Gender-Related Differences in Gas Exchange are not Related to Host Quality in the Xylem-Tapping Mistleoe, Phoradendron juniperinum (Viscaceae)

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GENDER-RELATED DIFFERENCES IN GAS EXCHANGE ARE NOT RELATED TO HOST QUALITY IN THE XYLEM-TAPPING MISTLETOE, PHORADENDRON JUNIPERINUM (VISCACEAE)[1]

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Male and female individuals of dioecious species often differ in morphology, physiology, growth, and habitat distribution. Where habitat distribution differences have been demonstrated, female plants generally occupy those habitats with greater resource availability ("rich" habitats). Gender-specific habitat preferences are often presumed to be a consequence of greater resource requirements, per gamete, of female reproduction. Previous work has shown that *Phoradendron juniperinum*, a xylem-tapping dioecious mistletoe that parasitizes *Juniperus* species in western North America, displays the opposite pattern: males are relatively more numerous than females in richer sites (i.e., branches with relatively high light and low evaporative demand within the host tree). We report here differences in host ("site") quality and gas-exchange properties between the sexes. To minimize environmental variation, all measurements were made on sunlit foliage between 9:00 a.m. and 2:00 p.m. Males had significantly higher photosynthetic rates (4.0 [SE = 0.2] μmol m^{-2} sec^{-1}) than either females (2.9 [0.3] μmol m^{-2} sec^{-1}) or nonreproductive individuals (3.0 [0.2] μmol m^{-2} sec^{-1}). Female photosynthetic rates were not statistically different from those of nonreproductive individuals. No concomitant differences in stomatal conductance were observed. Gas exchange data were independently confirmed by significant differences in carbon isotope ratio (δ^{13}C). Gender-related differences were not related to host quality as measured by foliar N, foliar δ^{13}C, or water potential of the host tree. The fate of the additional photosynthate in males is unknown, but we discuss the possibility that carbon costs of reproduction in males have been underestimated in past work.

Recent studies aimed at understanding the physiological ecology of the xylem-tapping mistletoes (including *Phoradendron juniperinum*) have revealed a complex set of traits interpreted as adaptations for parasitic life. Pulse-chase experiments using radioactive carbon on seven *Phoradendron* species revealed that no immediate photosynthate is transported from mistletoe to host, or vice versa (Hull and Leonard, 1964), and therefore *Phoradendron* was regarded as a "water parasite," dependent on its host only for water and perhaps mineral nutrients. Subsequent gas exchange measurements showed that photosynthetic water-use efficiency (A/E), expressed as the molar ratio of photosynthesis (A) to transpiration (E), was much lower in mistletoes than in their hosts (Schulze and Ehleringer, 1984; Ullmann et al., 1985). Low water-use efficiency has been described as a mechanism for gathering sufficient nitrogen from host xylem sap (Schulze and Ehleringer, 1984; Ehleringer et al., 1985) as well as to increase uptake of dissolved carbon from host xylem sap (Marshall and Ehleringer, 1990). Recent results suggest that partial heterotrophy may be more common among xylem-tapping hemiparasites than initially believed (see Marshall and Ehleringer, 1990; Schulze et al., 1991). It has also

been interpreted as a consequence of the low costs of water uptake by mistletoe haustoria (Givnish, 1986). It remains unclear which resource (nitrogen, carbon, or water) most influences mistletoe fitness; however, it is clear that xylem-tapping mistletoes are benefited by, and indeed may require, the resources they obtain from the host xylem due to their low water-use efficiency.

