HOST COMPATIBILITY OF THE CLOUD FOREST MISTLETOE PSITTACANTHUS SCHIEDEANUS (LORANTHACEAE) IN CENTRAL VERACRUZ, MEXICO

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The consequences of the seed deposition of the parasitic mistletoe Psittacanthus schiedeanus were evaluated in a 32-mo study. We conducted a field seed inoculation experiment to determine variation in seed adhesion, seed germination, seedling establishment, and plant survival to reproduction among five host species and to evaluate whether these post-dispersal processes explain mistletoe prevalence and specificity at the regional scale. Seeds without an exocarp were inoculated onto branches of individuals of the five most common host species identified in nature in central Veracruz, México. Seed fate was monitored for 2 yr, at weekly intervals for the first 2 mo and at 2-mo intervals thereafter. The height and diameter of experimental host branches and canopy cover above them were measured to see if these factors affected mistletoe establishment. Significant differences in seed attachment and seed germination were found among host species. Fewer seeds remained attached on experimental branches of Quercus germana than those of Liquidambar styraciflua. Although significant differences in seed germination were observed among species (significantly greater on A. pennatula), >70% of mistletoe seeds germinated within the first 5 wk on all host species. Towards the end of the inoculation experiment, more mistletoe seedlings survived, grew, and then flowered on Liquidambar styraciflua than on A. pennatula, P. mexicana, Q. germana, or Q. leiophylla. Host branch initial height and diameter did not affect seedling survival, but seedlings survived better on trees where the canopy was more open. Our results suggest that Liquidambar styraciflua is the most compatible host species with P. schiedeanus in central Veracruz. Not surprisingly, Liquidambar is by far the most common host tree for P. schiedeanus in this area as well. We suggest that the observed local specialization is a result of seed dispersal as consequence of bird foraging and territorial behavior, host abundance, and host species compatibility.

Key words: host–parasite interaction; Loranthaceae; parasitism; Psittacanthus schiedeanus; seed germination; seedling establishment.

Parasitism is a successful mode of life in many flowering plants (Knutson, 1983; Musselman and Press, 1995). Mistletoe parasitism constitutes a continuum of host specificity that ranges from specialized to generalized (Reid, 1989; Monteiro, Martins, and Yamamoto, 1992; Reid, Stafford, and Yan, 1995; Norton and Carpenter, 1998). Specialist mistletoes are typically restricted to a single host species (although they can infest other hosts), whereas generalist mistletoes use various host species with no apparent preference for any of them. Although most parasitic mistletoes have been described to behave as host generalists, they can show host specialization at a regional scale (Norton and Carpenter, 1998).

Radomiljac (1998) suggests that mistletoe seed germination is little influenced by the type of substrate to which seeds are adhered, and only suitable conditions of water, oxygen, temperature, and light are required for germination (Lamont, 1983). However, host stem size may have a strong effect on seed persistence and seedling establishment (Reid, 1987, 1989; Sargent, 1995; Yang and Reid, 1995; Ladley and Kelly, 1996; Norton and Ladley, 1998). Mistletoe seedlings can remain autotrophic for several months before penetrating the tissues of the host (Sallé, 1983; Boone et al., 1995). Establishing connection with the host vascular tissues is essential for longer term survival (Norton and Carpenter, 1998). Lamont (1983) divided the period of mistletoe post-dispersal establishment into four sequential phases: seed adhesion, seed germination, seedling establishment, and plant survival to reproduction. Seedling establishment in mistletoes involves the penetration of haustoria in host tissue. The number of plants that survive to flower and fruit can be diminished within each of the phases given the constraints and pitfalls that characterize each phase. Seed predation may be responsible for much seed disappearance (Yang and Reid, 1995; Norton and Ladley, 1998), as observed in Phoradendron robustissimum (Sargent, 1995), and twig size, seed clumping, and host bark characteristics may also explain the failure of further seedling development and growth of mistletoe plants (Reid, 1987, 1989; Howe, 1989; Sargent, 1995). Studies to determine the underlying mechanisms leading to mistletoe post-dispersal establishment across a spectrum of the most commonly used host species are needed.

