Host preference of a temperate mistletoe: Disproportional infection on three co-occurring host species influenced by differential success

ANDREA B. LEMAITRE, ALEJANDRA J. TRONCOSO AND
HERMANN M. NIEMEYER*
*Laboratorio de Química Ecológica, Departamento de Ciencias Ecológicas, Facultad de Ciencias,
Universidad de Chile, Casilla 653, Santiago, Chile (Email: niemeyer@abulafia.ciencias.uchile.cl)*

Abstract   The mistletoe *Tristerix verticillatus* (Loranthaceae) parasitizes within a small area of the Yerba Loca Nature Sanctuary near Santiago, Chile, three co-occurring hosts: *Schinus montanus* (Anacardiaceae), *Fabiana imbricata* (Solanaceae) and *Berberis montana* (Berberidaceae). Previous studies suggest that *T. verticillatus* may be favoured when parasitizing *S. montanus* relative to the other two host species. We hypothesize that infection of *S. montanus* is not proportional to its local abundance or appearance, that *S. montanus* is more intensively parasitized than other available hosts, and that host provenance is a determinant of the fate of the infecting seed. We compare the incidence of infection of *T. verticillatus* in relation to local availability and appearance variables, and the intensity of infection of *T. verticillatus*, on the three co-occurring host species. We then test the effects of host provenance on mistletoe seed establishment success with a seed cross inoculation experiment varying the donor and receptor hosts. Finally, we test whether there are differences in establishment success between manually processed seeds and seeds defecated by the avian disperser *Mimus thenca* (Passeriformes: Mimidae). Our results show that the three hosts have an aggregated spatial distribution. *Schinus montanus* was parasitized at a higher rate than expected by its local availability and appearance, and inoculated seeds showed differential development depending on the origin of the seeds: seeds from *T. verticillatus* parasitizing *S. montanus* inoculated to *S. montanus* twigs showed higher germination and lower mortality than seeds from *T. verticillatus* parasitizing *F. imbricata* inoculated to *S. montanus* twigs. Furthermore, seeds defecated by the avian disperser, *M. thenca*, had higher adherence and reduced mortality when compared to manually processed seeds. The disproportional host infection found is discussed in terms of the differential establishment of mistletoe seeds, morphological characteristics of hosts and the behaviour of dispersing birds.

Key words: disproportional infection, host–parasite interaction, host preference, Loranthaceae, seed cross inoculation.

INTRODUCTION

Parasitic plants are considered similar to herbivores in relation to interactions with their hosts (Attsat 1977; Pennings & Callaway 2002). Like herbivores, parasitic plants can preferentially infect hosts that provide greater return in nutrition, reproduction and/or survival (Pennings & Callaway 2002; Press & Phoenix 2005). Host preference by a parasitic plant refers to the disproportional infection in relation to the availability of hosts in the environment; this may result from an active selection of the host by the parasite (Runyon *et al.* 2006), from ecological factors such as preferential attraction of pollinators or dispersers (Troncoso *et al.* 2010), or from host–parasite compatibility mechanisms (Press & Phoenix 2005).

Mistletoes are parasitic plants of the Loranthaceae and Viscaceae that are considered key components of ecosystems on account of the variety of interactions they establish with other organisms (Watson 2001; Press & Phoenix 2005). Mistletoes vary widely in their degree of host specificity (Press & Phoenix 2005). This variation can be found even within a single genus, such as *Tristerix* (Loranthaceae). Thus, while *Tristerix aphyllus* and *Tristerix chodatianus* have been only found infecting species of Cactaceae and Rosaceae, respectively (in fact, *T. chodatianus* has only been collected on plants of the genus *Polylepis*), *Tristerix corymbosus* has been recorded infecting about 30 host species of 21 different plant families (Kuijt 1988; Troncoso unpubl. 2009). Nonetheless, generalist parasites are not fully unrestricted in their host range; on the contrary, they may show local preference for some hosts over others, and such pattern of host use has been related to the local abundance of

hosts (Norton & Carpenter 1998). In general, the pattern of mistletoe infection within a given area depends primarily on three factors: (i) the spatial distribution of hosts, which affects the likelihood of encounter with mistletoe dispersers (Norton & Carpenter 1998; Medel *et al.* 2002); (ii) vector (i.e. birds) occurrence and behaviour, which affect the probability of infection (Aukema & Martínez del Río 2002a; Aukema 2004; Medel *et al.* 2004; Roxburgh & Nicolson 2005); and (iii) the differential development of mistletoe seeds, which is generally higher on the host species of provenance (Clay *et al.* 1985; Rödl & Ward 2002) and hosts with higher resource availability (Watson 2009).

