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Survival and development of *Phoradendron californicum* and *Acacia greggii* during a drought

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SURVIVAL AND DEVELOPMENT OF *PHORADENDRON CALIFORNICUM* AND *ACACIA GREGGII* DURING A DROUGHT

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ABSTRACT.—Survival and development of parasitic and autoparasitic *Phoradendron californicum* (desert mistletoe) and their *Acacia greggii* (catclaw) hosts were quantitatively investigated during the 1997 drought in southern Nevada. *Phoradendron californicum* was parasitic on other individuals of the same species (autoparasitic), and these in turn were parasitic on *A. greggii* hosts. An extensive drought from February 1995 to mid-July 1997 was characterized by extremely low seasonal rainfall and high summer air temperatures. Extensively mistletoe-infested hosts had significantly less canopy volume and produced significantly fewer leaves, flowers, and fruits than uninfested (control) or lightly infested hosts. Mistletoe plants on *A. greggii* hosts with fewer infections produced significantly more leaves and fruits and survived better than mistletoe plants on *A. greggii* hosts with extensive infestations. Autoparasites had significantly less canopy volume and fruit production than their parasitic hosts and parasites on hosts with fewer infections. Severity of infestation was significantly negatively correlated with *A. greggii* and *P. californicum* survival, as it was with leaf, flower, and fruit development of *A. greggii* and parasitic and autoparasitic *P. californicum* during the 1997 drought in southern Nevada.

Key words: host, parasite, autoparasite, Acacia greggii, Phoradendron californicum, *drought, survival, development, Las Vegas valley, southern Nevada.*

Phoradendron californicum (desert mistletoe) is an autotrophic hemiparasite, surviving at the expense of its higher vascular plant hosts (Kuijt 1969, Holland et al. 1977, Calder and Bernhardt 1983, Ehleringer et al. 1985, 1986). Branches of these host plants often swell during infection by this leafy mistletoe (Holland et al. 1977). *Phoradendron californicum* taps its host xylem only to obtain water and mineral nutrients within xylem fluids (Leonard and Hull 1965, Raven 1983, Ehleringer et al. 1986, Holland et al. 1977).

Acacia greggii (catclaw) is often covered with thick masses of *P. californicum*, which may reduce host growth and reproductive success through time (Knute and Faber 1991). Serious long-term damage to host plants is largely caused by a combination of environmental and *Phoradendron*-induced physiological (water and nutrient) stress (Glatzel 1983, Hollinger 1983, Schulze and Ehleringer 1984, Schulze et al. 1984, Ehleringer et al. 1986). Weather extremes are an important environmental factor influencing survival and development of woody desert plants. Insufficient rainfall and above-average air temperatures during winter 1995–summer 1997 in southern Nevada may have been such an extreme. In general, precipitation during this 2.5-year period was well below average. From casual observations, it appears that some *P. californicum* individuals and their *A. greggii* hosts may be killed or damaged by drought alone.

Autoparasitism is a condition in which a parasite occurs facultatively on another individual of the same species. *Phoradendron californicum* parasitizes *A. greggii* and *Cercidium floridum* (blue palo verde) hosts and established *P. californicum* infestations in northwestern Arizona (Schulze and Ehleringer 1984) and southeastern California (Lei 1999). However, Schulze and Ehleringer (1984) note that autoparasitism involving *Phoradendron* species occurs infrequently.

Schulze and Ehleringer (1984) and Ehleringer and Schulze (1985) have greatly increased our knowledge regarding the water and nutrient status of *P. californicum* and its *A. greggii* hosts in northwestern Arizona. Yet, the response of parasites, autoparasites, and their hosts to severe drought remains poorly understood. The objective of this study was to describe survival and development of leaves, flowers, and fruits of a complex host-parasite-autoparasite

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pathosystem. Specifically, 2 questions are addressed in this study: (1) Does the severity of *P. californicum* infestation affect the survival and development of *A. greggii* hosts under drought stress? (2) Does the severity of infestation affect the survival and development of parasitic and autoparasitic *P. californicum* under drought conditions?