Psittacanthus schiedeanus (Cham. & Schiecht) Blume ex. Schultes (Loranthaceae) mistletoe parasitizes several host tree species in cloud forest remnants in central Veracruz, México (Cházar and Oliva, 1988). However, the number of infested individuals (prevalence of infection) is highest within and among Liquidambar styraciflua Oested (Hamamelidaceae) (López de Buen and Ornelas, 1999; López de Buen, Ornelas,
and García Franco, 2001). We have suggested that the preference of \textit{P. schiedeanus}-fruit eating birds for perching and consuming mistletoe fruits on some tree host species directly affects mistletoe seed dispersal (López de Buen and Ornelas, 1999). Our observations show that birds deposit more mistletoe seeds onto branches of \textit{L. styraciflua} individuals than other species (López de Buen and Ornelas, 1999). Although the behavior of frugivorous birds play an important role in seed deposition and may play a role in mistletoe host specialization, such specialization may also be the result of regional host abundance, and the influence of host compatibility on seeding establishment could also be an important component in explaining relative infection rates among host species (Norton and Reid, 1997; Norton and Ladley, 1998; Norton and de Lange, 1999). The nonrandom distribution of \textit{P. schiedeanus} on hosts (López de Buen and Ornelas, 1999; López de Buen, Ornelas, and García-Franco, 2001) was the motivation to undertake this study.

In this paper, we specifically asked to what extent seed adhesion, seed germination, seeding establishment, and plant survival explain the observed pattern of \textit{P. schiedeanus} host infection. Our inoculation experiments allowed us to evaluate whether these post-dispersal processes vary among host species and thus allowed us to explain mistletoe host specialization at the regional scale.

**MATERIALS AND METHODS**

**Study site**—Fieldwork was carried out from January 1997 to August 1999 in one of the few remaining cloud forest fragments (9 ha), near Xalapa, Veracruz, México (19°30’ N, 96°57’ W; at 1300 m above sea level). Mean annual precipitation is 1500 mm, and mean annual temperature is 18°C. The climate is mild and humid throughout the year, with a dry, cold season from November to March (Williams-Linera, 1997). The most common tree species in the study area include \textit{Liquidambar styraciflua} var. \textit{mexicana} Oest (Hamamelidaceae), \textit{Quercus germana} Cham. & Schldl., \textit{Quercus leiophylla} A. D. C. (Fagaceae), \textit{Platanus mexicana} Moric. (Platanaceae), \textit{Persea americana} Mill. (Lauraceae), \textit{Acacia pennatula} (L.) J. F. Ornelas and L. Jiménez (Fabaceae), \textit{Crataegus mexicana} Mociño and Sessé (Rosaceae), and \textit{Citrus maxima} (Burm.) Merr. C. (Rutaceae) (Cházaró and Oliva, 1988; López de Buen and Ornelas, 1999). Floristic details of the area are given by Castillo-Campos (1991).

**Study species**—\textit{Psittacanthus schiedeanus} mistletoes are distributed from central México to Panamá and often parasite tall trees in evergreen montane forests between 1300 and 3300 m elevation (Burger and Kuijt, 1983; Cházaró and Oliva, 1988). More than 20 tree species can be used by this mistletoe species (Cházaró and Oliva, 1988; López de Buen and Ornelas, 1999). In central Veracruz, México, this mistletoe is highly conspicuous in the summertime because it blooms copiously and continuously bright, red-orange flowers visited mainly by hummingbirds, \textit{Campylopterus caripensis} and \textit{Anazulía cyanoccephala} (J. E. Ornelas and L. Jiménez, Instituto de Ecología, AC, unpublished data) from June to November (López de Buen and Ornelas, 1999).