The mistletoe *Tristerix verticillatus* R. et P. (Loranthaceae) is a shrubby hemiparasite which is distributed east of the Andes from south-eastern Bolivia (Santa Cruz) to north-western Argentina (up to Mendoza), and west of the Andes in northern and central Chile (from La Serena to Valdivia) and from sea level up to 2500 m.a.s.l. (Kuijt 1988). Our study population occurs within the Yerba Loca Nature Sanctuary (YLNS), near Santiago (Metropolitan Region, Chile), where *T. verticillatus* parasitizes three co-occurring shrubby species: *Schinus montanus* Phil. (Sapindales: Anacardiaceae), *Fabiana imbricata* R. et P. (Solanales: Solanaceae) and *Berberis montana* Gay (Ranunculales: Berberidaceae). Previous studies have shown that *T. verticillatus* produces more nectar, receives more floral visits and has reduced herbivory levels when it parasitizes *S. montanus* compared to *F. imbricata* and *B. montana* (Cabezas 2007; Troncoso *et al.* 2010), suggesting that *T. verticillatus* may be favoured when parasitizing *S. montanus* relative to the other co-occurring host species (*F. imbricata* and *B. montana*). In the present study, we address the question of whether there is a preferential infection of *T. verticillatus* towards *S. montanus* when the other two hosts are available and enquire about possible proximate causes of the phenomenon. We hypothesize that infection of *S. montanus* is not proportional to its local abundance, that *S. montanus* is more intensively parasitized than other available hosts, and that host provenance is a determinant of the fate of the infecting seed. We test the hypothesis by comparing the incidence of infection of *T. verticillatus* in relation to local availability and the intensity of infection of *T. verticillatus*, on the three co-occurring host species; having found a disproportional infection pattern in the study area, we test the effects of host provenance on mistletoe seed establishment success with a seed cross inoculation experiment varying the donor and receptor hosts. In addition, we test whether there are differences in establishment success between manually processed seeds and seeds defecated by the avian disperser *Mimus thenca* (Passeriformes: Mimidae).

METHODS

Study area

The YLNS is located 25 km northeast of the city of Santiago (33°10′–33°22′S; 70°13′–70°24′W), between 900 and 5500 m.a.s.l. The study was conducted within the area called Villa Paulina (1900–2100 m.a.s.l.) situated on the west facing slope along the Yerba Loca creek. The plant community in this area is composed of graminaceous and cushion plants and small bushes with hard and perennial leaves (Gajardo 1994). Among these latter species, three hemiparasite–host systems co-occur (*T. verticillatus* parasitizing *S. montanus*, *F. imbricata* and *B. montana*, respectively). *Fabiana imbricata* grows on the drier slopes of the study area, *B. montana* is found by the Yerba Loca creek and nearby meadows, and *S. montanus* is predominantly found along the Yerba Loca creek. Other *Tristerix* species occurring in the YLNS (*T. corymbosus* and *T. aphyllus*) parasitize other hosts and do not occur in the study area.

Host availability and appearance

To determine the availability of hosts and the incidence and intensity of infection of *T. verticillatus*, the total study area was divided into a grid of 180 plots of 50 × 50 m. Each plot was numbered. Random numbers were used to designate 20 evaluation plots; however, if adjacent plots occurred (thus overemphasizing a given type of habitat), another set of random numbers was used until no adjacent plots occurred. Evaluation plots covered about 11% of the total study area. The availability and appearance of hosts in the evaluation plots were assessed through the estimation of their relative abundance, and their individual height, area and volume, respectively. Relative abundance was measured as the number of individuals of each host species in each evaluation plot. The height, area and volume were recorded for all host individuals within the evaluation plots. Because the three host species closely resemble hemiellipsoids, the area of their projection to the ground surface was calculated with the formula of an ellipse and the volume with the formula of a hemiellipsoid using the projected area and height of the individual. Host abundance was compared with one-way Kruskal–Wallis tests followed by post-hoc Tukey tests (Sheskin 2000) and host area, height and volume were compared with one-way Kruskal–Wallis tests followed by post-hoc Dunn's tests due to unbalanced data sets (Siegel & Castellan 1988).