METHODS

Study Site

Field studies were conducted in Las Vegas, Nevada (roughly 36°10′N, 115°05′W; elevation 780 m), from spring through fall 1997. The Tropicana Wash lies across the southern part of the Las Vegas valley. Although this intermittent wash remains dry throughout much of the year, it often collects excess running water during and shortly after major storms.

Las Vegas valley has experienced 3 episodes of extreme drought since 1985, with precipitation falling well below annual means in some years. The most recent drought in Las Vegas valley of southern Nevada occurred over a period of 2.5 years, February 1995 through mid-July 1997, with precipitation generally falling well below monthly averages (Fig. 1). An average reduction of 72.9% in precipitation occurred during the 1995–1997 drought compared to a normal, non-drought period (NOAA, Las Vegas). Mean annual air temperatures, however, did not vary considerably despite the erratic precipitation pattern occurring during this period. The 1995–1997 years generally had above-average air temperatures (Fig. 2).

Field Surveys and Laboratory Analyses

The sample included hosts with parasites only, and with both parasites and autoparasites; also included were adjacent individuals without any visible parasites (control). A total of 16 autoparasitic *P. californicum* individuals each infested another *P. californicum*, which in turn parasitized 8 *A. greggii* hosts.

Within my study site, 1017 *P. californicum* (parasitic and autoparasitic) individuals and 76 *A. greggii* (infested and uninfested) trees were surveyed for evidence of mortality. Because 13 host trees were not infested by parasites (control), 1017 *P. californicum* individuals, including 16 autoparasites, were found on 63 hosts. *Phoradendron californicum* are obligate parasites. Once a host dies, all *P. californicum* individuals parasitizing it also die. The condition of each *A. greggii* host was recorded as live without any dead branches (1), live with single or multiple dead branches (2), or dead (3). Each *P. californicum* was recorded as live with green foliage (1), live with reddish brown foliage (2), or dead (3). Host plants having completely bare branches and lacking leaves, flowers, or fruits (without phenophases) through the 1997 growing season were assumed dead. Similarly, parasites and autoparasites with dark brown foliage and extremely brittle stems, and without phenophases, were also assumed dead.

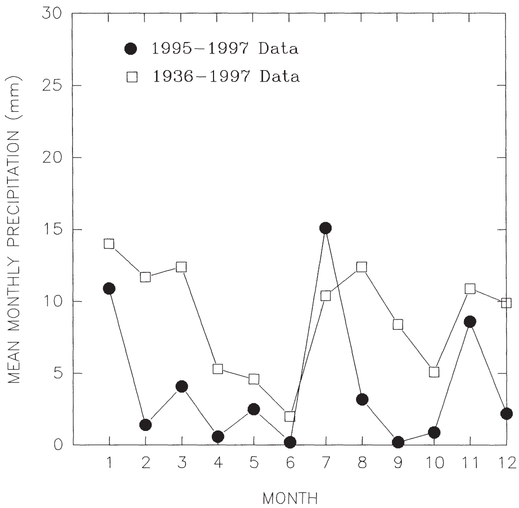

Fig. 1. Comparison of mean monthly precipitation from February 1995 through July 1997 with mean monthly precipitation of Las Vegas valley (NOAA, Las Vegas) in southern Nevada based on 1936–1997 data.

Development of *P. californicum* (parasitic and autoparasitic) and its *A. greggii* hosts was assessed by examining vegetative and reproductive characteristics. Thirty-two *A. greggii* trees were randomly selected and were evenly distributed among the 4 levels of *P. californicum* infestation (control, light, moderate, severe). Light, moderate, and severe infections implied fewer than 20, between 20 and 40, and more than 40 *P. californicum* individuals per host tree, respectively. Due to the paucity of autoparasites, all 16 autoparasites were found on 8 severely parasitized host trees.