Fruits are fleshy, one-seeded, and change in color from green when immature to purplish-black at ripening (López de Buen and Ornelas, 2001). Fruit development usually starts by early June, but fruit ripening occurs asynchronously from November to April (López de Buen and Ornelas, 2001). We observed numerous bird species consuming fruits of this mistletoe including \textit{Ortalis vetula} Wagler (plain chachalaca), \textit{Melaenepes aurifrons} Vigors (gold-fronted woodpecker), \textit{Myiozetes similis} Spix (social flycatcher), \textit{Cyanocorax morio} Wagler (brown jay), \textit{Turdus grayi} Bonaparte (clay-coloured robin), \textit{Dumetella carolinensis} Linnaeus (gray catbird), \textit{Bombycilla cedrorum} Vieillot (cedar waxwing), \textit{Pilogonys cinericeps} Swainson (gray silky-flycatcher), \textit{Chlorospingus ophthalmicus} Du Bus de Gisignies (common bush-tanager), \textit{Piranga rubra} Linnaeus (summer tanager), \textit{E. elegantissima} Bonaparte (elegant euphonia), \textit{Pheucticus ludovicianus} Linnaeus (rose-breasted grosbeak), and \textit{Icterus galbula} Linnaeus (baltimore oriole) (López de Buen and Ornelas, 1999; A. Cruz, Instituto de Ecología, AC, unpublished data). While it is not known which species are the most efficient seed dispersers (sensu Reid, 1989), social flycatchers, cedar waxwings, and gray silky-flycatchers are likely candidates, because they regurgitate complete viable seeds singly in safe sites, and those seeds germinate (López de Buen and Ornelas, 1999). Cedar waxwings are thought to be important seed dispersers in years when large groups stay over the winter in central Veracruz, because the fruit ripening peak coincides with the highest numbers of cedar waxwings (López de Buen and Ornelas, 2001).

**Experimental design**—A seed inoculation experiment was conducted on branches of the study host species and mistletoe seed fate was monitored from January 1997 through August 1999. The most common native host species occurring in our study site (López de Buen and Ornelas, 1999) were chosen for artificial seed inoculation: \textit{A. pennatula}, \textit{L. styraciflua}, \textit{P. mexicana}, \textit{Q. germana}, and \textit{Q. leiophylla}. These host species flush their leaves almost entirely between November and February, except \textit{Quercus spp.}, which flush leaves all year round (Pennington and Sarukhán, 1998). We collected 2500 recently fallen mistletoe fruits from the ground, below \textit{L. styraciflua} trees (\(N = 8\)). We then removed the exocarp to allow seed germination (Sargent, 1995; Ladley and Kelly, 1996; L. López de Buen, unpublished data). The source of seeds used in inoculation may influence the results in experiments like this one. Yet collecting seeds from under one host species only was a serious drawback to testing the question we have posed about host local specificity. Collecting fruits from all host species to undertake cross inoculation experiments among all host species would have been desirable. However, more than a month of daily harvesting and setting up the inoculation experiment with recently fallen fruits would be needed for such an enterprise. Keeping the collected fruits in the laboratory for \(>1\) mo would introduce unknown experimental bias because of seed viability. Instead, we only collected recently fallen mistletoe fruits from the ground below few \textit{L. styraciflua} trees. By doing so, we were able to set up a balanced inoculation experiment with sufficient viable seeds from the most common host species in \(<1\) mo.

Experimental seeds were used to inoculate branches (unit of replication) of the study host species in our study site. We applied sets of 20 seeds on each of five different branches of five individual trees (100 seeds per tree) per host species by sticking them in place with the natural viscis. In order to extend and develop viscin threads, the seeds were smeared around on the palm of the hand as suggested by Sargent (1995). Sets of experimental seeds were arranged linearly along the branch, separated from each other by \(-3\) cm. All seeds were “planted” in this manner in January 1997. Some species of mistletoes have seed dormancy (S. Sargent, Allegheny College, personal communication), so it is likely that the seedling will not die if host contact through the haustorium is not established during the cotyledon phase (Kuijt, 1969; Davidar, 1983). Despite this, seeds germinate in \(-30\) d under controlled conditions (L. López de Buen, unpublished data) and in Costa Rica this species opens its cotyledons within \(-2\)–\(-3\) d (S. Sargent, Allegheny College, personal communication). Seedlings were defined as those plants with cotyledons (Davidar, 1983). Seed fate was monitored for 2 yr, at weekly intervals for the first 2 mo and at 2-mo intervals thereafter. Flowering individuals were counted at the end of the study (128 wk after seed inoculation).