A previous investigation of the reproductive biology of *P. juniperinum* uncovered unusual characteristics as well. Unique among the mistletoes studied to date, the sex ratio of *P. juniperinum* populations is significantly male-biased (Dawson, Ehleringer, and Marshall, 1990). The mechanism by which this bias arises remains unclear, although it is known that sex in the related genus *Viscum* is genetically determined (Barlow and Wiens, 1975, 1976; Wiens and Barlow, 1979; Schink and Mechelke, 1989), making "sex-choice" in mistletoes an unlikely explanation. A detailed analysis of sex-ratio variation in individual host trees revealed a consistently male-biased sex-ratio in the south- and east-facing quadrants of the largest trees (Dawson, Ehleringer, and Marshall, 1990). These microsites are expected to be most favorable for growth due to their favorable energy balance. This finding opposes much of the literature on dioecious plants, which has almost uniformly shown that females more often occupy the highest quality sites (Dawson and Bliss, 1989; Dawson, Ehleringer, and Marshall, 1990; Dawson and Ehleringer, 1993). Segregation of the sexes between sites that differ in quality has been interpreted as an adaptive consequence of the presumed higher resource requirements (costs) that females incur for successful flowering and subsequent fruit maturation. Because males do not carry the burden of fruit maturation, their reproductive costs are confined to a shorter, and earlier, portion of the
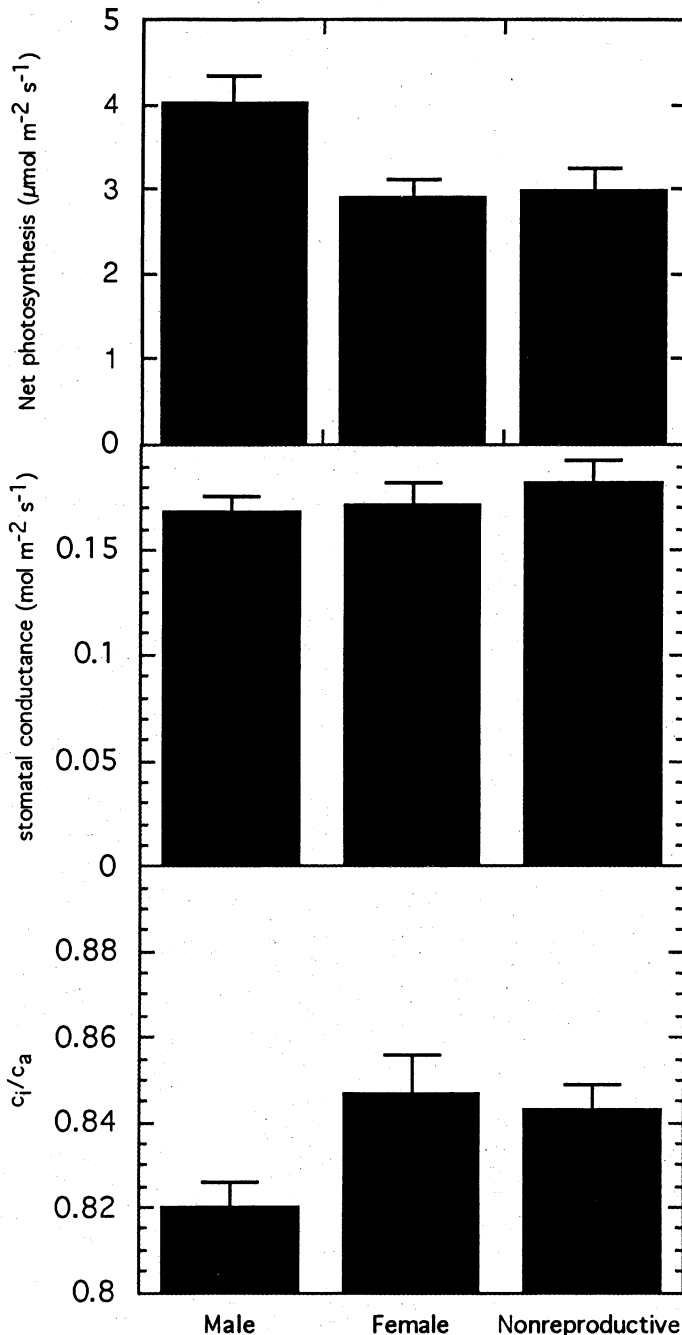
Fig. 1. Net photosynthesis, stomatal conductance, and c_i/c_a of male, female, and nonreproductive mistletoes (*Phoradendron juniperinum*). Photosynthetic rates and c_i/c_a differed significantly between males and females or nonreproductive individuals.

of increased sink strength driven by maturing fruits (Kramer and Kozlowski, 1979; Dawson and Bliss, In press).

Mistletoes provide an ideal test of the effect of changes in habitat quality on ecological and physiological characteristics because the mistletoe's "habitat" is almost entirely defined by the structural or physiological characteristics of its host and its position within the crown of the host (Dawson, Ehleringer, and Marshall, 1990). This circumvents the need to describe belowground conditions; the "soil" for a mistletoe is the xylem of its host.

