Host-preference and density of woodrose-forming mistletoes (Loranthaceae) on savanna vegetation, South Africa

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Abstract

In the Bushbuckridge region of South Africa host preference and density of two woodrose-forming mistletoes, *Erianthemum dregei* (Eckl. & Zeyh.) V. Tieghem and *Pedistylis galpinii* (Schinz ex Sprague) was quantified in relation to land-use (harvested or unharvested), rainfall (high > 660 or low < 660 mm year^{-1}) and catenal position (top or lower slope). These two mistletoes are generalist hemi-parasites of savanna trees and shrubs occurring on 25 and 17 hosts respectively, seven of which are shared. Thirty-six percent of woody plant species recorded were found to be hosts. Although *Sclerocarya birrea* (A. Rich.) Hochst. comprised only 4% of woody plant density in the environment, it was the principal host for both mistletoes, accounting for 71% of total *E. dregei* and 42% of *P. galpinii* infection. Mistletoe infection relative to density of *Ficus stuhlmanii, Trichilia emetica* and *Cassine transvaalensis* indicated that these were preferential hosts to *S. birrea*. Mistletoe host preference was negatively correlated with host wood density. Mistletoe number per tree had a weak relationship to canopy size. Mistletoes of all size classes were denser at high rainfall relative to low rainfall sites. Interestingly, the overall mistletoe size class distribution was similar between harvested and unharvested sites. The ratio of living to dead mistletoe was 2 to 1 for *E. dregei* and 1.5 to 1 for *P. galpinii*. There are sufficient dead mistletoes in unharvested and harvested areas to satisfy present market demand. Living *E. dregei* predominated in harvested rather than unharvested areas suggesting that current-harvesting levels had little or no negative effect on the population. In contrast, *P. galpinii* was denser in unharvested areas possibly owing to its higher market value and thus higher harvesting levels.

Introduction

Mistletoes may produce a "cancer"-like proliferation of host tissue at the point of attachment called a wood-rose (Dzerefos and Witkowski 1997). In some mistletoes host tissue proliferation may act as a physical barrier to penetration (Yan 1993) preventing the xylem connection necessary for the mistletoe to obtain water and mineral solutes (Kuijt 1969). In contrast the Loranthaceae mistletoes *Erianthemum dregei* (Eckl. & Zeyh.) V. Tieghem and *Pedistylis galpinii* (Schinz ex Sprague), successfully parasitise hosts even when diameters of 0.2 m (Schönland 1907), 0.5 m (Dzerefos 1996) and 1 m (Wiens and Tolken 1979) have been reached. In other parts of the world woodroses of diameters 0.15 and 0.23 m have been reported for *Tapinanthus bangwensis* (Engler and Krause) Danser (Williams 1963) and *Psittacanthus* spp. (Kuijt 1964) respectively.

The Loranthaceae mistletoes are represented in Africa by 22 genera and nearly 250 species (Calvin and Wilson 1995). In South Africa there are 11 genera and

37 species (Visser 1986). Of these *E. dregei* and *P. galpinii* are known to produce woodroses. Southern African savanna is richer in mistletoes than the other biomes in the region, i.e. forest, fynbos, grassland, nama-karoo and succulent-karoo (Dean et al. 1994).

In Swaziland, Mozambique and the northern and eastern regions of South Africa, *E. dregei* and *P. galpinii* are harvested and removed from the woodrose to reveal intricate flower-like patterns. The host tissue (woodrose) is sold as a curio to tourists after cleaning and polishing and provides a valuable source of revenue for rural people (Dzerefos et al. 1999). The gross monetary value of standing stock of woodroses in Bushbuckridge was estimated in 1995 as US $202 ha^{-1} in unharvested, protected areas and US $211 ha^{-1} in harvested communal areas (Dzerefos 1996). Woodrose harvesting is not detrimental to hosts as only the infected branch and mistletoe are cut off. About 20% of harvesters from Bushbuckridge harvested woodroses after the mistletoe had died. Sustainable harvesting is threatened with increasing commercialisation (Dzerefos 1996) and habitat destruction associated with expanding human populations, replacement of natural vegetation by agriculture or cattle farming and harvesting of hosts trees for fuel-wood, building materials and carving timber (Banks et al. 1996).

The need for an adaptive management regime as conditions change requires an understanding of the dynamics that affect mistletoe host preference and density. A distinction between principal mistletoe hosts and preferred hosts has not previously been made. Preferred hosts are those which are proportionally more frequently parasitised than their availability in the environment and may result from a combination of host attributes such as plant size, wood density and/or environmental factors. Although dispersal of mistletoe seeds is a random process associated with bird feeding and perching behaviour (Godschalk 1983), larger trees have been found to have more infections since a larger surface area to receive seed is available (Thomson and Mahall 1983) and they are also older. Juvenile mistletoes are vulnerable to desiccation for 6 to 9 months after germination (Menzies 1954) until a functional connection with the host xylem has been established. Transfer of water and mineral solutes will only occur to the mistletoe if the host has a higher water potential (Reid et al. 1995), which may be related to environmental factors such as rainfall, land-use and topographic position. Mistletoe establishment improved when planted during a humid winter rather than a dry summer (Reid 1987). Over its whole range *P. galpinii* has a shorter reproductive period (February to May) than *E. dregei*, which flowers over 9 to 12 months (Germishuizen et al. (1994a, 1994b)).

Within the above context the key questions for this study were: (a) do mistletoes exhibit a preference for certain hosts? (b) is mistletoe host selection related to host availability? (c) is mistletoe host selection related to host size or wood density? and (d) how is mistletoe density affected by land-use (harvested, communal areas or unharvested, conservation areas), rainfall (high > 660 or low < 660 mm year^{-1}) and catenal position (top or bottom slope).

Methods

Study area

The study was conducted in the Bushbuckridge region of South Africa. The area was defined by the Orpen Road leading to the Kruger National Park in the north and the Sabie River in the south (24°30–55′ S, 31°2–30′ E). There is a high population density ranging from over 300 people km^{-2} in the west to 146 km^{-2} in the east (Tollman et al. 1995).