Host spatial distribution

Thirty geographical coordinates (points) were randomly located within the study area and from each point the *T-square* method (Besag & Gleaves 1973; Krebs 1999) was used to measure the distances between two close neighbour host individuals. In this method, random points are located and at each of them two distances are measured: the distance from the random point to the nearest organism and the distance from the organism to its nearest neighbour, with the

restriction that the angle between the random point, the nearest organism and its nearest neighbour must be more than 90°. The pattern of spatial distribution was obtained by calculating Hines test statistic, h_t, and the level of statistical significance was compared with values obtained with the Fisher distribution. The rejection levels of the null hypothesis for random distribution were calculated for 60 degrees of freedom. A random pattern was inferred if $0.60 < h_t < 1.66$, a uniform pattern if $h_t < 0.60$, and an aggregated pattern if $h_t > 1.66$ (Krebs 1999). This method was used to assess the spatial distribution of all host individuals, jointly and each host species separately, and all hemiparasite infrapopulations (i.e. all individuals of the hemiparasite occurring on a given host individual; Huyse 2005) in the study area. In the case of the hemiparasite, the method was carried out for the totality of hemiparasite infrapopulations regardless of the host species parasitized, in order to obtain their overall spatial distribution; subsequently, the spatial distributions of the mistletoe parasitizing each of the three host species were re-evaluated separately to compare the distribution pattern in relation to the parasitized host species.

Incidence and intensity of infection

The incidence of infection was separately evaluated for each host species as the ratio between the number of all parasitized host individuals and the total number of available host individuals within the evaluation plots (Kelly et al. 1988; Norton & De Lange 1999; Dzerefos et al. 2003). In order to compare host use with host availability, Manly standardized selection indices (B_i) (Krebs 1999) were used. These indices indicate a host preference when the proportion of infected hosts is higher than expected from their local availability. The values of the selection indices were compared with the expected ratios for non-preference (0.33) using the G-test for partial samples of the total population (Krebs 1999).

The intensity of infection was determined in two ways: (i) as the ratio between the sum of the volumes of all parasitic plants per host individual and the volume of that host individual; and (ii) as the number of hemiparasite individuals per host individual. The intensities of infection were compared between hosts with the Kruskal–Wallis test. A posteriori comparisons were made using the non-parametric Dunn's test for comparisons of unbalanced designs (Siegel & Castellan 1988).

Germination, adherence, establishment and mortality

A cross inoculation experiment (Kawecki & Ebert 2004) was set up to study the effect of provenance and destination host species on the development of T. verticillatus seeds. One hundred and twenty fruits (ripe and without herbivore damage) were collected from 'donor' hosts (provenance effect): 60 of T. verticillatus parasitizing S. montanus and 60 of T. verticillatus parasitizing F. imbricata; no fruits were collected from T. verticillatus parasitizing B. montana because this system did not produce enough fruits for the experiments planned. The fruits collected were stored in a cooler

until planted the day after (Sargent 1995; Norton et al. 2002). Before placing the fruits on the receptor hosts (destination effect), the exocarp was removed from them by carefully squeezing the fruits to expose the seed's viscin (Ladley et al. 1997; Rödl & Ward 2002). In 60 uninfected receptor host individuals (30 replicates per host species), 7- to 20-mm-thick branches with similar orientation and at similar height were chosen and two peeled fruits were placed on each of them, one from S. montanus and one from F. imbricata. At the time of planting, twigs with inoculated seeds were swayed to verify if seeds were well stuck and then they were sprinkled with water to closely simulate the humidity present in a recent bird dropping. Seeds were checked after 5, 10, 20, 40 and 60 days of planting, to record if the haustorium had emerged and had began its growth in length (germination), the haustorial disk had formed and attached to the twig (adherence), the leaf primordia had appeared (establishment), or they had died (Powell & Norton 1994; Norton et al. 2002). Natural death of seeds was observed as a progressive dehydration, shrinkage and turning black, which eventually led to the seed falling off from the inoculated twig. Overall mortality encompassed seeds that died naturally, seeds that were predated and seeds that fell to the ground while alive. The number of seeds that accomplished or not a given stage of development and the number of dead seeds were counted, and these numbers were compared between different provenances (T. verticillatus from S. montanus and F. imbricata) using a one-tailed Fisher's exact test (Sheskin 2000).

Another experiment was set up to compare the performance of fruits whose exocarp had been manually removed with fruits that had passed through the digestive system of the disperser bird, M. thenca. Sixty ripe and undamaged fruits of T. verticillatus growing on S. montanus were collected. One set of 30 fruits were fed to a caged specimen of M. thenca caught at the study site and subjected previously to one day of fasting. Seeds were recovered from the bird's faeces. The exocarp of the other set of 30 fruits was removed manually as described above. Seeds (defecated and manually processed) were then placed pairwise on branches of infected S. montanus and observed as described above. Seeds were counted and their numbers analysed as described in the preceeding paragraph.

