and expected (striped bars) frequency of mistletoe infections as a function of height class within host trees of different size class. Height classes are in 1-m intervals (e.g., class 2 is from 1.05 to 2 m). Host tree size classes are as in Fig. 6; (A) 45–60 cm, (B) 70–95 cm, and (C) >105 cm circumference at base.

small size (our presurvey estimates of the total number of infections obtained from ground level were low by 36–52% when compared to the estimates obtained on the same trees but conducted from scaffolding next to each tree which allowed access to the canopy). A clear peak in the mistletoe distribution occurred at ages 5–7 and at a height of 3 m in all host trees

(Fig. 8). The age distribution of mistletoes across all canopy heights for ages greater that 10 years was even, and less than expected based on the results of the log-linear analysis (Fig. 8).

DISCUSSION—For any population of short-lived plants, age-structure can be reconstructed

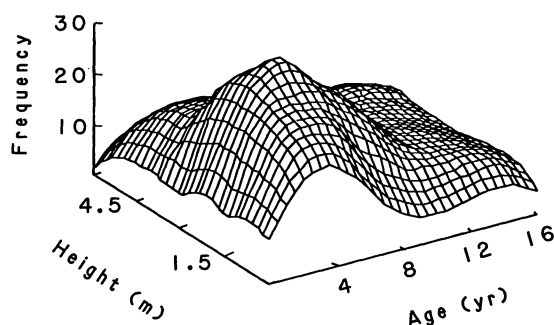Fig. 8. The frequency of mistletoe plants as a function of their age and height within 30 host trees from a population surveyed near the Coral Pink Sand Dunes State Reserve, Utah.

if one can determine how variable or constant the annual natality, mortality, and recruitment schedules are for that particular population (Silvertown, 1982). For long-lived plants this task is made more difficult because most often the schedules of natality, mortality, and/or recruitment are on much longer time-scales (well beyond the life of the investigator), and determining the ages of the extant set of individuals within that population is not easily accomplished. For this reason we must rely on being able to reconstruct the age-structure in perennial plant populations using reliable indices of age and inferring birth and death schedules through correlational analyses or population simulation models (Charlesworth, 1980). This approach has been successful in perennial plants that are easily aged such as trees growing in temperate climates where age can be determined using dendrochronological methods (Hett and Loucks, 1971; Hibbs, 1979; Sarukhan, 1977). However, for nonarborescent perennial plants, we have no reliable estimates of age and thus our ability to obtain age-structure information about these taxa is severely limited.

Anatomy, morphology, and aging—Srivastava and Esau (1961) and Calvin (1967) were among the first to demonstrate that the age of a mistletoe could be determined by anatomically sectioning host branches and counting the number of growth rings traversed by the "sinkers"; radial extensions of the mistletoe's endophytic system. Although this method is very reliable and was used in the present study to establish correlations with our nondestructive index, it is nonetheless destructive, time consuming, and labor-intensive, thus making it unsuitable for field work. Our method extends these early and important studies so that the individual age of a mistletoe (and from this

the age structure of a mistletoe population) can be reliably, and nondestructively, determined in the field.

Many ecological and physiological characteristics in the xylem-tapping mistletoe Phoradendron juniperinum have been shown to be correlated to the age of the plant (Schulze and Ehleringer, 1984; Dawson et al., 1990). Schulze and Ehleringer (1984) did estimate age in their study, but their protocol was not independently confirmed. Kuijt (1970) used the branching patterns of several species of Arceuthobium in evaluating their taxonomic relationships. Although he did not offer a precise set of protocols, Kuijt also suggested that the age of a dwarf mistletoe could be determined from its branch structure if "a detailed analysis of those features of branching habit repeat themselves from year to year" (Kuijt, 1970). The aging method presented here provides a formal, easily used, nondestructive method to determine the age of individual mistletoe plants.

Although the great majority of mistletoes could be aged accurately by our method, errors amounting to 1 or perhaps 2 years resulted when the method was applied to some plants. These included mistletoes with an "etiolated" branching structure resulting from significant shading and plants that were at or near the upper age limits of the species (e.g., >15 yr). Plants in which vegetative growth ceased or slowed during the current year, resulting in shorter internodes on the main stem, were also often difficult to age if the most distal "branch" order could not be distinguished from floral pedicels. This problem can easily be minimized by aging plants in the autumn after most of the growth has taken place, floral pedicels have abscised from male plants, and female plants are in fruit.

Age distributional patterns—Over all of the host trees surveyed we found that the peak abundance of mistletoe infections occurred between 2 and 12 years of age. The greater abundance of mistletoes during these years was correlated with the amount of precipitation which fell as summer rain. During the establishment phase of young mistletoe seedlings, if host plant water status was more favorable than in a normal year due to increased rainfall and if potential evaporation was not as great (due to lower leaf and ambient air temperatures), then these periods may have been especially conducive for plant establishment.