**Seed fate**—Seed adhesion, seed germination, seeding establishment, and plant survival to reproduction of \textit{P. schiedeanus} were analyzed separately according to post-dispersal phenological phases as defined by Lamont (1983). Each phenological stage was treated independently. Firstly, adhesion was estimated as a percentage of the number of seeds planted; then germination was estimated as a percentage of the number of seeds adhered; seeding establishment as a percentage of germinated seeds; seedling survival from week 10 to week 72 as a percentage of those present at week 10; and adult survival to reproduction (of flowering individuals) from week 72 to week 128 as a percentage of those present at week 72. Finally, we did an overall analysis on...
the number of seeds adhered to those remaining seedlings after 72 wk. This approach allowed us to see which stages contributed significantly to the overall pattern.

**Data analyses**—Differences among host species in the percentage of seeds that remained adhered were analyzed using one-way ANOVA (Zar, 1984), and differences in germination, establishment, and survival over time (weeks) were analyzed using repeated-measures ANOVAs (Zar, 1984). Post-hoc mean comparisons (Games-Howell procedure) were conducted to examine differences among host species in each of the phenological phases of *P. schiedeanus*. The overall analysis looking at the variation among host species in seed fate (from seed adhesion to week 72) was also compared using repeated-measures ANOVA (Zar, 1984). In the model, host species was treated as a fixed factor and the percentage of seeds or seedlings on each branch over time was the repeated measure. The percentage of flowering individuals remaining at week 128 was calculated from those seedlings present at week 72. Percentages were arcsine transformed to fulfill the requirements of the parametric analysis (Zar, 1984), but untransformed data are reported in graphs. All statistical analyses were run using General Linear Modeling with StatView and SuperANOVA (Abacus Concepts, 1989, 1996).

**Height and diameter of host branches**—Sargent (1995) found that twigs of the host species <5 mm died after mistletoe seed inoculation and those >40 mm did not (see also Reid, 1987; Yan and Reid, 1995; Ladley and Kelly, 1996; Norton and Ladley, 1998). Diameter of experimental branches ranged from 5 to 18 mm and height above the ground from 0.7 to 3.4 m. Results of one-way ANOVAs showed a significant variation among branches of five host species in height above the ground and diameter (Table 1).

Because experimental branches varied in diameter and height above the ground it was necessary to control for these initial differences in the analysis, as those factors might otherwise obscure the effects that host species per se have on seed fate. We analyzed the relationship between mistletoe seedling survival on the five host species and the branch characteristics using repeated-measures ANCOVA. Log-transformed height and diameter were used as covariates to control for the variability among branches at the beginning of the seed inoculation experiment. In the model, host species was a fixed factor, branch characteristics were the covariates, and percentages of seeds or seedlings that had survived every week (as the overall analysis) were the repeated measures. Along with the main effects for host species and branch characteristics, the interactions host species × branch characteristic were also included in the model.

**Canopy cover and seedling mortality**—Canopy cover above the experimental branches of host trees (overstory density) may influence the establishment and survival of mistletoe seedlings (Cházaro et al., 1992; Yan, 1993; Sargent, 1995). Canopy cover (in percentages) was measured with a Spherical Crown Densiometer (Forestry Suppliers, Jackson, Mississippi, USA) at 8-wk intervals after seed germination (weeks 40, 48, 56, 64, and 72). The effect of canopy cover of five host species on mistletoe seedling survival was also analyzed using repeated-measures ANCOVA in the same way as for branch characteristics. Mortality rates were measured in the same weeks as the percentage of seedlings that died in each individual. Differences among host species in mortality rates over time were compared with a two-way ANOVA (Zar, 1984). Canopy cover measures were arcsine transformed to fulfill the requirements of parametric analysis (Zar, 1984), but untransformed data are reported.

**Host abundance and host compatibility**—To test whether mistletoe host compatibility partially reflects relative host abundance, we compared the relative success of inoculated seeds (relative infection success) on different hosts (number established 128 wk after seed inoculation relative to number planted for each host species) with the prevalence of mistletoe infection on different hosts in the study site (number of infected trees relative to total number of individuals of each host species) (López de Buen and Ornelas, 1999). We compared relative infection success and prevalence using a paired *t*-test.