Altitude ranges from 400 to 700 m a. s. l. (Development Bank of South Africa (DBSA) 1989) and the area is locally known as the lowveld. A distinct rainfall gradient exists from the escarpment in the west (> 1 000 mm year^{-1}) to the Kruger National Park in the east (± 500 mm year^{-1}) and less obviously from south to north. Rain falls predominantly in summer between October and March. A twenty-year record indicates the likelihood of drought every 3.5 years where only 75% of the expected mean annual rainfall (MAR) is received. Evaporation rates of 1 750 to 2 500 mm year^{-1} exceed MAR (Development Bank of South Africa (DBSA) 1989).

The underlying parent rock is predominantly granite and gneiss with intrusions of gabbro and dolerite. Soil diversity is associated with the undulating topography as a result of gravitational redistribution of clay particles and bases in solution. Shallow, sandy, nutrient poor soils are common on the top of slopes. Clayey soils with high Na content occur in the catena bottom lands (Witkowski and O'Connor 1996).

The vegetation of the area is classified as Mixed Lowveld Bushveld (van Rooyen and Bredenkamp 1996). The top of the catena is dominated by large,

broad-leaved trees including *Combretum* spp., *Diospyros mespiliformis* Hochst. ex A. DC, *Peltophorum africanum* Sonder and *Sclerocarya birrea* (A. Rich.) Hochst. The catena bottom lands are dominated by *Acacia* spp., *Albizia harveyi* Fourn, *Euclea* spp. and *Gymnosporia* spp. Generally riparian vegetation consists of *D. mespiliformis, Schotia brachypetala* Sonder and *Ficus* spp.

Site selection

Twelve sites were selected with a harvested site and an unharvested site in relatively close proximity (Table A1). The main land-uses in the study area are government and private conservation areas, private commercial cattle farms and communal grazing areas used by rural villagers for livestock grazing and natural resource harvesting (Shackleton 1996). In this study the communal areas are referred to as "harvested" while the remaining land-uses are collectively called "unharvested". Half the sites receive high rainfall (> 660 mm year^{-1}) and half low rainfall (< 660 mm year^{-1}). At each site 10 transects of 375 m length were sampled, giving a total of 120 transects. Half of the 10 transects for each site were situated at the top of the catena (on the upper slope) and half at the bottom of the catena (on the lower slope) to incorporate soil type and vegetation variation associated with topography. Transects were scattered at various distances from peripheral homesteads, to account for decreasing woody plant density with distance away from villages (Shackleton et al. 1994).

Woody plants

For each transect 25 points, 15 m apart, were positioned to determine woody plant density (plants ha^{-1}) using the point centre quarter method (PCQ). For each quarter, the nearest woody plant taller than 1.5 m was identified to species and its distance from the point measured using a WILD TMO range finder. Distances < 4 m were visually estimated. The number of PCQ points used was calculated by plotting the running mean of plant density from preliminary data. Previous recommended host sampling heights were ⩾ 3 m (Lamont 1985), 2 m (Thomson and Mahall 1983) or 1.5 m (Yan 1990).

Three-way analysis of variance (ANOVA) was used to test the effects of rainfall, land-use and catenal position on woody plant density (SAS Institute 1985). Sample size was 15 transects (5 from each of the 3 sites) per treatment combination (transect scale). Data were transformed (log$_{10}$ or arcsin for percentages) where necessary to meet the assumptions for ANOVA, and/or data per site (5 transects) were pooled and analysed at the site scale. Occasionally the data for the three sites were pooled and analysed by ANOVA without replication (treatment scale). For finer-scale differences between treatment combinations the Student-Neuman-Keuls (SNK) multiple range test was used.

Attributes of infected woody plants

Three metres on either side of the transect (375 × 6 m) was examined for woody plants infected with *E. dregei* or *P. galpinii*. The following were recorded for infected woody plants: i) species, ii) circumference of the stem 0.5 m above ground level, iii) height (H), iv) height of the canopy base (LH), v) length of the longest diameter of the canopy (D$_1$) and vi) diameter of the canopy at 90° to D$_1$ (D$_2$). Total canopy area and volume were calculated for host species using the following equations: Canopy area = $\pi(D_1/2 \times D_2/2)$

$$\text{Canopy volume} = \pi(D_1/2 \times D_2/2 \times H - LH)$$

Mistletoe infection and its relationship with host canopy area ha^{-1} and host canopy volume ha^{-1} were analysed using the best-fit of linear, exponential, log$_{10}$ and power curve regressions. Contingency table χ^2 were used to compare the occurrence of mistletoe infection on *S. birrea* at high and low rainfall sites with land-use. Three-way ANOVAs and SNK were conducted to test for differences in i) number of host species, ii) density of mistletoe infection on all hosts combined and iii) density of mistletoe infection on *S. birrea* in relation to land-use, rainfall and catenal position.

Mistletoe host selection was assessed by means of preference ratios (PR; Petrides (1975)), namely the extent of host species infection in relation to its overall relative density in the community. The relationship between PR and host wood density (van Wyk 1984) was analysed by regression.

Attributes of the mistletoe

Mistletoes found within transects were identified to species level. Total number of mistletoes per host plant was recorded and a distinction was made between living versus dead mistletoes. Dead mistletoes

were further divided into useable (sellable) and not useable woodroses according to harvester's selection criteria (Dzerefos et al. 1999).

A glass slide was calibrated to measure woodrose size at a distance as these were frequently high up in the tree canopy. Objects of known size were placed at distances of 1, 5, 10, 15, 20 and 25 m, using a theodolite. Intervals of 10 mm were marked on the slide, which corresponded to actual size measurements at the six distances. The four mistletoe size classes (broadest diameter of the woodrose) were: i) small (< 0.1 m), ii) medium (0.1–0.25 m), iii) large (0.25–0.5 m) and iv) very large (> 0.5 m). Three-way ANOVAs were used to test for differences in i) the density of living, ii) dead and iii) dead-useable mistletoes in relation to land-use, rainfall and catenal position.

Results

Distribution and density of woody plants

A total of 117 woody species were recorded. Those infected with woodrose-forming mistletoes are listed along with authorities in Table 1. *Dichrostachys cinerea* occurred in every site and had the highest density of 52 ± 4 plants ha^{-1} overall. Other species found at all sites were *Terminalia sericea* (49 ± 2 ha^{-1}), *Combretum collinum* (27 ± 2 ha^{-1}), and *S. birrea* (16 ± 1 ha^{-1}), while *Combretum hereroense* (29 ± 2 ha^{-1}) and *Acacia exuvialis* (19 ± 1 ha^{-1}) occurred in 11 and 10 sites respectively. Nineteen species were restricted to high rainfall and two to low rainfall sites.