For each tree, volume of host canopies containing green leaves was computed by first assuming *A. greggii* architecture resembled an

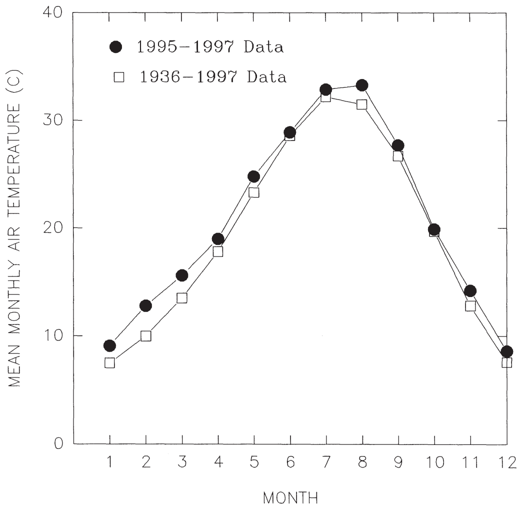

Fig. 2. Comparison of mean monthly air temperature from February 1995 through July 1997 with mean monthly air temperature of Las Vegas valley (NOAA, Las Vegas) in southern Nevada based on 1936–1997 data.

elliptical cylinder and then calculating the volume using the following equation: (πab)h, where a and b are radii and h is height of the elliptical cylinder (Larson et al. 1994). Since *A. greggii* canopies had small open spaces within the cylindrical shape, measured volumes are likely overestimated. Total number of leaflet pairs in each group of 100 compound leaves was counted. A compound leaf possesses 2 or more separate leaflets, with 2 relatively symmetrical leaflets making up a leaflet pair. The total number of leaflet pairs was then divided by 100 to determine average number of leaflet pairs per compound leaf. Flower and fruit production was determined by counting the number of floral spikes and pods (fruits) from individual host canopies, respectively. However, flower and fruit production of hosts was not compared because not all flowers will mature into fruits regardless of parasite severity.

Because only 8 autoparasitic *P. californicum* individuals were detected, only 8 parasitic *P. californicum* individuals in each of 3 levels of infestation (light, moderate, and severe) were randomly selected and measured, for a total of 32 individuals. Foliage of mistletoe plants also resembled an elliptical cylinder, and so the same formula (πabh) was used to calculate volume (Larson et al. 1994). Again, since *P. californicum* canopies had small open spaces and were not arranged in a perfect elliptical cylinder, calculated volumes are likely to be overestimates. Fruit production was determined by counting the number of berries from individual *P. californicum* canopies.

Statistical Analyses

Total numbers of live and dead *A. greggii* hosts with 4 levels of *P. californicum* infestation (control, light, moderate, and severe) were expressed in percentages. Similarly, total numbers of live and dead *P. californicum* individuals on *A. greggii* hosts with 4 levels of infestation (light, moderate, severe, and autoparasite) were also expressed in percentages. Thirty-two *A. greggii* hosts were randomly selected and evenly distributed among the 4 levels of *P. californicum* infestation to calculate the volume of *A. greggii* and *P. californicum* foliage and to determine fruit production of *P. californicum*. The remaining 44 *A. greggii* hosts were not selected in order to conduct appropriate statistical analyses using identical sample sizes. One-way analysis of variance (ANOVA; Analytical Software 1994) was used to detect significant differences in leaf, flower, and fruit production among uninfested hosts (control) and among hosts with 3 levels of infestation. Tukey's multiple comparison test (Analytical Software 1994) was then performed to compare means of vegetative, floral, and fruit characteristics when a significant infestation effect was detected.

Pearson's correlation analysis (Analytical Software 1994) was conducted to correlate severity of infestation with host and parasite survival, as well as severity of infestation with host and parasite development. Mean volume of and number of fruits on *P. californicum* canopies were presented with standard errors; P-values less than or equal to ($\leq$) 0.05 were reported as statistically significant.