## RESULTS

**Seed adhesion**—We found significant variation in *P. schiedeanus* seed attachment among host species (*F*₄,1₂₀ = 3.369, *P* = 0.012). More seeds fell off from experimental branches of *Q. germana* (12%) than other species (<5%) (Fig. 1A), but post-hoc mean comparisons showed no differences among species (Games-Howell test, *P* > 0.01).

**Seed germination**—Variation in seed germination was significantly different among host species (*F*₄,4₇₆ = 5.164, *P* = 0.0007). More than 90% of mistletoe seeds germinated on *A. pennatula*, and <85% did on the other species (Games-Howell test, *P* < 0.01) (Fig. 1B).

**Seeding establishment**—Variation in mistletoe seeding establishment was marginally significant among host species (*F*₄,3₇₄ = 2.535, *P* = 0.045). Almost 100% of seeds that germinate by week 5 get established in all host species, except those on branches of *Q. germana* (<90%) (Games-Howell test, *P* < 0.01; Fig. 1C).

**Seeding survival**—The percentage of seedlings that have survived after 72 wk of those present at week 10 was statistically different among branches of five host species (*F*₄,4₄₄ = 6.363, *P* = 0.0001), but more seedlings survived on *L. styraciflua* (Fig. 1D). More than 50% of the mistletoe plants established as seedlings survived on branches of *L. styraciflua*, and less than 40% on branches of the other host species (Games-Howell test, *P* < 0.01 for all species except *P. mexicana*) (Fig. 1D).

**Plant survival to reproduction**—By the end of the experiment (week 72), <10% of original seedlings remained on
Host species

Fig. 1. Results of seed inoculation experiments of *Psittacanthus schiedeanus* seeds or seedlings on the most common host species. (A) Seed adhesion (the percentage of the number of seeds planted); (B) Seed germination (the percentage of the number of seeds adhered); (C) Seedling establishment (the percentage of germinated seeds); (D) Seedling survival (the percentage of those present at week 10) (see text). Letters represent results of post-hoc mean comparisons (Games-Howell test, \( P < 0.01 \)). LS = *Liquidambar styraciflua*, AP = *Acacia pennatula*, PM = *Platanus mexicana*, QG = *Quercus germana*, and QL = *Q. leiophylla*. Data are means ± SE.

Because host species × height \( (F_{4,1176} = 1.766, P = 0.143) \), host species × diameter \( (F_{4,1176} = 0.479, P = 0.751) \), and host species × height × diameter \( (F_{4,1176} = 0.673, P = 0.612) \) interactions were not significant, we removed them from the model. After doing this, the \( F \) value for host species was significant \( (F_{4,1358} = 9.415, P = 0.0001) \). The nonsignificant \( P \) value for diameter \( (P = 0.471) \) shows that this factor does not explain variation in seedling survival, but the initial differences in branch height among host species affected seedling survival \( (P = 0.015) \).

**Canopy cover and seedling mortality**—Canopy cover (in percentages) above experimental branches during the mistletoe fruiting period was significantly different among host species in October, December, and February (Table 1). Canopy cover varied over time in deciduous *A. pennatula* and *L. styraciflua*, but stayed almost constant for *P. mexicana*, *Q. germana*, and *Q. leiophylla* (Table 1).

A relatively high seedling mortality (35%), calculated as the percentage of seedlings that died in each individual at 8-wk intervals after seed germination, was observed at the beginning of our observations (week 40) and then increased dramatically by week 56 (56%). Seedling mortality since week 40 then decreased again to 27% in week 64 and to 29% in week 72 (Fig. 4). This variation in mortality rates over time was significant \( (F_{16,378} = 5.547, P = 0.0002) \) and the host species × time interaction was significant as well \( (F_{16,378} = \)...
2.135, $P = 0.0067$). Mortality rates were only significantly higher at week 56 (February) (56%; Fig. 4) (Games-Howell test, $P < 0.01$). These data suggest that seedling mortality rates are higher during dry and cooler months (January–March).

We also observed significant variation in mortality rates among host species ($F_{4,179} = 11.933, P = 0.0001$): mortality rates were significantly higher on branches of $Q. leiophylla$ (53%) and $A. pennata$ (51%) than those of $Q. germana$ (39%), $P. mexicana$ (35%), and $L. styraciflua$ (21%) (Games-Howell test, $P < 0.01$).