Woody plant density was significantly higher at high rainfall relative to low rainfall sites, at unharvested relative to harvested sites and at the bottom relative to the top of the catena (Table 2). There was also a significant rainfall by land-use interaction. However, the ratio of mistletoe density to woody plant density was significantly higher only at the top of the catena. Contingency table χ^2 analyses confirmed an association between woody plant density and land-use for both high ($\chi_1^2 = 260$; $P < 0.0001$) and ($\chi_1^2 = 446$; $P < 0.0001$) low rainfall sites.

Host species and size selection

Forty-one host species were recorded. Seven of these hosted both mistletoe species. Eighteen hosted *E. dregei* only, 10 hosted *P. galpinii* only and six hosted unidentified dead mistletoes (Table 3). Of *P. galpinii*

hosts, only *Combretum imberbe*, *Diospyros mespiliformis* and *Peltophorum africanum* had infections > 1%. Dead mistletoes were found on *Acacia caffra*, *Cassine transvaalensis*, *Dombeya rotundifolia*, *Heteropyxis natalensis*, *Pappea capensis* and *Spirostachys africana*. *E dregei* was observed on *Manilkara mochisia* (Baker) Dubara at Bushbuckridge but not within the transects. *P. galpinii* (17) had fewer host species than *E. dregei* (25).

Significantly more host species occur at high rainfall sites ($F_{1,112} = 11.93$; $P < 0.001$). There was also an interaction between rainfall and land-use ($F_{1,112} = 5.72$; $P < 0.05$), with more host species in high rainfall-harvested areas. *Albizia versicolor*, *Faurea saligna*, *Heteropyxis natalensis* and *Trichilia emetica* were recorded only in high rainfall sites.

Mistletoes were mostly encountered on *S. birrea*, which constituted 58% of total infections. Seventy-one percent of *E. dregei* and 42% of *P. galpinii* infections were hosted by *S. birrea*. The occurrence of *S. birrea* was influenced by an association with land-use at high ($\chi_1^2 = 216$; $P < 0.0001$) and low rainfall sites ($\chi_1^2 = 5$; $P < 0.022$), with higher densities in communal, harvested areas where this species is traditionally protected from felling.

Strychnos madagascariensis had 7% (74 mistletoes) of the total *E. dregei* infection. Although *S. madagascariensis* was found in 83% of sites, *E. dregei* infections were only found at one pair of high rainfall sites and limited to 20 trees. *Terminalia sericea* and *Euclea crispa* had 5% of total *E. dregei* infection (50 and 53 mistletoes, respectively) but were only infected in high rainfall sites even though they occurred throughout the study area. *Bauhinia galpinii* had 3% (28 mistletoes) infection and was recorded in all high rainfall sites but only 33% occurred in high rainfall sites. The remaining host species all displayed < 2% *E. dregei* infection. Other *E. dregei* hosts occurring exclusively in high rainfall sites were *Albizia versicolor* and *Trichilia emetica*.

Second to *S. birrea*, 13% of *P. galpinii* infection occurred on *Acacia nigrescens* (52 mistletoes) and *Peltophorum africanum* (51 mistletoes). *A. nigrescens* occurred throughout the area except at four high rainfall sites. Although *P. africanum* occurred in all but one site, infections were only in three high rainfall sites. Eight percent of *P. galpinii* infections were on *Diospyros mespiliformis* (34 mistletoes), 8% on *Ficus stuhlmanii* (31), 4% on *Combretum hereroense* (16), 3% on *C. imberbe* (10), 2% on *Albizia harveyi* and 2% on *Combretum collinum*. *D. mespiliformis* was

Table 1. Relative density of host species in the field, percentage infected by woodrose-producing mistletoes and preference ratios. Wood density (air dried) is provided where available (van Wyk 1984). Categories were selected on the basis of the preference ratio.

Host species	Relative density (%)	Infected (%)	Pref. Ratio	Wood density (kg/m³)	Category
Ficus stuhlmanii Warb.	0.04	1.87	46.75	600	Preferred
Trichilia emetica Vahl	0.03	0.90	30.00	560	
Cassine transvaalensis (Burtt Davy) Codd	0.08	1.33	16.63	960	
Sclerocarya birrea (A. Rich.) Hochst.	3.67	57.65	15.71	560	
Schotia brachypetala Sonder	0.23	1.57	6.83	800	
Rhus pentheri Zahlbr.	0.16	0.72	4.50	-	
Euclea crispa (Thunb.) Sonder ex Gürke	1.19	3.43	2.88	-	Favoured
Peltophorum africanum Sonder	1.33	3.13	2.35	900	
Diospyros mespiliformis Hochst. ex A. DC	1.31	2.47	1.89	850	
Strychnos madagascariensis Poiret	2.43	4.58	1.88	850	
Bauhinia galpinii N. E. Brown	0.93	1.69	1.82	-	
Rhus rehmanniana Engl.	0.11	0.18	1.64	-	
Rhus pyroides Burch.	0.08	0.12	1.50	-	
Acacia nigrecens Oliver	2.22	3.37	1.52	1100	
Spirostachys africana Sonder	0.49	0.6	1.22	960	
Faurea saligna Harvey	1.07	1.27	1.19	770–900	Neutral
Combretum imberbe Wawra	0.78	0.84	1.08	1200	
Albizia versicolor Welw. ex Oliver	0.28	0.30	1.07	650	
Acacia burkei Benth	0.13	0.12	0.92	900	
Antidesma venosum E. Meyer ex Tul.	0.61	0.54	0.89	670	
Acacia nilotica (L.) Willd. ex Delile	0.42	0.36	0.86	1100	
Pappea capensis Ecklon & Zeyher	0.08	0.06	0.75	860	

Table 1. continued.