Our purpose in this study was to test whether gender-related differences in physiological performance occurred in *Phoradendron juniperinum* and if so, whether they were consistent with previous findings, i.e., that females outperform males in higher quality microsites to meet their higher costs of reproduction (Dawson and Bliss, 1989; Dawson and Ehleringer, 1993). Specifically, we tested the hypothesis that female plants would have higher photosynthetic rates than males, which would in turn exceed nonreproductive individuals. Stomatal conductance, nitrogen concentrations, and carbon isotope ratios of mistletoes were also measured to aid in interpreting the photosynthetic data. Differences in habitat quality due to branch position were avoided by measuring only mistletoes growing in full sun during the late morning, i.e., those in the outer branches of the southeast quadrant of the crown. Habitat quality was therefore equivalent to host quality, which was also tested by measuring host characteristics. These characteristics included predawn water potentials, nitrogen concentrations, and carbon isotope ratios of host trees.

MATERIALS AND METHODS

Photosynthetic gas exchange was measured on one mistletoe plant growing on each of 42 host trees. Host trees were chosen from within a 1-ha stand dominated by *Juniperus osteosperma* located near Coral Pink Sand Dunes State Reserve, in southern Utah (lat. 37°3'N, long. 112°45'W, elevation 1,855 m). Trees were chosen randomly from among the trees in the stand that were 1) infected with mistletoe and 2) more than 5 m from the nearest selected tree. Mistletoes on the host trees were chosen subjectively for vigor and sunlit foliage. Photosynthetic gas exchange was measured with a LICOR-6200 Portable Photosynthesis System when foliage was in full sunlight, between 9:30 a.m. and 1:00 p.m. MST (Mountain Standard Time). Measured leaf tissue was collected, returned to the laboratory, and weighed. Projected area of a subsample was also measured using a LICOR 3100 Leaf-Area Meter. Because specific leaf area ($cm^2 g^{-1}$) was inversely correlated with size of the sample, regression equations with positive y-intercept were used to estimate leaf area from leaf weight. Gas exchange measurements analyzed both on a leaf area and a weight basis yielded similar results; in fact, *t*-tests were almost identical. Leaf tissue was ground and subsamples analyzed for Kjeldahl nitrogen (Lillivek, 1970) and the ratio of the stable isotopes of carbon ($\delta^{13}C$) (Ehleringer and Osmond, 1989). Water potential of the host trees was measured before dawn and in midafternoon. Samples of foliage from host trees were collected, and a subsample was analyzed for nitrogen and $\delta^{13}C$.

growing season (Lloyd and Webb, 1977; Dawson and Bliss, 1989; Dawson, Ehleringer, and Marshall, 1990). Dawson and Ehleringer (1993) discuss in detail possible reasons underlying the differential distribution of the sexes.

Among the resources presumed needed in greater quantities by females is photosynthate. One might therefore expect that selection on improved carbon acquisition, via higher photosynthetic rates, might be particularly favorable for females compared to males (Dawson and Ehleringer, 1993). Such differences might also arise as a result

TABLE 1. *T-tests comparing photosynthetic rates (μmol m^{-2} sec^{-1}) of male, female, and nonreproductive individuals*

Comparison	t	df	Significance
Female-Male	2.7	103	0.007
Female-Nonreproductive	0.2	81	0.815
Male-Nonreproductive	3.0	116	0.004

Proportion of heterotrophic (host) carbon in the mistletoe tissues was estimated using the procedure of Press et al. (1987). This procedure demands an estimate of $\delta^{13}C$ of mistletoe photosynthate, which is calculated from the known linear relationship between c_i/c_a ratios and $\delta^{13}C$ (Farquhar, O'Leary, and Berry, 1982). An estimate of actual $\delta^{13}C$ of host tissues is also required. Because $\delta^{13}C$ of the two sources of photosynthate are conserved, it is possible to calculate the relative contributions of each. The data are discussed in this paper as proportional heterotrophy.

Measurements were made only when both sexes of mistletoe plants could be identified with certainty, between the appearance of male flowers, in late July or early August, and their senescence, sometime in September. Four measurements were made between July 1988 and August 1990. We tested for differences between males, females, and nonreproductive individuals using simple t-tests.