RESULTS

Compared to adjacent unparasitized *A. greggii* hosts (Fig. 3), more severely parasitized hosts were either dead or had multiple dead branches. Substantial insect damage was found on dead and dying *A. greggii* hosts. Insects, including bark beetles, invaded many weakened *A. greggii* hosts. However, all unparasitized hosts and a majority of lightly to moderately parasitized hosts survived the 1997

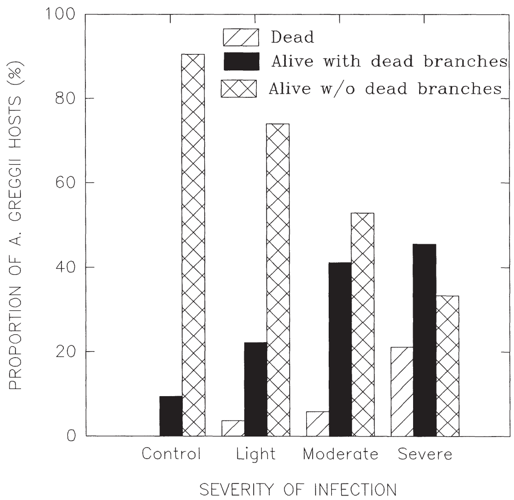

Fig. 3. Condition (live and dead, n = 76) of uninfected *A. greggii* hosts (control) and hosts with various levels of *P. californicum* infection in southern Nevada. Total numbers of live and dead *A. greggii* trees are expressed in percentages. Total number of trees in each infection class: control, n = 13; light, n = 27; moderate, n = 28; and severe, n = 8.

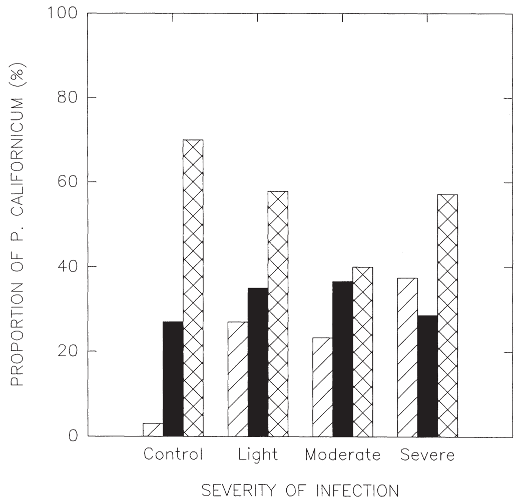

Fig. 4. Condition (live and dead, n = 1017) of *P. californicum* growing on *A. greggii* hosts with various levels of infection in southern Nevada. Total numbers of live and dead *P. californicum* individuals are expressed in percentages. Total number of individuals in each infection class: light, n = 130; moderate, n = 562; severe, n = 309; autoparasite, n = 16.

TABLE 1. Vegetative, floral, and fruit characteristics of uninfected *A. greggii* hosts (control) and hosts with various levels of *P. californicum* infestation in southern Nevada (n = 100 in each infection class). Mean values in columns followed by different letters are statistically significant at $P \leq 0.05$.

Infection class	Leaflet pairs per leaf	Green canopy volume (m^3)	Number of spikes	Seeds per pod	Pods per tree
Control	5.2a	7.0a	389.7a	6.9a	234.2a
Light	5.2a	7.2a	374.1a	6.7a	223.1a
Moderate	5.0a	4.9b	334.6b	6.4a	201.3b
Severe	4.9a	2.8c	296.0c	6.3a	175.5c

drought and produced abundant flowers or fruits (Table 1) despite some dead branches.

Mortality of *P. californicum* was considerably greater (Fig. 4) on severely parasitized hosts than on adjacent unparasitized hosts and hosts with light to moderate infestation. Regardless of the extent of infestation, a large percentage of *P. californicum* plants had reddish brown foliage with relatively low flower or fruit production throughout the 1997 growing season. All 16 autoparasites were found on 8 heavily parasitized *A. greggii* hosts; 6 autoparasites were dead, as were their parasitic hosts.