Host species	Relative density (%)	Infected (%)	Pref. Ratio	Wood density (kg/m³)	Category
Lannea discolor (Sonder) Engl.	0.09	0.06	0.67	540	Avoided
Lannea schweinfurthii (Engl.) Engl.	0.41	0.24	0.59	570	
Euclea divinorum Hiern	0.90	0.48	0.53	820	
Albizia harveyi Fourn.	1.64	0.78	0.48	800	
Strychnos spinosa Lam.	0.70	0.30	0.43	730	
Heteropyxis natalensis Harvey	0.98	0.42	0.43	800	
Acacia gerrardii Benth.	2.12	0.78	0.37	900	
Terminalia sericea Burch. ex DC	10.93	3.55	0.32	880	
Combretum apiculatum Sonder	3.40	0.84	0.25	1230	
Combretum collinum Fresen.	6.06	1.33	0.22	960	
Combretum hereroense Schinz	6.60	1.08	0.16	900	Highly Avoided
Combretum zeyheri Sonder	1.61	0.24	0.15	750	
Acacia caffra (Thunb.) Willd.	0.41	0.06	0.15	980	
Dombeya rotundifolia (Hochst.) Planchon	2.17	0.30	0.14	960	
Dichrostachys cinerea (L.) Wight & Arn.	11.76	0.84	0.07	960	
Ziziphus mucronata Willd.	2.08	0.12	0.06	880	
Gymnosporia senegalensis (Lam.) Loes.	2.22	0.12	0.05	-	
Combretum molle R. Br. ex G. Don	2.58	0.12	0.05	860	
Gymnosporia buxifolia (L.) Szyszyl.	1.63	0.06	0.04	660	

Table 2. Woody plant density and its relation to mistletoe density (mean ± S.E.; No. ha⁻¹) in areas of different rainfall (R), land-use (L) and catenal position (C), where n = 15 transects. Significance by three-way ANOVAs (*P*-values; *d.f.* = 1,112). Different superscript letters indicate significant differences between means (SNK; $P < 0.05$).

Rain	Land-use	Top	Bottom	ANOVA: R	L	C	R×L	R×C	L×C	R×L×C
a) Woody plant density										
High	Harvested	735 ± 31[bc]	962 ± 24[ab]	0.0001***	0.0037**	0.0248*	0.0467*	0.9622	0.1164	0.9726
	Unharvested	1452 ± 63[a]	1472 ± 46[a]							
Low	Harvested	391 ± 14[c]	686 ± 29[c]							
	Unharvested	478 ± 14[c]	516 ± 16[c]							
b) Mistletoe density/woody plant density										
High	Harvested	0.12 ± 0.02[a]	0.09 ± 0.11[a]	0.7889	0.4068	0.0004***	0.5680	0.5017	0.1666	0.6997
	Unharvested	0.06 ± 0.003[a]	0.04 ± 0.003[a]							
Low	Harvested	0.31 ± 0.03[a]	0.08 ± 0.01[a]							
	Unharvested	0.16 ± 0.01[a]	0.07 ± 0.01[a]							

* $P < 0.05$,
** $P < 0.01$,
*** $P < 0.001$

Table 3. Woody plants infected by living woodrose-forming mistletoes, *Erianthemum dregei* and *Pedistylis galpinii*.

Hosts common to both mistletoe species	Specific hosts	
	Erianthemum dregei	*Pedistylis galpinii*
Acacia gerrardii,	*Albizia versicolor,*	*Acacia burkei,*
Acacia nigrescens,	*Antidesma venosum,*	*Combretum apiculatum,*
Acacia nilotica,	*Bauhinia galpinii,*	*Combretum collinum,*
Albizia harveyi,	*Combretum molle,*	*Combretum hereroense,*
Dichrostachys cinerea,	*Euclea divinorum,*	*Combretum imberbe,*
Euclea crispa,	*Faurea saligna,*	*Combretum zeyheri,*
Sclerocarya birrea	*Gymnosporia buxifolia,*	*Diospyros mespiliformis,*
	Gymnosporia senegalensis,	*Ficus stuhlmanii,*
	Lannea discolor,	*Lannea schweinfurthii,*
	Rhus pentheri,	*Peltophorum africanum.*
	Rhus pyroides,	
	Rhus rehmanniana,	
	Schotia brachypetala,	
	Strychnos spinosa,	
	Strychnos madagascariensis,	
	Terminalia sericea,	
	Trichilia emetica,	
	Ziziphus mucronata	

recorded throughout the study area and was infected in high and low rainfall sites.

Using preference ratios (PR), host species ranged from preferred to highly avoided by mistletoes (Table 1). PR was negatively related to wood density (PR $= 856.543^{-0.021(\text{wood density})}$; $r^2 = 0.178$; $n = 35$). There was a significant positive relationship between mistletoe density and host canopy area ha⁻¹ for high rain-fall-harvested and unharvested sites (Table 4). Low rainfall-unharvested sites showed the same relationship. The number of *E. dregei* infections increased with host canopy area ha⁻¹ on high rainfall-harvested and on low rainfall-unharvested sites. *P. galpinii* density only increased with host canopy area on low rainfall-unharvested sites.

Table 4. Regressions of the number of *Erianthemum dregei* and *Pedistylis galpinii* infections (number ha^{-1}) (y) on host canopy area (m^2 ha^{-1}) (x) at high or low rainfall and at harvested or unharvested sites. Only regressions with *P*-values < 0.1 are given.

Environmental Factors	r^2	P	Regression equation	n
a) Combined species				
High harvested	0.276	< 0.001	y = 5.813x$^{0.561}$	88
High unharvested	0.109	< 0.001	y = 0.882x + 31.89	116
Low unharvested	0.261	< 0.001	y = 1.220x + 66.073	62
b) *Erianthemum dregei*				
High harvested	0.305	< 0.001	y = 27.439x$^{0.544}$	66
High unharvested	0.087	< 0.1	y = 165.933x + 3.289	33
Low unharvested	0.303	< 0.001	y = 4.919x + 323.974	39
c) *Pedistylis galpinii*				
Low unharvested	0.202	< 0.1	y = 6.939x + 291.044	18

A linear relationship was evident for number of *E. dregei* on *S. birrea* in low rainfall-unharvested sites (r^2 = 0.35; *P* < 0.01; *n* = 27). *S. birrea* had larger canopy areas ha^{-1} relative to other hosts, such as *Acacia, Combretum, Diospyros* and *Strychnos* species. Of these *Acacia* and *Combretum* had comparable numbers of mistletoes but no relationship with canopy size. The number of small (r^2 = 0.003), medium (r^2 = 0.04) and large (r^2 = 0.07) sized mistletoes was not related to canopy size. The relationship between mistletoe number and host canopy volume are not presented as these are similar to those for canopy area (Dzerefos 1996).