RESULTS

Contrary to expectation, photosynthetic rates were significantly lower in female mistletoe plants when compared to males. There were no differences in photosynthetic rates between females and nonreproductive individuals (Fig. 1; Table 1). Male plants maintained the highest photosynthetic rates when compared to either females or nonreproductive individuals. This pattern was consistent throughout all of our sampling periods, although the differences were not always statistically significant for a given sampling date. The pattern was also found whether photosynthetic rates were expressed per unit leaf area (Fig. 1) or per unit weight (males 4.7 [SE = 0.3] nmol g^{-1} sec^{-1}, females 3.3 [0.4] nmol g^{-1} sec^{-1}, nonreproductives 3.4 [0.3] nmol g^{-1} sec^{-1}). Analysis of stomatal conductance measurements revealed no differences between sexes or between reproductive and nonreproductive individuals. Differences in photosynthetic rates, but no differences in stomatal conductances, resulted in lower c_i/c_a ratios in male plants (with highest photosynthetic rates; Table 2). The $\delta^{13}C$ of tissues collected from the mistletoes also differed between male and female plants and between female and nonreproductive plants (Tables 2, 3). Proportional heterotrophy was not different among the sexes,

TABLE 3. *T-tests comparing ancillary gas-exchange measurements of male, female, and nonreproductive mistletoe plants*

Comparison	t	df	Significance
Female-Male			
Stomatal conductance (mol m^{-2} s^{-1})	0.21	105	0.834
c_i/c_a	2.60	109	0.011
$\delta^{13}C$ (‰)	2.60	77	0.011
Specific leaf area (cm^2/g)	1.05	109	0.295
Nitrogen (mmol g^{-1})	0.35	53	0.726
Heterotrophy index	0.32	73	0.750
Female-Nonreproductive			
Stomatal conductance (mol m^{-2} s^{-1})	0.68	82	0.500
c_i/c_a	0.33	83	0.745
$\delta^{13}C$ (‰)	2.07	66	0.042
Specific leaf area (cm^2/g)	0.53	85	0.598
Nitrogen (mmol g^{-1})	0.50	37	0.621
Heterotrophy index	0.730	63	0.468
Male-Nonreproductive			
Stomatal conductance (mol m^{-2} s^{-1})	1.63	118	0.106
c_i/c_a	2.74	120	0.007
$\delta^{13}C$ (‰)	0.29	87	0.770
Specific leaf area (cm^2/g)	1.11	108	0.268
Nitrogen (mmol g^{-1})	0.42	52	0.673
Heterotrophy index	1.190	84	0.237

nor were nitrogen concentrations or specific leaf areas (Tables 2, 3).

Host quality was assessed by measuring the degree of host plant water stress and the foliar nitrogen and $\delta^{13}C$ of host leaf tissues (Table 4). Predawn water potentials, host $\delta^{13}C$, midday water potentials, and host foliar nitrogen concentrations were not statistically different between the two sexes. By these measures, therefore, hosts of male and female plants were indistinguishable.

DISCUSSION

It is often presumed that female individuals of dioecious plants have higher resource requirements than males because of the need not only to flower, but also to mature fruit (reviewed by Lloyd and Webb, 1977). As an extension of this argument, one might predict that reproductively active plants, be they female or male, would require more resources than nonreproductive plants, although the magnitude of any difference would be less when males are compared to nonreproductive plants than when females are compared to nonreproductive plants (Silvertown, 1987). The findings we report here do not fit these predictions, and therefore both the data and the basis of

TABLE 2. *Comparison among male, female, and nonreproductive mistletoe plants of ancillary measurements. Data collected as in Table 1, except that a subset was analyzed for nitrogen and $\delta^{13}C$*

Variable	Female $\bar{X}$	Female SE	Male $\bar{X}$	Male SE	Nonreproductive $\bar{X}$	Nonreproductive SE
$\delta^{13}C$ (‰)	−27.4	0.15	−26.9	0.13	−27.0	0.17
Specific leaf area (cm^2/g)	11.15	0.14	11.36	0.12	11.03	0.16
Nitrogen (mmol g^{-1})	0.58	0.09	0.61	0.03	0.64	0.06
Heterotrophy index	0.60	0.02	0.59	0.02	0.62	0.02