Results of repeated measures ANCOVAs showed that mistletoe seedling survival was affected by canopy cover in October and February (Table 2). The host species $\times$ canopy cover interaction was not significant for the December data, so we removed it from the model. After doing this, only the $F$ value for host species was significant ($P = 0.0001$), suggesting that canopy cover variation in December does not explain seedling survival.

**Host abundance and host compatibility**—By August 1999 (128 wk after seed inoculation), plant survival to reproduction differed among host species (Table 3). More $P. schiedeanus$ survived to reproduction on $L. styraciflua$ than on any other host species, and the number of seedlings established on $L. styraciflua$ was higher than expected in experimental trees ($\chi^2 = 34.55, P < 0.001$) relative to prevalence of infection of $L. styraciflua$ in the area (Table 3). No differences between relative infection success and prevalence were observed ($t = -1.72, df = 4, P > 0.05$).

### Discussion

**Patterns driven through vector–mistletoe interactions**—Loranthaceous mistletoes typically require birds as vectors for seed dispersal to hosts (Davidar, 1983; Monteiro, Martins, and Yamamoto, 1992; Overton, 1994; Reid, Stafford, and Yan, 1995; Martínez del Rio et al., 1996). Frugivorous birds habitually perch in trees and are effective at depositing seeds onto perches (Docters van Leeuwen, 1954; Davidar, 1983; Godschalk, 1983; Restrepo, 1987; Reid, 1989; Sargent, 1995; Martínez del Rio et al., 1996; López de Buen and Ornelas, 1999). Large seeds are often deposited singly (typically by regurgi-
tation), and small seeds are voided in fecal samples and are sometimes wiped onto branches where they stick in place with the viscous tissue that surrounds the seeds (Kuijt, 1969; Davidar, 1983). The viscid tissue typically hardens in 1 or 2 d (Sallé, 1983; Murphy et al., 1993; Yan and Reid, 1995) gluing the seed to the branch. Adequate seed dispersal of mistletoes involves seed deposition by birds to the branch’s surface of a compatible host (Yan, 1993), and the exocarp needs to be removed to facilitate seed germination (Lamont, 1983; Murphy et al., 1993; Sargent, 1995). Studies have shown that mistletoe seeds will not germinate without exocarp removal (Lamont, 1983; Sargent, 1995; Ladley and Kelly, 1996; L. López de Buen, unpublished data), an action normally performed by birds. Despite birds helping to disperse mistletoe seed successfully, only a fraction of seed production is adequately dispersed. In *P. schiedeanus* mistletoe, we have observed that only 35% of ripe fruits are removed very likely by birds, and the remaining 65% are lost (dried out attached to the plant or dropped to the ground) (López de Buen and Ornelas, 2001). However, even ripe fruits removed by the birds would not necessarily end up in safe places, given the wide disperser potential of these birds. Although dispersal success is likely affected by this possibility because seeds were hand planted.

### Patterns driven through host–mistletoe interactions

In the absence of possible effects imposed by host selection by birds, we think that *P. schiedeanus* prevalence can be explained in part by host compatibility with *L. styraciflua*.

Even if mistletoe seeds are adequately dispersed to hosts, not all of them will germinate and become established. In this study, we have shown that 88 ± 6.82% (mean ± 1 SE) of the seeds germinate in the field, regardless of host species on which they were planted. However, the subsequent establishment and survival of seedlings varied depending on host species (Fig. 2). Our seed inoculation experiment showed that patterns of seed adhesion, seed germination, seedling establishment, and seedling survival vary among the five most common host species in central Veracruz. We observed that 10–20% of inoculated seeds fell off the branches (see also Norton and Ladley, 1998), but differences in seed adhesion among host species were not significant. Our results on *P. schiedeanus* seed germination are congruent with those of Ladley and Kelly (1996). They showed that removal of the exocarp is necessary for germination of five endemic New Zealand Loranthaceae and that once this has happened there is a high level of germination, regardless of substrate. As they suggested for three mistletoe species, dispersal limitation is a likely explanation for the 65% of *P. schiedeanus* seeds that never get dispersed. Ladley and Kelly also showed that survival of adult mistletoes was >90% per year for most species.

