

## Reduced mycorrhizae on *Juniperus monosperma* with mistletoe: the influence of environmental stress and tree gender on a plant parasite and a plant-fungal mutualism

Catherine A. Gehring and Thomas G. Whitham

Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA

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**Summary.** We examined how an important plant mutualist (fungal mycorrhizae) interacted with a common tree parasite, a xylem-tapping mistletoe (*Phoradendron juniperinum* Engelm.) growing on one-seeded juniper (*Juniperus monosperma* Engelm.). We also examined how host tree gender and environmental stress might be involved in this interaction. Four major patterns were observed. First, the mycorrhizal levels of trees of both sexes were negatively correlated with mistletoe density. In comparisons of heavily and lightly infested trees at the stressful site, high mistletoe levels were associated with 27% less mycorrhizae on male trees and 38% less mycorrhizae on the roots of female trees. Second, the reduction of mycorrhizae on trees with high mistletoe levels was slightly but significantly greater for female trees than male trees. These results are consistent with the hypothesis that severe mistletoe infestation suppresses mycorrhizae and that this suppression is more severe in female trees because of their greater energetic investment in reproduction. Third, female junipers growing in the stressful ash and cinder fields averaged three-fold higher levels of mistletoe infestation than male trees. Fourth, no differences in mistletoe infestation were observed between male and female trees growing in the more favorable soils. Comparisons with other systems suggest that both mistletoes and herbivores have similar interactions with mycorrhizae.

**Key words:** Dioecy – Environmental stress – Parasitic mistletoe – Mutualist – Mycorrhizal fungi

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Mycorrhizal fungi enhance host plant nutrient uptake and provide protection from some pathogens in exchange for photosynthate from host plants (Hacskeylo 1972; Harley and Smith 1983). Mycorrhizae vary in density depending upon environmental conditions, and are generally more abundant on plants growing in margin-

nal environments where the need for enhanced nutrient and water uptake is greater (Meyer 1973; Tinker 1975, 1984). Because mycorrhizal fungi are dependent upon host plants for energy in the form of photosynthate (e.g., up to 60% of a plant's photosynthate may be used by mycorrhizae (Stribley et al. 1980)), any factor that affects plant energy allocation patterns could influence the relationship between mycorrhizal fungi and host plants. Such factors could include plant gender and the degree of parasitism or herbivory experienced by a plant.

Among dioecious plants, males and females often allocate energy differently. For example, females of many dioecious plants have been shown to invest relatively more energy in sexual reproduction and defense (Putwain and Harper 1972; Lloyd and Webb 1977; Armstrong and Irvine 1989; Boecklen et al. 1990), while males invest more energy in vegetative growth (Harper 1977; Boecklen et al. 1990). Because of these differences in allocation patterns, male and female plants could differ both in their need for mycorrhizal mutualism or in the amount of photosynthate they must provide to establish and maintain mycorrhizal fungi. The high nutrient requirements of female plants during fruit production could be met in part by increased levels of mycorrhizae. Alternatively, greater investment in sexual reproduction by female plants could result in reduced photosynthate available to mycorrhizal fungi.

The level of parasitism experienced by a plant could also affect the amount of water, minerals, and photosynthate available, and any sexual differences in parasitism load therefore could have important impacts on mycorrhizal mutualism. Herbivores and parasites have been demonstrated to respond to the differential patterns of resource allocation between the sexes (Bawa and Opler 1978; Dannell et al. 1985; Lovett Doust and Lovett Doust 1985; Boecklen et al. 1990), and the mutualistic mycorrhizal fungi associated with the roots of higher plants may respond to these differences as well. Herbivores have been shown to cause dramatic reductions in level of mycorrhizal colonization in grasses, crops, and gymnosperms (Bethlenfalvy and Dakessian 1984; Beth-

lenfalvay et al. 1985, 1988; Trent et al. 1988; Gehring and Whitham 1991) and parasitic plants may have similar impacts. Because the occurrence of mistletoe parasitism (Hawksworth 1983) and mycorrhizal mutualism (Newman and Reddell 1987) is widespread among plants, the relationships between these two could have important consequences for plant survival and reproduction. The present study is the first to examine how parasitic mistletoes might influence mycorrhizal mutualism.