TABLE 4. *Comparison of host quality among male, female, and nonreproductive mistletoe plants. Data as in Table 1*

Variable	Female		Male		Nonreproductive	
Xylem pressure potential (MPa)						
Predawn	−0.98	0.12	−0.98	0.08	−0.87	0.07
Midday	−2.36	0.08	−2.41	0.07	−2.30	0.07
Host $\delta^{13}C$ (‰)	−24.2	0.16	−24.4	0.10	−24.7	0.22
Host N (mmol g^{-1})	0.55	0.02	0.53	0.03	0.54	0.04

the presumptions may require further consideration and refinement.

Our data demonstrate that mean photosynthetic rates of males were higher than those of females, and females were similar to nonreproductive individuals on every sampling date. The differences in photosynthetic rates at the same stomatal conductance led to differences between the sexes in c_i/c_a. Differences in c_i/c_a among plants should also show up as differences in $\delta^{13}C$, because in many nonparasitic C_3 plants, $\delta^{13}C$ provides a time-integrated, or average estimate of c_i/c_a (Farquhar, O'Leary, and Berry, 1982). However, with parasitic plants, such corroboration is possible only if proportional heterotrophy and host $\delta^{13}C$ are similar. These conditions were met for the male-female comparison, and the differences indeed match the theoretical pattern previously outlined (Marshall and Ehleringer, 1990). The evidence presented here shows that male mistletoes maintain a significantly lower instantaneous and time-integrated c_i/c_a (a less negative in $\delta^{13}C$) than do female mistletoes (Tables 2, 3). The data obtained for nonreproductive individuals do not meet the conditions described above, however, and therefore they cannot be compared. Comparison of the $\delta^{13}C$ of male and female mistletoes to previously published data for *Phoradendron juniperinum* (Schulze and Ehleringer, 1984; Ehleringer et al., 1985; Marshall and Ehleringer, 1990) shows a high degree of similarity, and thus we are confident in the gas-exchange differences we have described.

These findings required us to reconsider the notion that female mistletoes may have a higher set of resource requirements to meet their reproductive demands than males. Dawson and coworkers (1990) earlier noted that the sex ratio of this population of mistletoes tended to be male biased in microsites that were conjectured to be of higher quality for the mistletoes. They pointed out that this pattern was in marked contrast to that commonly reported in the literature. Furthermore, they estimated higher reproductive effort (RE; mass of reproductive tissues divided by mass of current growth) among females than among males. They suggested that the explanation for the marked differences in RE among the sexes might lie in our incomplete understanding of the physiological ecology of the mistletoes (Dawson, Ehleringer, and Marshall, 1990). In particular, they proposed that the sexes might differ in the proportion of resources they obtained from their host, including carbon obtained from the xylem. Data presented here invalidate this hypothesis, however, as proportional heterotrophy between the sexes was not different (Tables 2, 3), nor were differences in host quality detected (Table 4).

It is conceivable that xylem carbon concentrations might be higher in the branches supporting females, compensating for their lower photosynthetic rates. Marshall and Ehleringer (1990) presented the following equation to describe mistletoe $\delta^{13}C$, accounting for host carbon from the xylem:

$$\delta^{13}C_{mistletoe} = \frac{[A\delta^{13}C_{predicted}] + [Ec_{xylem}\delta^{13}C_{xylem}]}{A + Ec_{xylem}} \quad (1)$$

where $\delta^{13}C_{predicted}$ is the value obtained using the c_i/c_a data in the equation of Farquhar, O'Leary, and Berry (1982), E = transpiration rate, c_{xylem} = the concentration of carbon dissolved in the xylem stream, $\delta^{13}C_{xylem}$ = the $\delta^{13}C$ of xylem carbon, and A is the photosynthetic rate. The equation can be rearranged to solve for xylem carbon concentrations, yielding:

$$c_{xylem} = \frac{A(\delta^{13}C_{predicted} - \delta^{13}C_{mistletoe})}{E(\delta^{13}C_{mistletoe} - \delta^{13}C_{xylem})}. \quad (2)$$

Using equation 2, we estimated xylem carbon concentrations, assuming a constant vapor pressure deficit of 30 mbar bar^{-1}, and using the means in Tables 1 and 3 and host $\delta^{13}C$. This yielded values of 39 mM C for females, 68 mM for males, and 57 mM for nonreproductive individuals. This estimate leads us to suggest that it is unlikely that females obtain heterotrophic carbon at higher rates than males or nonreproductive individuals; in fact, the opposite appears to be true; therefore the hypothesis that xylem carbon uptake compensates for differences in photosynthesis can be rejected. Males gain more carbon from both autotrophy and heterotrophy.