Norton and Ladley (1998) did a hand planting experiment with *Alepis flaviga* on branches of *Nothofagus solandri* and showed that 17% fell off the branches, a similar percentage to what we observed for *P. schiedeanus* on branches of *Quercus germana*. In their study, establishment was much higher on thin branches (48% on <5 mm diameter) than fatter ones (6% on >20 mm diameter). Branch diameter varied significantly among host species on which *P. schiedeanus* was established, but this factor did not explain a significant portion of variation in seedling establishment. Differences in bird foraging could potentially alter the dispersal efficiency of *P. schiedeanus*, especially if large frugivores (e.g., plain chachalacas, brown jays) avoid using small-diameter branches as perch and defecation sites. However, the interpretation of our results is not affected by this possibility because seeds were hand planted.

As our experiment progressed, differences from previous similar studies started to emerge. For instance, more seedlings survived to flowering the third year on branches of *L. styraciflua* (L. López de Buen, unpublished data). Ladley and Kelly (1996) and Norton, Ladley, and Owen (1997) showed that growth of the New Zealand species seems to be much slower than *Psittacanthus*, with seedlings often still having only 5–10 leaves after 2–3 yr and flowering not occurring until they are 5–8 yr old or more.

Possible genetic effects may confound the interpretation of our results. Differences in host utilization may be genetically based leading to differential success of individuals of one mistletoe population when grown on a different species. In fact, we observed that more seedlings survived on the source host species than expected given the prevalence of mistletoe infection on various hosts in our study site. Norton and Carpenter (1998) suggested that local host specificity could be genetically based. In addition, Clay, Dement, and Rejmanek (1985) showed significant differences in haustorial disk formation when *Phoradendron tormentosum* individuals were cross-inoculated between host species, with greatest success when they were grown on the source host species. Nevertheless, we assumed that the experimental seeds corresponded to one mistletoe population and that genetic effects are unlikely as all host species included in this study are closely intermixed in our study site.

In most parasitic angiosperms, seed germination follows host stimulation by chemical signaling of compatibility. This feature enables the parasite to determine its distance from the host species. Parasitic species with tiny seeds (<0.5 mm in length) require host stimulation, whereas those with seeds >0.5 mm in length do not (Musselman and Press, 1995). In Loranthaceae, this seems not to be the pattern (Norton and Carpenter, 1998). *Psittacanthus schiedeanus* is a typical large-
seeded Loranth (11.7 ± 1.5 mm, mean ± 1 se; López de Buen and Ornelas, 2001), and it germinated similarly on all five host species. In contrast, P. schiedeanus seedling survival was similar among host species during the first 3 mo after seed inoculation, but then decreased drastically by the second year (Fig. 2). This pattern may be an outcome of host resistance to haustorium penetration; the resistance may operate when the haustorium makes contact with the bark layer or the xylem (Yan, 1993; Sargent, 1995). The relationship between mistletoe haustorium and host xylem changes constantly during mistletoe growth in Viscaceae mistletoes (Calvin and Wilson, 1995). Host penetration with the haustoria through axial parenchyma occurs in earlywood, but the haustorium-host contact with the parenchyma cells and the tracheary elements or sinkers occurs in the latewood (Calvin and Wilson, 1995). Mistletoe sinkers, like Phoradendron species, need almost a year to reach the host wood and xylem, and the host needs almost the same time to develop its resistance to the haustorial penetration (Yan, 1993; Calvin and Wilson, 1995). The morphology and functional development of haustoria differs between the two families of mistletoes, however. In viscaceous mistletoes, the more endophytic haustorium, having entered the host bark, grows along the longitudinal axis of the host branch in the phloem and develops into the cortical or primary haustorium (Yan, 1993). Connections with host xylem are maintained through sinkers derived from the primary haustoria that run up and down the branches of the host under the bark (Yan, 1993). In contrast, loranthaceous mistletoes, such as Psittacanthus, have secondary haustoria that form rootlike structures that run up and down the branches outside the bark (S. Sargent, Allegheny College, personal communication).

Mistletoe-host compatibility is determined by host resistance and mistletoe infectivity. The ability of a mistletoe to establish on a potential host depends on the ability of its haustorium to penetrate the host bark and establish a functional connection with the host (Yan, 1993). Unfortunately, little is known on mistletoe haustorial system in Loranthaceae. However, we believe that the observed differences in later seedling and plant survival are the consequences of host compatibility (second and third years).