Moderate to heavy infestation, with or without autoparasites, significantly ($P \leq 0.001$) decreased host canopy volume and flower and fruit production (Table 1) compared to uninfested or lightly infested hosts. Conversely, total number of leaflet pairs per leaf and total number of seeds per pod did not differ significantly ($P > 0.05$; Table 1). Mistletoe plants on hosts with more infections produced significantly ($P \leq 0.001$) less canopy volume (Fig. 5) and had lower fruit production (Fig. 6) than mistletoe plants on hosts with fewer infections. Autoparasites exhibited significantly ($P \leq 0.001$) less canopy volume (Fig. 5) and fruit

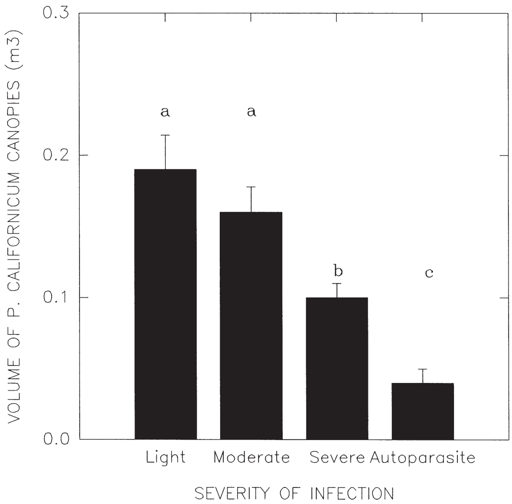

Fig. 5. Canopy volume (mean ± $s_{\bar{x}}$, n = 32) of *P. californicum* growing on *A. greggii* hosts with various levels of infection in southern Nevada. Different letters at the tops of columns indicate significant differences at $P \leq 0.05$.

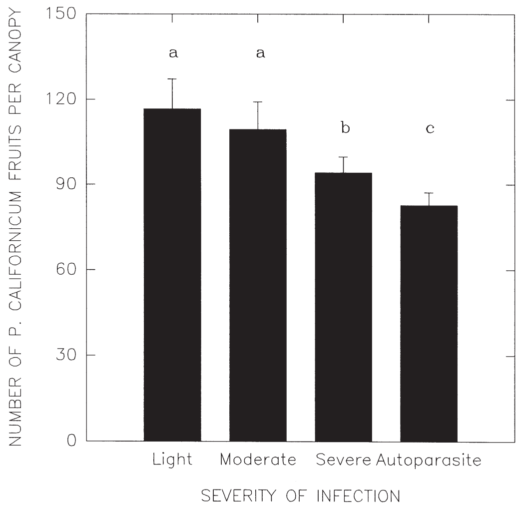

Fig. 6. Fruit production (mean ± $s_{\bar{x}}$, n = 32) of *P. californicum* growing on *A. greggii* hosts with various levels of infection in southern Nevada. Different letters at the tops of columns indicate significant differences at $P \leq 0.05$.

production (Fig. 6) than their parasitic hosts and parasites on hosts with fewer infections.

Severity of infestation was significantly negatively ($P \leq 0.001$; Table 2) correlated with (1) host and parasite survival; (2) leaf, flower, and fruit production of hosts; and (3) leaf and fruit production of parasites and autoparasites.

DISCUSSION

Survival and development of parasitic and autoparasitic *P. californicum* and *A. greggii* hosts were compared during the severe drought of 1995–1997 in southern Nevada. *Phoradendron californicum* had adverse impacts on its *A. greggii* hosts as well as on other *P. californicum* individuals.

Long-term climatically extreme conditions, such as drought, tend to episodically lower host, parasite, and autoparasite populations. The drought in southern Nevada began in February 1995 and reached its greatest intensity during the first 6 months of 1997, followed by well above-average monsoonal rainfalls in July and September (NOAA, Las Vegas). This prolonged drought was characterized by extremely low seasonal rainfall and high summer air temperatures. The well below-average seasonal rainfall and above-average air temperatures during winter 1995–summer 1997 likely resulted in low soil water content and high soil temperatures. Although not investigated in this study, active transpiration with soils of low available moisture during growing seasons may result in substantial branch damage or even mortality of *A. greggii* hosts that support abundant *P. californicum* individuals on their branches. Severely infested *A. greggii* hosts would be expected to exhibit greatest branch damage or mortality compared to uninfested or lightly infested hosts in drought years. Mistletoe infestation greatly reduces host growth and the ability to survive drought and insect outbreak (Calder and Bernhardt 1983). However, uninfested *A. greggii* hosts appear to be fairly tolerant of extreme water and heat (drought) stress, and are more capable of growing in periodically stressful desert environments than moderately or severely infested hosts.