To examine the relationship between tree gender, degree of parasitism, and level of mycorrhizal colonization, we examined the levels of mistletoe parasitism, and mycorrhizal mutualism on *Juniperus monosperma* Engelm. (McDougall 1973), a dioecious tree known to be colonized by vesicular-arbuscular endomycorrhizae (McDougall and Jacobs 1927). We chose this system, in part, because the mistletoe parasite (*Phoradendron juniperinum* Engelm. (McDougall 1973)) taps the xylem of the host plant thereby removing water, mineral nutrients, and carbon (Hull and Leonard 1964; Ehleringer et al. 1985, Marshall and Ehleringer 1990), materials which are transported from mycorrhizal fungus to host plant or vice versa. We addressed the following questions: 1) Do mistletoe levels differ between male and female junipers, and is this relationship affected by the degree of environmental stress experienced by the plant?, 2) Does the level of mycorrhizal colonization differ in male and female junipers?, and 3) Is there a relationship between level of mistletoe infestation and level of mycorrhizal colonization?

## Materials and methods

### Study sites

This study was conducted near Sunset Crater (2000 m elevation), northeast of Flagstaff in Coconino County, Arizona. Soil in the major study area consisted of lava, ash, and cinders characterized by low moisture and nutrient levels (Mopper et al. 1990; Gehring and Whitham, in prep.). Dominant plants included pinyon pine (*Pinus edulis* Engelm.), one-seeded juniper (*Juniperus monosperma* Engelm.), apache plume (*Fallugia paradoxa* (D. Don.) Endl.), mormon tea (*Ephedra viridis* Coville), and squawbush (*Rhus trilobata* Nutt.). We also examined mistletoe levels at a second, less stressful site approximately 9 miles northwest of the cinder site and at the same elevation. Soils were composed of noncinder, sandy-loam and had nine-fold higher rates of soil nitrate mineralization and 40% higher levels of soil phosphate than those at the cinder site (Gehring and Whitham, in prep.). In addition, soil moisture levels were approximately two times higher at this off-cinder site during the dry season (May), as well as during the wet season (early September) (Gehring and Whitham, in prep.). The differences in the conditions of the sites is also reflected in the growth rates of pinyon pine (*Pinus edulis*). Annual shoot growth at the off-cinder site was twice that of pinyon pine at the cinder site in each of the past three years (Gehring and Whitham, in prep.).

### Mistletoe density

To determine whether male and female junipers differed in level of mistletoe infestation, we counted the number of mistletoe plants on 18 randomly selected, mature, reproductively active male and female juniper trees at each site. To control for slight differences in

tree size, the total volume of each tree canopy was estimated and the level of mistletoe infestation expressed as number of mistletoe plants per m<sup>3</sup>. Mistletoe infestation data were square root transformed and analyzed using a one-way analysis of variance followed by a Student-Newman Keuhl's multiple comparison test to determine the location of treatment differences (Zar 1984).

To assess mistletoe density on a population level, we categorized 100 randomly selected, similarly sized trees at each site according to degree of mistletoe infestation. Trees were sexed and designated as having high mistletoe levels if the number of mistletoes on the tree exceeded 50, medium mistletoe levels if the number of mistletoes ranged from 6–49, and low mistletoe levels if the number of mistletoes was 5 or fewer. These data enabled us to estimate the frequency of high, medium, and low mistletoe males and females at the two sites, and to determine the sex ratio of junipers at these sites. The frequency of males and females in each category were compared using a Chi-squared contingency table (Zar 1984).