Density of mistletoes

In total, 1 660 mistletoes, at a mean density of 63 ± 9 ha^{-1}, were sampled. There were more *E. dregei* (1 066 plants; 64%) than *P. galpinii* (404 plants; 24%). Dead mistletoes (190 plants; 12%), could not be identified to species level. Most size classes tended to be more abundant in high than low rainfall regions: i.e. small (54 ± 6 & 29 ± 2 ha^{-1} respectively), medium (23 ± 1 & 14 ± 1 ha^{-1}) and very large (0.4 ± 0.1 & 0 ha^{-1}) while large were equally distributed (3 ± 0.4 & 3 ± 0.2 ha^{-1}). In harvested and unharvested sites small mistletoes had the highest density (39 ± 4 & 44 ± 5 ha^{-1} respectively), followed by medium (18 ± 1 & 19 ± 2 ha^{-1}), large (3 ± 0.4 & 3 ± 0.2 ha^{-1}) and very large (both 0.2 ± 0.1 ha^{-1}).

Mistletoe density was higher for high rainfall sites (Table 5), with a significant rainfall-catenal position interaction. Top land sites had higher mistletoe density than bottom land sites ($F_{1,112}$ = 365.23; *P* = 0.033). The top lands of Xanthia (176 ha^{-1}) and Flew

de Lys (115 ha^{-1}), both high rainfall sites, had the highest number of mistletoes.

Woody plant density and total mistletoe (r^2 = 0.022; *n* = 120) as well as *E. dregei* (r^2 = 0.0002; *n* = 70) and *P. galpinii* (r^2 = 0.046; *n* = 38) density showed no significant relationship. *E. dregei* was denser at top relative to bottom land positions, and at high relative to low rainfall sites (Table 5). There was a tendency for *E. dregei* to be denser in harvested areas. There was a significant rainfall-catena interaction for *E. dregei* density. This interaction was evident in top land transects of Xanthia, which had a particularly high level of *E. dregei* infection (159 ha^{-1}). Lower densities of mistletoes occurred in the bottom lands of Huntington (1 ha^{-1}), a low rainfall-harvested site, and Alicecot and Manyeleti, low rainfall-unharvested sites, where none were found.

P. galpinii density was higher on unharvested relative to harvested sites (Table 5). Significant rainfall-land-use and rainfall-catena interactions were found for *P. galpinii* density. There was considerable variation in *P. galpinii* density between sites. Highest *P. galpinii* density occurred at Fleur de Lys (45 ha^{-1} in bottom lands and 63 ha^{-1} in top lands) while three sites scored zero infection.

Mistletoe infection on *S. birrea* was significantly higher on the top relative to the bottom of the catena ($F_{1, 16}$ = 17.09; *P* = 0.001). The greatest difference in number of mistletoes ha^{-1} on *S, birrea* was recorded at low rainfall harvested sites where 276 ± 98 occurred at the top relative to 9 ± 9 at the bottom of the catena. Less variation was recorded at high rainfall harvested sites where 320 ± 161 mistletoes ha^{-1} were found at the top and 224 ± 185 at the bottom of the catena. Contingency table χ^2 analyses of mistletoe

Table 5. Density of mistletoe infection (mean ± S.E.; No. ha^{-1}) in areas of different rainfall (R), land-use (L) and catenal position (C), where $n = 8$. Significance by three-way AN0VAs without replication (treatment scale; *P*-values, *d.f.* = 1,1).

Rain	Land-use	Top	Bottom	ANOVA: R	L	C	R×L	R×C	L×C
a) Combined species									
High	harvested	86 ± 25	83 ± 45	0.0282*	0.0560#	0.0333*	0.0589#	0.0360*	0.3262
	unharvested	55 ± 17	54 ± 18						
Low	harvested	66 ± 14	13 ± 6						
	unharvested	62 ± 18	16 ± 6						
b) *Erianthemum dregei*									
High	harvested	81 ± 24	74 ± 41	0.0335*	0.0871#	0.0355*	0.0906#	0.0432*	0.6046
	unharvested	37 ± 12	28 ± 13						
Low	harvested	43 ± 13	43 ± 13						
	unharvested	41 ± 17	6 ± 4						
c) *Pedistylis galpinii*									
High	harvested	5 ± 3	9 ± 8	0.2048	0.0245*	0.0635#	0.0245*	0.0199*	0.0704#
	unharvested	18 ± 10	27 ± 12						
Low	harvested	23 ± 10	8 ± 5						
	unharvested	20 ± 11	11 ± 6						

\# $P < 0.1$,
* $P < 0.05$,
** $P < 0.01$,
*** $P < 0.001$

infection on *S. birrea* indicated an association between land-use for both high ($\chi^2_1 = 58.4$; $P < $ O.0001) and low ($\chi^2_1 = 48.6$; $P < 0.0001$) rainfall sites. *E. dregei* on *S. birrea* was significantly higher on the catena top ($F_{1, 16} = 14.91$; $P = 0.0014$) relative to the bottom. At low rainfall-harvested sites 204 ± 123 *E. dregei* mistletoes ha^{-1} occurred at the top relative to 9 ± 9 at the bottom of the catena. At high rainfall-harvested sites, 320 ± 161 *E. dregei* mistletoes ha^{-1} were found at the top and 221 ± 182 at the bottom of the catena. In contrast, there were no significant differences between treatments for *P. galpinii* on *S. birrea*.

Density of living and dead mistletoes

At the site scale, there was a significant interaction between rainfall and catenal position for the density of living mistletoes ($F_{1, 16} = 4.55$; $P = 0.0488$), with higher densities in high rainfall topland sites (Table A2). Dead-useable mistletoes had a significantly higher density at high rainfall sites ($F_{1, 16} = 6.22$; $P = 0.0240$; Table A2). Significant interactions between rainfall and land-use, as well as between rainfall and catenal position for the density of dead-useable mistletoes were found. In contrast there was no signifi-

cant differences between treatments for the density of dead-not useable mistletoes (Table A2).