Environmental factors—Mistletoes are hemiparasites, meaning that they obtain only water and minerals from their host; however, some of them obtain high levels of nutrients by higher transpiration rates than their hosts (Ehleringer et al., 1985; Stewart and Press, 1990). These parasitic plants need to control their water loss in coordination with their hosts by stomatal action, and so environmental factors, such as humidity and temperature, influence this parasite–host relationship. In fact, Ullmann et al. (1985) demonstrated that mistletoe water loss is higher among deciduous host species than in evergreen host species. Norton and Ladley (1998) suggested that Alepis flavida establishment in Nothofagus salandri forests of New Zealand might be better on branches experiencing higher light levels. We have shown in central Veracruz that seedling survival of P. schiedeanus is not affected by the initial diameter of experimental host branches, but seedlings survived better on trees with more open canopies (e.g., L. styraciflua). Although branch height contributed significantly to explaining seedling survival, these variables were only weakly correlated ($R^2 = 0.24$) at week 40 in P. mexicana (ANOVA, $F = 5.554$, df = 1, $P = 0.03$). In addition, mistletoe seedling mortality increased during dry and cooler months on all host species, except on L. styraciflua (Fig. 4). Although these environmental factors were not totally controlled in our inoculation experiment, these data suggest that more attention is needed to within-tree establishment patterns in future studies of mistletoe establishment.

Host specificity—We have previously suggested that the differences among host species in P. schiedeanus infestation are influenced by host selection by seed dispersing birds, perching while foraging (López de Buen and Ornelas, 1999); the primary mistletoe consumers preferred the most parasitized trees, L. styraciflua. Our earlier results suggest that mistletoe prevalence and reinfection of highly parasitized individuals are the consequence of bird foraging and territorial behavior (see also Reid, 1989; Martínez del Río et al., 1996; Silva and Martínez del Río, 1996; López de Buen and Ornelas, 1999). Here, we have shown that after controlling for bird foraging behavior, more seedlings will survive until flowering on branches of L. styraciflua than on branches of other host species. Mistletoe-host compatibility is frequently referred to as one of the primary causes of mistletoe host specificity (Calder, 1983 and references therein). Mistletoes are only likely to develop specificity to hosts on which they are frequently deposited (Monteiro, Martins, and Yamamoto, 1992; Norton and Carpenter, 1998). López de Buen and Ornelas (1999) have documented that the main mistletoe consumers typically deposit seeds on upper branches of L. styraciflua. Here, we show that high P. schiedeanus prevalence on L. styraciflua is not simply the consequence of being frequently encountered by frugivores, but the result of a higher host compatibility. Given the high abundance of L. styraciflua, the benefits to P. schiedeanus of specializing on it may outweigh the disadvantage of interacting with less common host species.

Norton and de Lange (1999) suggested that the variation in the relative host abundance over time is the key factor determining the degree of host specialization in mistletoes. We have previously shown that L. styraciflua is the most abundant host species in the area and had the highest mistletoe infestation, but have no historical record on host abundance variation. At best, our inoculation experiment showed that, by controlling host abundance and bird behavior, host compatibility emerges as an important factor explaining host specificity at the regional scale.

In conclusion, Psittacanthus schiedeanus is a host-generalist mistletoe, like other species in the genus (Burger and Kuijt, 1983; Cházarro and Oliva, 1988; Cházarro et al., 1992; Monteiro, Martins, and Yamamoto, 1992; Norton and Carpenter, 1998). Even so, it is most compatible at the regional level with one host. This pattern may change, however, over the geographic range of the interaction (see also Norton and de Lange, 1999). Liquidambar styraciflua is distributed from North America to middle Central America (Williams-Linera, 1997), whereas P. schiedeanus is distributed from central Mexico to Panama (Burger and Kuijt, 1983; Cházarro and Oliva, 1988). It is likely that the interactions among this mistletoe, its hosts, and assemblage of frugivorous birds vary across its geographic distribution, which has a wide spectrum of host species and seed dispersers, and that these interactions show local specialization.