### Levels of mycorrhizal colonization

To determine whether mycorrhizal colonization varied with either host plant sex or level of mistletoe parasitism, we examined the levels of mycorrhizal colonization of 6 trees in each of the following groups at the cinder site: low mistletoe density males, low mistletoe density females, high mistletoe density males, and high mistletoe density females. Mistletoe densities on these trees were quantified to ensure that mistletoe levels in the high and low groups were comparable in male and female junipers. By collecting from these groups, we were able to separate the impacts of tree sex and level of mistletoe parasitism on mycorrhizal colonization. Male and female trees sampled grew intermixed within the site and were matched for size. Fine root samples (150–200 cm of roots < 5 mm in diameter) were collected at the north side of all trees along the dripline so that roots from both inside and outside the tree canopy were represented. Fine roots were traced to a main root to ensure they were from the desired tree. Roots were collected in early May of 1990 and stored in plastic bags at 5° C for 48 h until processing.

Entire root samples were cleared in KOH, and stained using acid fuchsin in lactic acid (Kormanik and McGraw 1982). Percentage mycorrhizal colonization was determined using a gridline intersect method in which at least 150 intersection points were examined (Giovanetti and Mosse 1980). Data were analyzed using a one-way analysis of variance followed by a Student-Newman Keuhl's multiple comparison test to determine the location of treatment differences (Zar 1984).

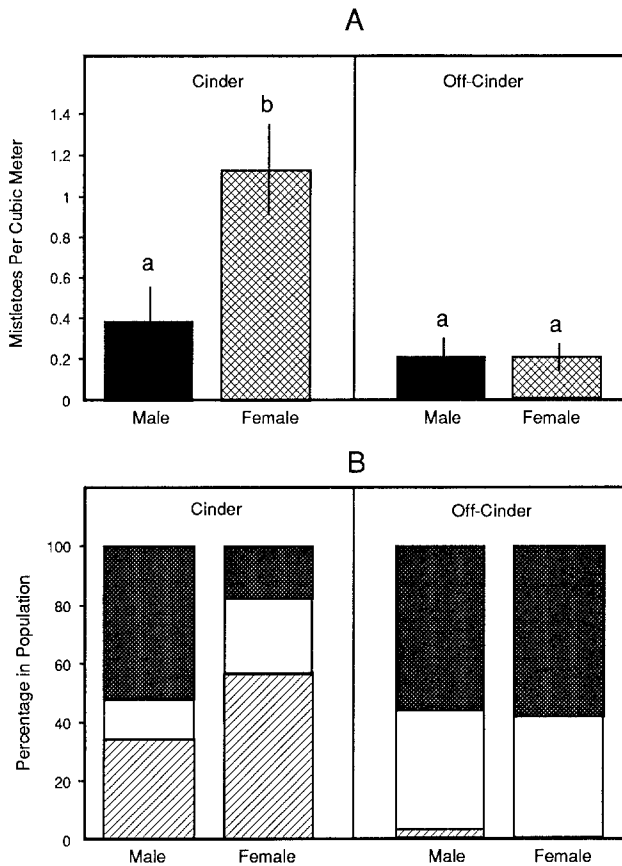
## Results

### Sex ratio

The juniper sex ratio was male biased at the stressful cinder site (1.56 males for every female,  $n = 100$  trees) but was 1.0 at the less stressful off-cinder site ( $n = 100$  trees). This finding is consistent with data on a variety of other dioecious species where males tend to dominate in poor environments (Freeman et al. 1976; Lloyd and Webb 1977; Grant and Mitton 1979), and with theoretical models (Charnov 1982) for species such as junipers that are capable of sex change (Vasek 1966).