RESULTS

Host availability and appearance

The three host species differed significantly in their relative abundance ($H = 26.918$, $P < 0.001$), area ($H = 10.75$, $P = 0.005$), volume ($H = 8.87$, $P = 0.01$) but not in height ($H = 3.64$, $P = 0.16$). Fabiana imbricata was the most abundant host with 75.9 ± 15.1 (mean $\pm$ SE) individuals per hectare on average followed by B. montana (18.8 ± 6.8 individuals per hectare) and S. montanus (5.7 ± 2.2 individuals per hectare). Moreover, F. imbricata was the most voluminous host with 44.29 ± 25.19 m³ on average followed by B. montana (8.45 ± 0.47 m³) and S. montanus
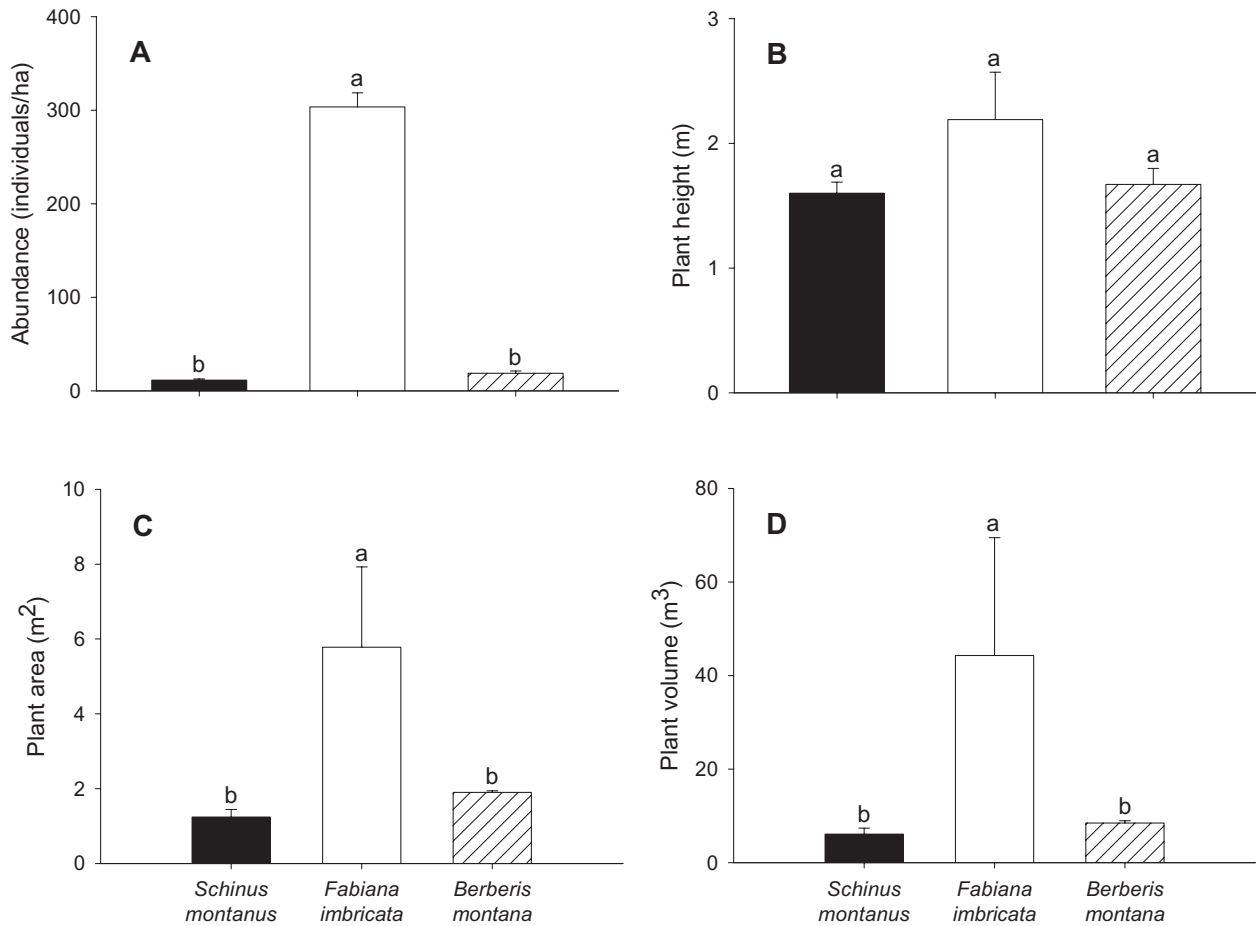
Fig. 1.   Availability of hosts, measured as number of individuals per hectare, and appearance of hosts, measured as height, area of projection to the ground and volume. Different letters in each graph denote significant differences at $P < 0.05$ between hosts.