In this experiment, differences in habitat between males and females were either controlled, by sampling only plants in full sunlight during late morning, or were undetectable, as indicated by the host quality data (Table 4). Thus, the physiological basis for the difference in photosynthetic rates among sunlit males, females, and nonreproductive individuals remains to be identified.

What is the fate of the extra photosynthate in male plants? One possibility is that males simply accumulate biomass faster than females; no data are currently available on this point. A second possibility is that the additional photosynthate is used for male reproduction. Published evidence demonstrating differences in reproductive costs between sexes provides little insight, partly due to methodological difficulties. There is little doubt that reproductive costs per gamete are higher in female than in male plants. No pollen grain has ever been shown to contain more resources than a seed. However, costs of reproduction are determined not only by cost per gamete, but also by number of gametes produced. Wallace and Rundel (1979) estimated that females of an evergreen shrub (*Simmondsia chinensis*) would have lower costs of reproduction than males, but only if seed set were below 30%. Similarly, Hancock and Bringhurst (1980) and Dawson and Bliss (1989) presented data showing that reproductive effort can be greater in male plants than in female plants on the same site (see also review by Goldman and Willson, 1986). This seems particularly likely given that mistletoes are wind-pollinated. Wind-pollinated species often have high pollen/ovule ratios, presumably due to inefficient pollen transfer (Cruden, 1977; Givnish, 1980).

Estimation of reproductive effort is difficult and likely to underestimate male reproductive effort. An estimate can be obtained by measuring biomass of the tissues associated with reproduction, or with its nutrient or caloric content (Dawson and Bliss, 1989). However, it is likely that biomass underestimates total costs, especially of male function (Goldman and Willson, 1986). Male reproductive effort is underestimated because the construction costs of lipid-rich pollen grains are likely higher (on a per-weight basis) than carbon-based costs of pistillate structures. A second methodological problem is that reproductive structures frequently contain chlorophyll and can fix re-

spired CO_2 (Bazzaz, Carlson, and Harper, 1979) or even have net carbon assimilation (Galen, Dawson, and Staton, unpublished data). Previous work on the seeds and seed germination in *Phoradendron juniperinum* demonstrated that stomata are present on the "green" epicotyls (Dawson and Ehleringer, 1991) and may be involved in gas exchange early in the life of a mistletoe plant. Carbon fixation or refixation in fruits or seeds could substantially reduce construction costs and thereby reduce the overall cost of reproduction in female mistletoes. Again, accounting for CO_2 fixation by fruit could reduce our estimates of female reproductive effort. Finally, a greater proportion of the resources allocated to female reproduction are allocated late in the growing season, after male reproductive effort is already complete. Early expenditure of resources increases the time during which lost productivity is compounded, which again means that there is a greater loss in males (Gross and Soule, 1981). Each of the above considerations increases actual costs of male reproduction over what one would estimate from biomass comparisons. We are led to agree with Goldman and Willson (1986) that "the physiological expense of being male in some organisms may be far higher than what is generally expected."

Applying these ideas to the biology of *Phoradendron juniperinum*, we note that published estimates of reproductive effort for females of this species are about double that of males (Dawson, Ehleringer, and Marshall, 1990). However, these data are susceptible to each of the criticisms described above. We have not yet tried to measure differences in energy content between pollen and seed of *P. juniperinum*, CO_2 fixation or refixation, or the greater compounding of photosynthate losses due to the earliness of male flowering. We recognize that earlier estimates of reproductive effort of this species, based solely on biomass, may be low (in Dawson, Ehleringer, and Marshall, 1990), and believe that a more rigorous analysis of reproductive effort in mistletoes might bring our understanding of mistletoe reproductive biology more in line with the gas exchange data presented here.

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