### Sex-biased mistletoe parasitism

Two independent data sets suggest that the degree of environmental stress experienced by juniper trees is im-



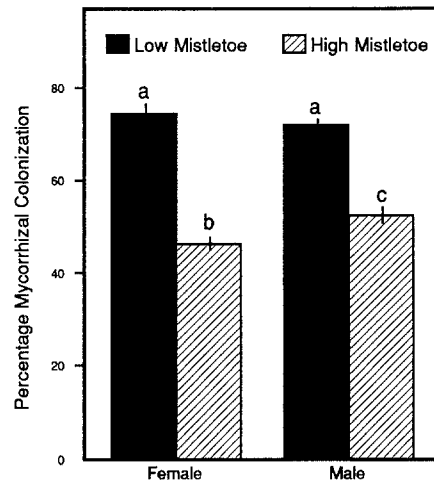
**Fig. 1.** Mistletoe levels of juniper trees growing in a stressful cinder environment and a less stressful off-cinder environment. Figure A shows the mistletoe levels per unit canopy volume ( $m^3$ ) of 18 male junipers and 18 female junipers at each site. Data are expressed as means  $\pm 1$  SE. Different letters above bars denote significant differences at  $p < 0.05$ . Figure B shows the percentage of 100 junipers of both sexes in low (dotted bars), medium (open bars), and high (right-hatched bars) mistletoe categories at the cinder and off-cinder sites. Categories are defined in the methods section of the paper

portant in determining parasite abundance on female trees but not on male trees. First, female junipers averaged three times higher mistletoe densities than either males at the stressful cinder site, or males and females at the less stressful site ( $F = 13.55$ ,  $p < 0.0001$ ; Fig. 1A). No significant differences were observed between the latter three categories (Fig. 1A).

Second, our population census data set also showed that female-biased mistletoe parasitism occurred only at the stressful site. There was a significant difference between the number of males and females in low, medium, and high mistletoe categories at the cinder site ( $X^2 = 13.32$ , d.f. = 2,  $p < 0.005$ ; Fig. 1B). However, no differences in mistletoe densities were observed at the off-cinder site where males and females both tended to have mistletoe densities primarily in the low and medium categories ( $X^2 = 1.016$ , d.f. = 2,  $p > 0.500$ ; Fig. 1B).

#### Levels of mycorrhizal colonization

In both sexes, we found a strong negative relationship between degree of mistletoe parasitism and level of



**Fig. 2.** Mycorrhizal levels of male and female junipers with low (solid bars) and high (right-hatched bars) levels of mistletoe parasitism at the stressful (cinder) site. Data are expressed as means  $\pm 1$  SE. Different letters above bars denote significant differences between means at  $p < 0.05$

mycorrhizal colonization, indicating that either mistletoe parasitism suppresses mycorrhizal formation or high levels of mycorrhizae allow trees to resist parasite attack. The levels of mycorrhizal colonization in high mistletoe density male junipers were on average 27% lower than those of low mistletoe density males; while the levels of mycorrhizal colonization in high mistletoe density females were 38% lower than those of low mistletoe density female junipers. The levels of vesicular-arbuscular mycorrhizal colonization observed in juniper with low mistletoe densities were similar to those reported for *Juniperus osteosperma* in northwestern Colorado (Reinsvold and Reeves 1986). However, we did not observe ectomycorrhizal colonization as has been observed in *Juniperus osteosperma* (Klopatek and Klopatek 1986, Reinsvold and Reeves 1986).

The decline in mycorrhizae with increased mistletoe density suggests that the fungal-plant mutualism is more severely affected in female trees than in male trees. Although the sexes did not differ in level of mycorrhizal colonization when mistletoe densities were low, female junipers had significantly lower levels of mycorrhizal colonization than male junipers when mistletoe densities were high (Fig. 2). This sexual difference was not due to higher mistletoe loads on the female vs. male junipers surveyed for mycorrhizae (i.e., mistletoe densities on heavily infested trees averaged  $1.11 \pm 0.200$  mistletoes/ $m^3$  for male junipers and  $1.03 \pm 0.156$  mistletoes/ $m^3$  for female junipers ( $t = 0.326$ , d.f. = 11,  $p = 0.751$ )).