$(6.08 \pm 1.28$ m$^3)$, and *F. imbricata* was also the host with the greatest area with 1.24 ± 0.20 m^2, followed by *B. montana* $(1.90 \pm 0.04$ m$^2)$ and *S. montanus* $(1.24 \pm 0.20$ m$^2)$ (Fig. 1).

Spatial distribution

All hosts considered as one group independent of the species and also each host species separately, presented an aggregated spatial distribution, h_t being greater than 1.66 in all cases (all hosts = 3.58, *S. montanus* = 2.95, *F. imbricata* = 3.44, *B. montana* = 3.81). Similarly, the total mistletoe population (all infrapopulations on the three host species) presented an aggregated spatial distribution (h_t value for *T. verticillatus* = 1.90); furthermore, mistletoe infrapopulations also showed aggregated spatial distribution when analysed independently for each host species (h_t values for *T. verticillatus* on *S. montanus* = 2.07, *T. verticillatus* on *F. imbricata* = 1.92, *T. verticillatus* on *B. montana* = 2.74).

Incidence and intensity of infection

Tristerix verticillatus did not parasitize the three available hosts to the same extent (*G*-test: $X^2 = 17256.93$, $P < 0.05$). While *S. montanus* was parasitized in a proportion higher than that expected by its abundance ($B_i = 0.971$), *B. montana* and *F. imbricata* were parasitized in a lower proportion than that expected on the basis of their abundance ($B_i = 0.029$ and 0.0003, respectively).

The intensity of infection was measured in terms of number of hemiparasites per host individual and in terms of hemiparasite biomass (ratio of hemiparasite/host volumes). The mean number of hemiparasite individuals per host individual did not differ significantly between the three host species (7.8 ± 2.5, 13.3 ± 10.4 and 4.0 ± 3.0 for *S. montanus*, *F. imbricata* and *B. montana*, respectively; $H = 0.176$, $P = 0.916$). Nonetheless, in terms of biomass, the most intensively infected host was *S. montanus* ($H = 11.9$, $P < 0.005$) on which the hemiparasite occupied almost 10% of the total host volume ($10.4 \pm 0.03\%$) whereas

it occupied less than 1% of the host volume when infecting *F. imbricata* and *B. montana* (0.4 ± 0.3 and 0.3 ± 0.2%, respectively). Moreover, neither the mean number of hemiparasite individuals per host individual nor the hemiparasite/host volume ratio were correlated with any of the variables of host appearance, that is, plant height ($r = 0.18$, $P = 0.31$; $r = -0.15$, $P = 0.42$, respectively), area ($r = 0.19$, $P = 0.28$; $r = -0.29$, $P = 0.10$, respectively) and volume ($r = 0.19$, $P = 0.28$; $r = -0.28$, $P = 0.12$, respectively).

Germination, adherence, establishment and mortality

Of the total of 120 seeds planted at the beginning of the cross inoculation experiment, five seeds (2.8%) were lost during the study (fell off or suffered predation), 69 (57.5%) germinated, 21 (out of 69; 30.4%) adhered, and only seven (out of 21; 33.33%) successfully established on the host twig. At the end of the study, the mortality of seeds of *T. verticillatus* was 94.2% (113 seeds).

Seeds from *S. montanus* inoculated on *S. montanus* showed higher germination and reduced mortality than seeds from *F. imbricata* inoculated on *S. montanus* (Table 1). In the inoculation of *F. imbricata* with seeds of *T. verticillatus* from *S. montanus* and *F. imbricata*, the number of seeds did not differ in germination, adherence, establishment or mortality (Table 1). Furthermore, seeds defecated by *M. thenca* showed higher adherence than manually processed seeds and mortality was highest for manually processed seeds (Table 1).

DISCUSSION

Our results show that *T. verticillatus* infected *S. montanus* with the greatest incidence and intensity

(hemiparasite/host biomass ratio); however, the most abundant and apparent host (in terms of volume and area) was *F. imbricata*. Hence, infection was disproportional in relation to the availability of hosts in the study site; moreover, it was not correlated with host appearance. The disproportional use of hosts in relation to their availability has previously been observed in parasitic plants belonging to different plant families, for example, Loranthaceae (Dzerefos *et al.* 2003), Convolvulaceae (Kelly *et al.* 1988), Orobancheaceae (Marvier & Smith 1997) and Santalaceae (Aukema & Martínez del Río 2002a), and has been attributed to three main mechanisms: the spatial distribution of hosts (Medel *et al.* 2002), the dispersing behaviour of birds (Aukema & Martínez del Río 2002b; Roxburgh & Nicolson 2005) and the differential establishment of mistletoe seeds (Aukema & Martínez del Río 2002a).