Although comparative water relations were not examined in this study, prolonged drought would result in widespread host-plant water stress, which in turn could increase mortality of established parasitic and autoparasitic infections. *Phoradendron californicum*, which is characterized by low water-use efficiencies, must maintain more negative water potentials than its *A. greggii* hosts to obtain water (Jordan et al. 1997). Some *P. californicum* individuals are more vulnerable to water stress than their hosts. Jordan et al. (1997) propose that drought may have a greater detrimental effect

TABLE 2. Correlation (r-value) between parasite severity and *A. greggii* survival ($n = 76$) and development ($n = 100$), and between parasite severity and *P. californicum* survival ($n = 1017$) and development ($n = 32$). Significance levels: * ≤ 0.05; ** ≤ 0.01; *** ≤ 0.001; NS: non-significant.

Interaction	r-value
Host survival × parasite severity	–0.99***
Host leaflet pairs/leaf × parasite severity	–0.94***
Host canopy volume × parasite severity	–0.93***
Host flower production × parasite severity	–0.98***
Host fruit production × parasite severity	–0.98***
Host seeds/pod × parasite severity	–0.98***
Parasite survival × parasite severity	–0.96***
Parasite canopy volume × parasite severity	–0.99***
Parasite fruit production × parasite severity	–0.98***

on *P. californicum* than on its hosts because some *P. californicum* individuals die although their host branches do not. Extremely low host-plant water potentials appear to result in substantial mortality of established *P. californicum* infections and may limit long-term *P. californicum* infection success under severe drought conditions in southeastern California (Jordan et al. 1997). The final cause of mortality in mistletoe-infested *A. greggii* during drought in southern California was bark beetle infestation. Jordan et al. (1997) observed extensive insect damage on mistletoe-infested *A. greggii.* This could be the main cause of mortality under drought stress.

In this study *Acacia greggii* experiencing moderate to massive infestations had a significant reduction in canopy volume and flower and fruit production. Large clumps of *P. californicum* were visible on host branches and canopies. Within a single, heavily infested host, live branches supported abundant parasites, while dead branches revealed dead and dying parasites and autoparasites. Despite infrequent host-parasite-autoparasite interactions, infection and reproduction of autoparasitic *P. californicum* were successful as evidenced by abundant green canopy and fruit production, respectively, at the expense of parasitic and nonparasitic hosts. Under extreme moisture stresses, *A. greggii* hosts died, as did their parasites and autoparasites.

A very limited number of autoparasitic *P. californicum* can be found in Las Vegas valley of southern Nevada. Host, parasite, and autoparasite survival and development are a function of parasite severity and drought stress. Relationships between severity of infestation and host, parasite, and autoparasite survival, and between severity of infestation and host, parasite, and autoparasite plant development, may have occurred in the absence of drought. Perhaps these phenomena are normal patterns irrespective of drought stress. Host trees with severe leafy mistletoe infestations are slowly declining and will eventually die long before similar trees without infestation. This decline will occur over many years if not several decades. Reductions in canopy volume of *A. greggii* likely occurred long before the 1995–1997 drought. The severe drought in 1997 may have accentuated or accelerated detrimental effects of mistletoe infestation on *A. greggii* hosts. Severely infested hosts are expected to be the first to die during periods of drought. *A. greggii* trees are already under infestation stress, and additional drought stress will weaken them enough that insects, including bark beetles, can successfully attack and kill them. Under extreme conditions in southern Nevada, *A. greggii* hosts supported abundant *P. californicum* before *P. californicum* experienced autoparasitic- and drought-induced mortality that killed parasites, autoparasites, and their hosts.

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