## Discussion

### *Mistletoe-driven mycorrhizal mutualism or vice versa?*

The negative correlation between mistletoe density and level of mycorrhizal colonization in male and female junipers could be explained by two hypotheses. First, if mycorrhizal fungi provide protection from mistletoe par-

asitism as they do from some pathogens (Dehne 1982), junipers with inherently lower mycorrhizal levels would have higher levels of mistletoe parasitism than juniper with high mycorrhizal levels. Few studies have examined the potential for mycorrhizae-mediated resistance to pathogenic organisms other than root-associated fungi, rootknot nematodes, and viruses (Dehne 1982), so the likelihood for this hypothesis is difficult to evaluate.

Alternatively, the lower mycorrhizal levels of heavily mistletoe-infested trees could be a consequence of mistletoe parasitism that reduces the carbon available to the fungal mutualists. Two major symptoms of mistletoe infestation include dieback of infected limbs and increased host plant water stress (Knutson 1983). Branch dieback above the site of mistletoe infestation is prevalent among junipers at our study site and has been reported for other juniper species (Hedgcock 1915). Such tissue loss could result in significant reductions in photosynthetic tissue that could prevent trees from maintaining their fungal mutualists. Similarly, plant water stress is also known to reduce photosynthesis because of stomatal closure (Knutson 1983). In addition, Marshall and Ehleringer (1990) have suggested that *Phoradendron juniperinum* may derive a significant amount of carbon via the xylem sap of their Utah juniper (*Juniperus osteosperma*) hosts. Carbon allocation to mycorrhizal fungi could thus be reduced via direct carbon losses to mistletoe parasites, as well as via photosynthetic tissue losses resulting from mistletoe parasitism. Similarly, both low light availability and herbivory have been shown to cause reduced mycorrhizal colonization relative to controls, presumably due to carbon limitation (Daft and El-Giahmi 1978; Bayne et al. 1984; Gehring and Whitham 1991).

A similar carbon limitation argument could be used to explain the lower mycorrhizal levels of female trees relative to male trees when both experience the same degree of mistletoe parasitism. If females invest more energy in reproduction, they may be more carbon limited than males, and may be less able to provide carbon to mycorrhizal fungi. Lower levels of mycorrhizal colonization and mycorrhizal benefits could result.

Although we have shown that low mistletoe density and high mistletoe density juniper trees differed by 27–38% in level of mycorrhizal colonization, whether greater colonization yields greater benefits remains to be tested in this system. Benefits of mycorrhizal mutualism, such as enhanced phosphate inflow into roots have been shown to be positively correlated with levels of vesicular-arbuscular mycorrhizal colonization in laboratory experiments (e.g., Sanders et al. 1977). Likewise, plant growth was positively correlated with mycorrhizal abundance in two ectomycorrhizal plant species (Cline and Patrick-Reid 1982; Last et al. 1990). No consistent positive correlation between level of vesicular-arbuscular mycorrhizal colonization and host plant yield has been observed in field studies (McGonigle 1988), although this may be due to methodological problems involved in eliminating or reducing mycorrhizal colonization in the field (Read 1991).

Differences in levels of mycorrhizal colonization would probably be most important at study areas similar

to the ones we report on which have low nutrient soils and are subject to annual drought conditions. Our study was performed during the warmest and driest time of the year when shoots were elongating and reproductive structures were being produced. Unless the uptake and utilization of nutrients by junipers is completely decoupled, this time of year should represent the peak need for mycorrhizal fungi. Mycorrhizal fungi have been hypothesized to be most important in stressful environments (Tinker 1975, 1984), and under stressful circumstances termed “ecological crunches” (Allen and Allen 1986). Vesicular-arbuscular mycorrhizae have been shown to alleviate drought stress either by enhancing phosphate uptake or by utilizing soil water not available to the nonmycorrhizal plant (Bethlenfalvay et al. 1988). Vesicular-arbuscular mycorrhizal mutualism is likely to be important in our study, and plants with reduced mycorrhizal colonization are likely to benefit less from mycorrhizal mutualism. Even the small difference observed between male and female trees might be significant during this dry time of year when females grow and produce berries under drought conditions.