The pattern of host spatial distribution affects the probability of host contact with the mistletoe (Norton & Carpenter 1998; Medel *et al.* 2002). We have found that all hosts taken together as well as each of the three hosts taken separately have an aggregated spatial distribution; hence, it would be expected that after arriving on a host plant, mistletoes would spread to neighbouring host plants at rates independent of host species. Therefore, spatial aggregation cannot be considered an important factor leading to the disproportional infection of hosts.

The morphological characteristics and growth habitat of hosts have been shown to affect their infection by mistletoes (Watson 2009). *Fabiana imbricata*, in spite of being the most apparent and abundant host, grows on the drier slopes of the study area; hence, it may represent a non-preferred host causing water stress to the mistletoe (host quality hypothesis: Watson 2009). On the other hand, *B. montana* is found by the Yerba Loca creek and nearby meadows, which would seem advantageous in terms of avoiding water stress to the mistletoe while attracting the avian vector of the

Table 1. Performance of cross-inoculated seeds of *Tristerix verticillatus* in relation to the origin and inoculation hosts, and passage through *Mimus thenca* digestive tract

Inoculated host	Origin of *T. verticillatus* seeds	Germination		Adherence		Establishment		Overall mortality	
		Yes	No	Yes	No	Yes	No	Died	Survived
Schinus montanus	*Fabiana imbricata*	12	18	2	10	0	2	30	0
	S. montanus	24	6	11	13	5	6	25	5
		P = 0.002		P = 0.09		P = 0.35		**P = 0.03**	
F. imbricata	*F. imbricata*	18	12	4	14	2	2	28	2
	S. montanus	15	15	4	11	0	4	30	0
		P = 0.30		P = 0.65		P = 0.25		P = 0.25	
S. montanus	*S. montanus*, defecated	21	9	11	10	5	6	25	5
	S. montanus, peeled	25	5	1	24	0	1	30	0
		P = 0.18		**P = 0.002**		P = 0.58		**P = 0.03**	

Fisher's exact tests were used to compare the two origins of seeds at each stage of development; significant *P*-values are shown in bold.

mistletoe, thus enhancing the probability of the vector spreading; however, its spiny branches might deter the avian vector and thus reduce its chance of infection (Sargent 1995; Norton & Ladley 1998). Finally, *S. montanus* lacks spines and is predominantly found along the Yerba Loca creek. Overall, these data are not inconsistent with the prevalent infection of *S. montanus* relative to the other two co-occurring hosts.

Another factor which has been shown to affect mistletoe prevalence is the differential development success of seeds on different host species; hence a seed cross inoculation experiment was performed. The overall success of the inoculation experiment did not differ substantially from those reported in comparable experiments. Thus, germination (57.5%) was not far from the range reported for other mistletoes (between 69 and 98%: Clay *et al.* 1985; Ladley & Kelly 1996; Norton & Ladley 1998; Norton *et al.* 2002; Rödl & Ward 2002; Roxburgh & Nicolson 2005; all reports on Loranthaceae mistletoes) while adherence (30.4% – values reported between 6 and 26%: Clay *et al.* 1985; Rödl & Ward 2002), establishment (33.3% – values reported between 2 and 48%: Clay *et al.* 1985; Ladley & Kelly 1996; Norton *et al.* 2002) and mortality (94.2% – values reported between 71 and 97%: Clay *et al.* 1985; Ladley & Kelly 1996; Roxburgh & Nicolson 2005) were within the range reported for other mistletoes.

Germination of seeds in the mistletoe is generally high and occurs under almost all circumstances (Kuijt 1969, 1988; Lamont 1983; Norton & Carpenter 1998). However, seeds of *T. verticillatus* from *S. montanus* showed higher germination than seeds from *F. imbricata* when inoculated to *S. montanus*. A host provenance effect has been reported previously for the mistletoe *Psyttacanthus calyculatus* (Loranthaceae) thriving on five different host species (Lara *et al.* 2009). We do not have a clear explanation for this phenomenon; the properties of *T. verticillatus* seeds of different provenances deserve further investigation. Furthermore, seeds of *T. verticillatus* from *S. montanus* showed lower mortality than seeds from *F. imbricata* when inoculated to *S. montanus*, consistent with higher performance of mistletoe seeds on the host species of provenance (Clay *et al.* 1985; Rödl & Ward 2002),

Seeds of *T. verticillatus* germinated to similar extent when the fruit exocarp was manually removed and when defecated by *M. thenca*. Successful germination of seeds whose exocarp had been manually removed was also found for *T. aphyllus* (Gonzáles *et al.* 2007) although it was previously reported that such seeds needed to pass through the digestive tract of *M. thenca* to start germination (Soto-Gamboa & Bozinovic 2002). Likewise, adherence was also greater and mortality lower for bird-defecated seeds than for manually

peeled seeds. It is likely that differences between performance of fruit whose exocarp was manually removed and when defecated by *M. thenca* may have been greater had fasting time been shorter (Murphy *et al.* 1993). At any rate, it may be expected that survival in the cross inoculation experiment would have been greater if bird-defecated seeds had been used.