For every two living *E. dregei* mistletoes, one dead specimen was recorded. Of the dead specimens one out of three was useable. The density of living *E. dregei* was higher at top land versus bottom land ($F_{1, 16} = 8.94$; $P = 0.0087$), and at high versus low rainfall sites ($F_{1, 16} = 5.03$; $P = 0.0395$), with a tendency to be higher in harvested versus unharvested sites ($F1, 16 = 4.02$; $P = 0.0621$). High rainfall-top land sites had a higher density of dead-useable *E. dregei* woodroses. The ratio of living to dead *P. galpinii* was 1.5 to 1. Half of the dead *P. galpinii* recorded were useable.

Discussion

Host specificity

Mistletoe hosts that were disproportionally parasitised in relation to their relative density were *Ficus stuhlmanii*, *Trichilia emetica*, *Cassine transvaalensis* and *S. birrea*. Although *S. birrea* constituted 4% of trees recorded it supported 58% of total infection (71% for *E. dregei* and 42% for *P. galpinii*) indicat-

ing that it is a principal as well as a preferred host. In contrast *Combretum collinum* (6%), *C. hereroense* (7%), *Dichrostachys cinerea* (12%) and *Terminalia sericea* (11%) were more frequently recorded but combined infection was 7%. Similarly, in Pakistan a single species hosted 33% of mistletoe infections, while 22 other woody plant species were occasionally infected (Zakaullah et al. 1984). In southern Australia, 90% of *Lysiana exocarpi* (Behr.) Tieghem mistletoes were supported by only two of the eight host species (Yan 1990).

E. dregei and *P. galpinii* occurred on 36% of woody plant species recorded which comprised 41 indigenous host species from 14 families. In the Cape karroid vegetation the mistletoe *Moquinella rubra* (Spreng. F.) Balle and two Viscaceae species parasitised approximately 33% of 24 common woody plant species (Lamont 1982). The important host genera, *Acacia, Combretum, Gymnosporia* and *Rhus*, identified for South African mistletoes (Dean et al. 1994) were all infected by *E. dregei* in this study but *P. galpinii* did not occur on the latter two genera.

Host species recorded for the first time for *E. dregei* were *Albizia versicolor, A. harveyi, Antidesma. venosum, Bauhinia galpinii, Dichrostachys cinerea, Faurea saligna, Lannea discolor, S. birrea* and *Terminalia sericea. E. dregei* infection has been recorded on *Acacia, Brachylaena, Chrysopyllum, Combretum, Euclea, Grewia, Gymnosporia, Rhus, Schotia, Spirostachys, Strychnos, Trichilia* (Germishuizen et al. 1994a), *Lumnitzera* (Briggs 1985), *Burkea* (Thoday 1960) and *Ziziphus* (Schönland 1907). Relatively fewer genera have been recorded as hosts for *P. galpinii*, i.e. *Acacia, Combretum, Dichrostachys, Sclerocarya, Trichilia* and *Terminalia* (Germishuizen et al. 1994b). First time records for *P. galpinii* hosts were *Albizia harveyi, Diospyros mespiliformis, Ficus stuhlmanii, Lannea schweinfurthii* and *Peltophorum africanum*. Hosts shared by *E. dregei* and *P. galpinii*, included five species from the family Mimosaceae (*Acacia gerrardii, A. nigrescens, A. nilotica, Albizia harveyi* and *Dichrostachys cinerea*) as well as *Euclea crispa* (Ebenaceae) and *S. birrea* (Anacardiaceae).

E. dregei and *P. galpinii* are generalist parasites (i.e. over 10 hosts) having 25 and 17 hosts respectively. Research indicates generalist host selection for Viscaceae such as *Phomdendron flavescens* (Pursh) Nutt. (Ferguson and Hemmerly 1976) and Loranthaceae such as *T. bangwensis* (Room 1973) and *L. exocarpi* (Reid and Lange 1988). Fewer specialist

mistletoes restricted to one or two hosts have been documented (Reid and Lange 1988 Yan 1990).

Host size per hectare

In this study the number of medium and large mistletoes per tree was not related to host canopy area ha^{-1}. Smaller trees have been found to have relatively fewer large *Amyema preissii* (Miq.) Tieghem than larger trees partly because the mistletoes have not had sufficient time to grow (Reid and Stafford Smith 2000). Lamont (1985) measured host tree height and diameter and confirmed that larger trees had more infection than smaller ones. Similar data were reported for a Viscaceae mistletoe on *Quercus* spp. (Thomson and Mahall 1983); and Loranthaceae mistletoes e.g. *Amyema* spp. on *Acacia* and *Eucalyptus* spp. (Lamont 1985 Reid and Lange 1988). Larger trees are more likely than smaller trees to be reinfected by *A. preissii* following removal from a control area (Reid and Stafford Smith 2000). Apart from *S. birrea*, other primary host genera (*Acacia, Combretum, Diospyros*, and *Strychnos*) showed no significant correlations between level of mistletoe infection and host canopy area ha^{-1}. *A. preissii* was shown to have a significant water and nutrient drain on hosts (Lamont and Southall 1982) and may constrain host tree growth, keeping them in smaller size classes for longer.

The density of *E. dregei* and of combined mistletoes were not always directly proportional to host canopy area ha^{-1} (Table 4). Harvested sites were subjected to greater woodrose and fuel-wood harvesting, and it appears that low relative to high rainfall is less favourable for mistletoe establishment and recruitment. For *P. galpinii*, infection was a function of host canopy size ha^{-1} only in low rainfall-unharvested sites.

Mistletoe density

Woody plants occurred in higher densities in high relative to low rainfall sites and to a lesser degree at the bottom relative to the top of the catena. There is a positive correlation between woody plant species richness and rainfall in southern Africa (O'Brien 1993). Tree harvesting for fuel, building, carving and medicinal requirements was reflected by a lower woody plant density in areas where harvesting was permitted, however, combined mistletoe density data showed no significant response to land-use. One explanation for this may be that wood harvesters select

non-fruit bearing trees (Campbell and Du Toit 1988 Wilson 1989) and leave the principal mistletoe host, *S. birrea*, as its fruit are highly valued (Shackleton 1996).

The top lands showed relatively more combined *E. dregei* and *P. galpinii* infection than the bottom lands. The dense vegetation in the bottom lands may create more shade than occurs in the top lands. Dense vegetation may shade mistletoe seeds deposited by birds and inhibit germination (Room 1973) and establishment (Room 1971 Lamont and Southall 1982 Monteiro et al. 1992) due to insufficient light. *S. birrea* is typically one of the tallest trees found on the catena top lands and contributes to higher mistletoe density. Living *E. dregei* density was greater on the top relative to the bottom of the catena.