There was a peak in the age distribution at ages 5–7 years and at approximately 3 m height within the host tree canopy. This pattern suggests that particular aspects of the host tree's

architecture may further influence the age-structure in this mistletoe population and the distribution of individuals within the host tree canopy. The overall canopy shape of *J. osteosperma* can be highly variable (Bunderson, 1983; Bunderson, Weber, and Nelson, 1986; Welsh et al., 1987). Trees rarely exceed 10 m in height, are more commonly 5–7 m tall, and commonly have their greatest branch biomass and leaf area distribution between 2.5 and 4 m above ground (Vasek, 1966; Born and Chojnacky, 1985; Chojnacky, 1985, 1987). These canopy characteristics may serve to attract seed-eating and seed-dispersing birds, such as the Phainopepla (*Phainopepla nitens*), Steller's Jay (*Cyanocitta stelleri*), the common Robin (*Turdus migratorius*), or the Dark-eyed Junco (*Junco hyemalis*), which may perch and defecate or regurgitate seeds (Hawksworth and Scharpf, 1981; Nicholls, Hawksworth, and Merrill, 1984). This could explain, at least in part, why a peak in mistletoe abundance occurred at this level in the host tree canopy, an observation also reported for the mistletoe *Alepis flavida* found parasitizing *Nothofagus solandri* from New Zealand (Hollinger, 1989) and *Loranthus europaeus* on two oaks in southeastern Europe (Eliás, 1988).

A greater number of infections and younger mistletoes on larger host trees suggests that there is a great amount of seedling establishment from *within* that particular tree. This "intra-tree-dispersal" could result in lower genetic diversity in subpopulations of mistletoes on larger but not smaller host trees (Glazner, Devlin, and Ellstrand, 1988). Further work on the role of bird vs. other types of dispersal and its influences on both the genetic structure and population age-structure in all mistletoes is needed before these hypotheses can be properly evaluated (but see Davidar, 1983; Godschalk, 1983; Linhart, 1984).

Previous work with *Phoradendron* suggested that periods of extreme winter cold were an important cause of mortality and hence a major control over distribution in these hemiparasites (Wagener, 1957; Lightle et al., 1964; Spooner, 1983). We found no correlation between the marked decline in the number of mistletoes greater than 10 years of age and abnormally cold winters. In fact, in 1985 (one of the coldest winters recorded for the area) and in several additional years during the past 20-year period, extremely low temperatures have been observed that approached the record low value. Had these low temperatures caused significant mortality, all individuals older than 3 years should have died. This did not occur (Fig. 5). The most likely climatic factor contributing to the mortality of individuals older than 10 years of age is lack of summer rain. Over the entire population age-distribution, marked decreases in the number of infections were seen following years when precipitation was below normal and summer rainfall was very low. For example, the drought years of 1976 and 1977 (83% and 77% of normal precipitation, respectively) correspond to the marked decline in the total number of mistletoe infections that would have been present on the host trees during these periods (> 10 years old). One likely explanation for the reported observation of mistletoe death under low-temperature winters could be the significant correlation between minimum winter temperatures and precipitation. For example, at our site, precipitation and minimum winter temperatures are highly correlated ($r = 0.395, P < 0.01$, $N = 47$). Thus, mortality that has in the past been attributed to cold temperatures may in fact have been associated with lack of water.

Physiological characteristics may also play an important role in structuring these mistletoe populations. We offer two testable hypotheses. First, *P. juniperinum* is known to be a water and nutrient parasite (Schulze and Ehleringer, 1984; Ehleringer, Cook, and Tieszen, 1986). Although autotrophic, it has very low rates of photosynthesis (Schulze and Ehleringer, 1984; Ehleringer et al., 1986; Marshall, Flanagan, and Dawson, unpublished data) as do other hemiparasitic mistletoe species (Hollinger, 1983; Schulze, Turner, and Glatzel, 1984; Ehleringer et al., 1985) and may even obtain some carbon via xylem water (Marshall and Ehleringer, unpublished data). If the respiratory costs associated with maintaining "old," largely nonproductive leaf area exceed the carbon income the plant may secure by having greater photosynthetic area, then age-dependent mortality (= population turnover) driven by the carbon and perhaps nitrogen economy may lead to the age-structure we have reported here. Alternatively, hydraulic resistance to water flow may increase significantly across the haustorial interface between host and parasite (Fisher, 1983; Glatzel, 1987). As plants age, stems grow and hydraulic resistance increases as a function of both mass and length (Zimmerman, 1983). Supporting and maintaining these stems in a favorable hydraulic state may again be costly and hence place an upper limit on the size of individuals. Such processes may help explain the age distributions reported here. In the future, we hope that the application of the aging method derived here increases the likelihood of evaluating age-dependent processes in higher-plant parasites.

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