This study is an approximation to factors affecting host use by a hemiparasitic plant, an issue which has seldom been addressed in the literature (Marquardt & Pennings 2010). The results showed that incidence and intensity of parasitic infection by *T. verticillatus* in the YLNS was disproportional to the availability and appearance of the three co-occurring hosts, *S. montanus* being the least abundant and less apparent host but that with the highest incidence and intensity of infection. Thus, *S. montanus* appears as the preferred host for *T. verticillatus* at the YLNS. Several features of the system may account for the effect: perching opportunities for avian dispersers, accessibility to water, morphological compatibilities between host and mistletoe and germination rate and mortality of seeds. A more detailed study evaluating the behaviour of avian dispersers in relation to the three available hosts at the study site, and the effect on mistletoe development of features related to nutritional, morphological and biochemical mistletoe–host compatibility would be welcome.

ACKNOWLEDGEMENTS

REFERENCES

Attsat P. R. (1977) The insect herbivore as a predictive model in parasitic seed plant biology. *Am. Nat.* **111,** 579–86.

Aukema J. E. (2004) Distribution and dispersal of desert mistletoe is scale-dependent, hierarchically nested. *Ecography* **27,** 137–44.

Aukema J. E. & Martínez del Río C. (2002a) Variation in mistletoe seed deposition: effects of intra-and interspecific host characteristics. *Ecography* **25,** 139–44.

Aukema J. E. & Martínez del Río C. (2002b) Where does a fruit-eating bird deposit mistletoe seeds? Seed deposition patterns and an experiment. *Ecology* **83,** 3489–96.

Besag J. E. & Gleaves J. T. (1973) On the detection of spatial pattern in plant communities. *B. Int. Statist. Inst.* **4,** 153–8.

Cabezas N. J. (2007) *Efecto del hospedero sobre la composición de metabolitos secundarios del hemiparasito* Tristerix verticillatus *(Loranthaceae) y sobre sus interacciones con insectos* (PhD Thesis). University of Chile, Santiago.

Clay K., Dement D. & Rejmanek M. (1985) Experimental evidence for host races in mistletoe (*Phoradendron tomentosum*). *Am. J. Bot.* **72,** 1225–31.

Dzerefos C. M., Witkowski E. T. F. & Shackleton C. M. (2003) Host-preference and density of woodrose-forming mistletoes (Loranthaceae) on savanna vegetation, South Africa. *Plant Ecol.* **167,** 163–77.

Gajardo R. (1994) *La vegetación natural de Chile. Clasificación y distribución geográfica.* Editorial Universitaria, Santiago.

Gonzáles W. L., Suárez L. H. & Medel R. (2007) Outcrossing increases infection success in the holoparasitic mistletoe *Tristerix aphyllus* (Loranthaceae). *Evol. Ecol.* **21,** 173–83.

Huyse T., Poulin R. & Théron A. (2005) Speciation in parasites: a population genetics approach. *Trends Parasitol.* **21,** 469–75.

Kawecki T. J. & Ebert D. (2004) Conceptual issues in local adaptation. *Ecol. Lett.* **7,** 1225–41.

Kelly C. K., Venable L. & Zimmerer K. (1988) Host specialization in *Cuscuta costaricensis*: an assessment of host use relative to host availability. *Oikos* **53,** 315–20.

Krebs C. J. (1999) *Ecological Methodology.* Addison-Wesley Longman, Menlo Park.

Kuijt J. (1969) *The Biology of Parasitic Flowering Plants.* University of California Press, Berkeley.

Kuijt J. (1988) Revision of Tristerix (Loranthaceae). *Syst. Bot. Mon.* **19,** 1–61.

Ladley J. J. & Kelly D. (1996) Dispersal, germination and survival of New Zealand mistletoes (Loranthaceae): dependence on birds. *NZ J. Ecol.* **20,** 69–79.

Ladley J. J., Kelly D. & Norton D. A. (1997) A guide to hand-planting of New Zealand mistletoes (Loranthaceae). *NZ Bot. Soc. News.* **49,** 16–19.