A year after removing 78 *E. dregei* mistletoes from 12 hosts, 68 'new mistletoes' were recorded on the same hosts, possibly resprouting from internal, longitudinal cortical strands (Dzerefos et al. 1998). The possibility of resprouting after harvesting is supported by the fact that living *E. dregei* also predominated in harvested rather than unharvested areas. Growth of *E. dregei* and its hosts may be promoted in harvested, communal areas because thinning the mistletoe population and in particular thinning of the woody vegetation results in greater resource availability for the remaining plants (e.g. Luoga et al. (2001); submitted). In contrast, *P. galpinii* was significantly denser in unharvested areas indicating that use may be adversely affecting density of this species, or alternatively that post harvest recruitment is lower than for *E. dregei*.

High rainfall sites had significantly more host species than low rainfall sites. In the case of *Albizia versicolor* and *Trichilia emetica* this was a function of host tree distribution according to mean annual precipitation. Hosts such as *S. birrea* were infected in both high and low rainfall sites but *Euclea crispa, Peltophorum africanum, Strychnos madagascariensis* and *Terminalia sericea*, although recorded throughout the study area, were only infected at high rainfall sites. Further investigation is required to determine if mistletoe-host compatibility is related to reduced water stress in the host or dilution of host-produced chemical inhibitors.

Small, medium and very large mistletoes were more abundant in high relative to low rainfall sites, suggesting that establishment and rates of growth are promoted when hosts are less water stressed. Combined *E. dregei* and *P. galpinii* densities were also higher at high rainfall relative to low rainfall sites.

Furthermore, living and dead *E. dregei* density was significantly greater at high relative to low rainfall sites. Correlations between annual rainfall and presence of the mistletoes, *L. exocarpi* and *A. miraculosum* (Yan 1990), indicated that water availability may determine mistletoe occurrence. Preferential selection of hosts along watercourses, where water supplies vary from adequate to high, has been reported in two Viscaceae and a Loranthaceae mistletoe (Lamont 1982). In arid central Australia, mistletoes were more abundant along roads, where they occurred on host plants with higher relative water contents than plants of the same host species further away from the road (Lamont and Southall 1982 Norton and Stafford Smith 1999). Roadside plants generally grow larger and are more fecund than plants away from roads as more water and nutrients are available through road run-off and interspecific competition is also reduced (Lamont et al. (1994a, 1994b)). The mistletoe density/ woody plant density data (Table 1) shows that trees in harvested areas have twice the woodrose load of trees in unharvested areas (the only exception was in low rainfall bottomlands). Although it is well known that high mistletoe densities can effect tree health detrimentally, all trees sampled in this study did not indicate any signs of stress or ill-health as a result of infestation. Because of lower tree densities in harvested areas, each tree may have assess to greater levels of resources than trees in unharvested areas (similar to roadsides trees), and consequently are able to withstand higher levels of mistletoe infestations.

Figure 1 summarises the main factors which impact on the density of the two woodrose-forming mistletoe species. *E. dregei* and *P. galpinii* are relatively prevalent generalist mistletoes that differ in overall density, size distribution, and diversity of hosts, as well as host use (Dzerefos et al. 1999), post-harvest recovery (Dzerefos et al. 1998) and growth rate (Dzerefos 1996). There are sufficient dead mistletoes in unharvested and harvested areas to satisfy present market demand (Dzerefos et al. 1999). Living *E. dregei* predominated in harvested rather than unharvested areas suggesting that current-harvesting levels had little or no negative effect on the population. In contrast, *P. galpinii* was denser in unharvested areas possibly owing to its higher market value and thus higher harvesting levels. It will therefore be necessary to reassess woodrose densities of the two species in future to ensure that overutilization of this useful resource does not take place.
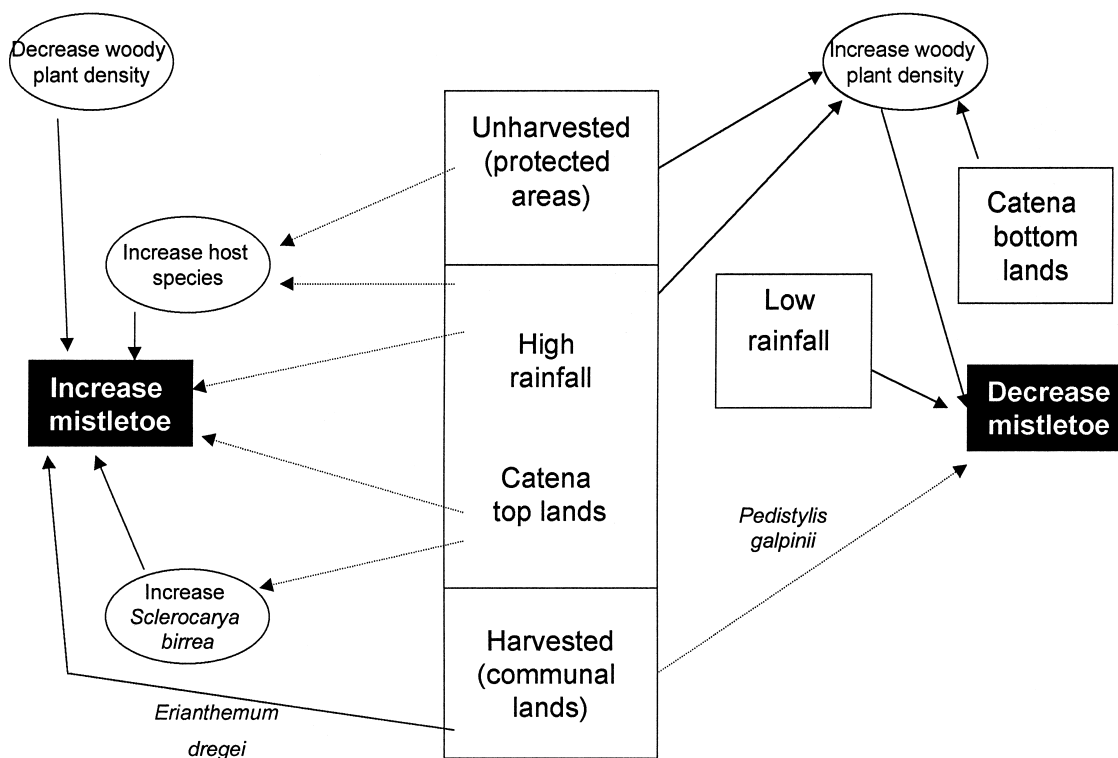
Figure 1. Factors influencing the abundance of *Erianthemum dregei* and *Pedistylis galpinii*. The predominant host species is *Sclerocarya birrea*. A dotted line indicates a significant relationship. Unless otherwise stated both mistletoe species are affected.