#### *Sex-biased mistletoe parasitism*

Two hypotheses may account for the observed patterns of sex-biased mistletoe parasitism. First, the higher mistletoe levels of female trees at the stressed site could result from greater numbers of mistletoe seeds being deposited by seed dispersers onto female junipers than male junipers. Most mistletoes are bird dispersed (Calder 1983), and a variety of birds feed on the fruits of *Phoradendron juniperinum* at Sunset Crater (e.g., Western bluebirds, Townsend’s solitaires, and American robins). Because many of these birds are likely to feed on juniper berries as well as the fruits of mistletoes, avian dispersers may spend more time on female junipers than male junipers. As a consequence, more mistletoe seeds may be deposited, germinate, and grow on female trees than male trees. However, this hypothesis is not supported by the fact that the mistletoe densities of male and female junipers at the nearby less stressful site were not significantly different although the same avifauna was present. If differential dispersal according to tree gender was occurring, female junipers would be expected to have higher mistletoe levels at this site as well as the stressful site.

A second hypothesis more consistent with our data is that mistletoe growth and survival is greater on female trees than on male trees when the trees are growing in a stressful environment. If female junipers are under greater stress than male junipers, as in other dioecious plants (Stark 1970; Hikmat et al. 1972; Freeman and MacArthur 1982), females may be least able to resist mistletoe attack. Other members of the genus *Phoradendron* are known to occur at higher densities in arid areas with low moisture levels and reduced tree growth (Knutson 1983). Many researchers have also documented increased incidence of herbivores and parasites on stressed plants (e.g., White 1969, 1976). Furthermore, at similar sites to those used in this study, Mopper et al. (1991),

Mopper and Whitham (1992), and Christensen and Whitham (1991) found herbivore loads on pinyon pine in the cinders at Sunset Crater to be several orders of magnitude higher than in nearby off-cinder soils. Our finding that sex-biased mistletoe loads occurred only at the stressful cinder site is consistent with these other studies.

Our results differ from studies on sex-biased herbivory in which male plants have been shown to experience higher levels of herbivory than females (Bawa and Opler 1978; Boecklen et al. 1990); but are similar to studies of fungal pathogens in which pathogens often attain higher densities on female plants (Lee 1981; Lovett Doust and Lovett Doust 1985). Although the mechanisms of sex-biased attack have not been documented for fungi or herbivores, lower herbivore loads on female plants have been correlated with higher levels of secondary compounds in these plants (Bawa and Opler 1978, Boecklen et al. 1990). The importance of chemically-based host plant defenses in deterring mistletoe parasitism is difficult to evaluate. Dawson and Ehleringer (1991) showed that mistletoe germination was inhibited by extracts from host plant foliage, suggesting a chemically-based defense. However, Khanna et al. (1968) found no significant relationship between host plant mistletoe levels and phenolic levels in five tree species. Elucidation of the mechanisms of sex-biased attack by plant parasites, fungi, and herbivores will require further research on each of these taxa.

In summary, we have shown that high levels of mistletoe parasitism are correlated with low levels of mycorrhizae in both male and female juniper trees. We have also shown that female junipers experience three-fold higher levels of mistletoe parasitism than male junipers when growing in a stressful environment, and that the negative association between mistletoe and mycorrhizae is slightly stronger in female trees. If mistletoes cause reduced mycorrhizal colonization, the impacts of mistletoe infestation on plants could be far greater than just those experienced through the loss of water and nutrients to the parasite. In addition, the sexual differences we observed not only suggest that male and female trees represent fundamentally different resources to mistletoe parasites in a stressful environment, but also that males and females may respond differently to the same levels of parasite attack.

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