Lamont B. (1983) Germination of mistletoes. In: *The Biology of Mistletoes* (eds M. Calder & P. Bernhardt) pp. 129–43. Academic Press, Sidney.

Lara C., Pérez G. & Ornelas J. F. (2009) Provenance, guts, and fate: field and experimental evidence in a host-mistletoe-bird system. *Ecoscience* **16,** 399–407.

Marquardt E. S. & Pennings S. C. (2010) Constraints on host use by a parasitic plant. *Oecologia* **164,** 177–84.

Marvier M. A. & Smith D. L. (1997) Conservation implications of host use for rare parasitic plants. *Conserv. Biol.* **11,** 839–48.

Medel R., Botto-Mahan C., Smith-Ramírez C. *et al.* (2002) Historia natural cuantitativa de una relación parásito-hospedero: el sistema *Tristerix*-cactáceas en Chile semiárido. *Rev. Chil. Hist. Nat.* **75,** 127–40.

Medel R., Vergara E., Silva A. & Kalin-Arroyo M. (2004) Effects of vector behavior and host resistance on mistletoe aggregation. *Ecology* **85,** 120–6.

Murphy S. R., Reid N., Yan Z. G. & Venables W. N. (1993) Differential passage time of mistletoe fruits through the gut of honeyeaters and flowerpeckers – effects on seedling establishment. *Oecologia* **93,** 171–6.

Norton D. A. & Carpenter M. A. (1998) Mistletoes as parasites: host specificity and speciation. *Trends Ecol. Evol.* **13,** 101–5.

Norton D. A. & De Lange P. J. (1999) Host specificity in parasitic mistletoes (Loranthaceae) in New Zealand. *Funct. Ecol.* **13,** 552–9.

Norton D. A. & Ladley J. J. (1998) Establishment and early growth of *Alepis flavida* in relation to *Nothofagus solandri* branch size. *NZ J. Bot.* **36,** 213–17.

Norton D. A., Ladley J. J. & Sparrow A. D. (2002) Host provenance effects on germination and establishment of two New Zealand mistletoes (Loranthaceae). *Funct. Ecol.* **16,** 657–63.

Pennings S. C. & Callaway R. M. (2002) Parasitic plants: parallels and contrasts with herbivores. *Oecologia* **131,** 479–89.

Powell G. R. & Norton D. A. (1994) Contrasts in crown development of the mistletoes *Alepis flavida* (Hook. f.) Tiegh. and *Peraxilla tetrapetala* (L. f.) Tiegh. (Loranthaceae) parasitic on *Nothofagus solandri* (Hook. f.) Oerst., Craigieburn Ecological District, New Zealand. *NZ J. Bot.* **32,** 497–508.

Press M. C. & Phoenix G. K. (2005) Impacts of parasitic plants on natural communities. *New Phytol.* **166,** 737–51.

Rödl T. & Ward D. (2002) Host recognition in a desert mistletoe: early stages of development are influenced by substrate and host origin. *Funct. Ecol.* **16,** 128–34.

Roxburgh L. & Nicolson S. W. (2005) Patterns of host use in two African mistletoes: the importance of mistletoe-host compatibility and avian disperser behaviour. *Funct. Ecol.* **19,** 865–73.

Runyon J. B., Mescher M. C. & De Moraes C. M. (2006) Volatile chemical cues guide host location and host selection by parasitic plants. *Science* **313,** 1964–7.

Sargent S. (1995) Seed fate in a tropical mistletoe: the importance of host twig size. *Funct. Ecol.* **9,** 197–204.

Sheskin D. J. (2000) *Handbook of Parametric and Nonparametric Statistical Procedures.* Chapman & Hall/CRC, Boca Ratón.

Siegel S. & Castellan Jr. N. J. (1988) *Nonparametric Statistics for the Behavioral Sciences.* McGraw-Hill, London.

Soto-Gamboa M. & Bozinovic F. (2002) Fruit disperser interaction in a mistletoe-bird system: a comparison of two mechanisms of fruits processing on seed germination. *Plant Ecol.* **159,** 171–4.

Troncoso A. J., Cabezas N. J., Faúndez E. H., Urzúa A. & Niemeyer H. M. (2010) Host-mediated volatile polymorphism in a parasitic plant influences its attractiveness to pollinators. *Oecologia* **162,** 413–25.

Watson D. M. (2001) Mistletoe – a keystone resource in forests and woodlands worldwide. *Ann. Rev. Ecol. Syst.* **32,** 219–49.

Watson D. M. (2009) Determinants of parasitic plant distribution: the role of host quality. *Botany* **87,** 16–21.