Acknowledgements

Table A1. Characteristics of the 12 study sites in Bushbuckridge, South Africa.

Site pair	Land Use	MAR (mm)	Altitude (m)	Co-ordinates	Dominant woody species
Bushbuckridge	Unharvested	850	640	24°50′10″ S, 31°5′30″ E	*Combretum* spp., *Dichrostachys cinerea, Terminalia sericea, Sclerocarya birrea, Trichilia emetica, Pterocarpus angolensis* and *Faurea saligna*
Xanthia	Harvested	695	588	24°50′10″ S, 31°10′1″ E	
Fleur de Lys	Unharvested	795	600	24°30′15″ S, 31°2′1″ E	*Combretum* spp., *Dichrostachys cinerea, Euclea* spp., *Terminalia sericea, Sclerocarya birrea* and *Peltophorum africanum*
Boelang	Harvested	850	680	24°35′1″ S, 31°5′45″ E	
Mangwazi	Unharvested	785	480	24°55′10″ S, 31°15′2″ E	
Madras	Harvested	750	580	24°55′15″ S, 31°5′50″ E	

Table A1. continued.

Site pair	Land Use	MAR (mm)	Altitude (m)	Co-ordinates	Dominant woody species
Alicecot	Unharvested	610	465	24°50′15″ S, 31°20′30″ E	*Combretum* spp., *Dichrostachys cinerea, Terminalia seri-cea, Sclerocarya birrea* and *Acacia nigrescens*
Dumphries	Harvested	655	420	24°45′45″ S, 31°15′45″ E	
Sabi Sabi	Unharvested	500	381	24°55′1″ S, 31°30′15″ E	
Huntington	Harvested	595	390	24°55′5″ S, 31°25′00″ E	
Manyeleti	Unharvested	500	415	24°40′15″ S, 31°25′48″ E	
Gottenburg	Harvested	590	415	24°40′27″ S, 31°25′15″ E	

Table A2. Density of living, dead-not useable and dead-useable mistletoe infection (mean ± S.E.; No. ha^{-1}) in areas of different rainfall (R), land-use (L) and catenal position (C), where n = 15 transects. Significance by three-way ANOVAs without replication (treatment scale; P values, $d.f.$ = 1,1).

Rain/Land-use	Living Top	Living Bottom	Dead-not useable Top	Dead-not useable Bottom	Dead-useable Top	Dead-useable Bottom
a) Combined species						
High Harvested	67.3 ± 18.2	63.4 ± 30.2	18.4 ± 8.4	19.3 ± 15.3	11.9 ± 6.5	3.0 ± 1.8
Unharvested	35.0 ± 13.6	25.8 ± 10.1	20.2 ± 7.2	28.4 ± 10.2	8.9 ± 4.0	8.6 ± 3.1
Low Harvested	53.3 ± 11.4	9.8 ± 3.8	12.7 ± 3.9	3.6 ± 2.9	5.3 ± 1.8	3.0 ± 2.7
Unharvested	49.8 ± 16.1	9.2 ± 4.0	11.9 ± 3.4	7.1 ± 4.3	4.4 ± 1.4	4.2 ± 3.0
b) *Erianthemum dregei*						
High Harvested	63.1 ± 17.3	54.5 ± 29.3	17.8 ± 8.4	19.3 ± 15.3	11.3 ± 6.4	3.0 ± 1.9
Unharvested	24.0 ± 9.3	9.9 ± 4.2	13.3 ± 6.9	18.1 ± 9.4	5.6 ± 3.9	3.9 ± 2.6
Low Harvested	34.1 ± 10.6	5.0 ± 3.2	8.9 ± 3.7	0.6 ± 0.6	4.4 ± 1.7	0 ± 0
Unharvested	35.3 ± 15.5	5.0 ± 3.4	6.2 ± 2.4	0.6 ± 0.6	2.1 ± 0.7	0.3 ± 0.3
c) *Pedistylis galpinii*						
High Harvested	4.2 ± 2.3	8.9 ± 8.0	0.6 ± 0.4	0 ± 0	0.6 ± 0.4	0 ± 0
Unharvested	11.0 ± 6.5	16.3 ± 8.4	6.8 ± 3.9	10.4 ± 4.4	3.3 ± 1.9	4.7 ± 2.3
Low Harvested	19.3 ± 8.2	4.7 ± 2.1	3.9 ± 2.3	3.0 ± 2.7	0.9 ± 0.5	3.0 ± 2.7
Unharvested	14.5 ± 8.5	4.2 ± 2.7	5.6 ± 3.2	6.5 ± 4.4	2.4 ± 1.4	3.9 ± 2.7

ANOVA (P-values)

	a) Combined species Living	Dead-not useable	Dead useable	b) *Erianthemum dregei* Living	Dead-not useable	Dead useable	c) *Pedistylis galpinii* Living	Dead-not useable	Dead useable
R	0.0715#	0.2548	0.0152*	0.1038	0.1163	0.0102*	0.9546	0.4697	0.2775
L	0.0859#	0.7284	0.0584#	0.1009	0.7873	0.1167	0.2464	0.2802	0.1677
C	0.0513#	0.3201	0.0694#	0.0759#	0.1224	0.0185*	0.176	0.9441	0.5471
R×L	0.0979#	0.778	0.0206*	0.0982#	0.5257	0.9816	0.135	0.393	0.225
R×C	0.0667#	0.5	0.0309*	0.1476	0.2132	0.0158*	0.0736#	0.4803	0.5845
L×C	0.658	0.3492	0.0637#	0.4492	0.2649	0.1415	0.7953	0.6591	0.4061

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