

Photosynthesis and water relations of the mistletoe, *Phoradendron villosum*, and its host, the California valley oak, *Quercus lobata*

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Summary. Water vapor and CO₂ exchange characteristics were studied in *Phoradendron villosum*, a hemiparasitic mistletoe and its host, *Quercus lobata*. The hemiparasite had stomatal conductances equal to or higher than the host but a much lower capacity to fix carbon. Respiration was high in the mistletoe relative to maximum photosynthesis because of the high leaf specific weight (weight per unit area) in this species. The temperature optima for photosynthesis were similar in both species although photosynthesis in *Phoradendron* declined more steeply below 20 degrees C. Consequences of the high conductance and low rate of photosynthesis in the mistletoe include a low water-use efficiency and a relatively high internal concentration of CO₂.

tor had higher rates of photosynthesis, respiration, higher water deficits, and lower osmotic potentials than its host *Acacia grasbyi*. Rates of transpiration were slightly higher in the host.

Here I describe the carbon dioxide exchange and transpiration of a hemiparasite *Phoradendron villosum* Nutt., the oak mistletoe, in relation to that of its host, *Quercus lobata* Née., the California valley oak. This work shows that the hemiparasitic *P. villosum* has a significantly lower capacity to fix carbon than its host despite a relatively high rate of transpiration. These results are considered in the context of the host-parasite relationship and plant water-use efficiency.

Introduction

Mistletoes are hemiparasites. As such, they rely upon their hosts for a source of water and minerals but produce, to at least a certain extent, their own supply of assimilate (Kuijt 1969). Despite this unusual partitioning of plant water and carbon economy, there have been few recent studies of the water relations or photosynthetic capacities of mistletoes or other hemiparasitic species. Early work (Kamerling 1914) indicated that the European mistletoe *Viscum album* had an unusually high rate of transpiration although later work (Härtel 1937) showed that this rate was quite variable. Glatzel (1983) has recently reviewed much of the early work dealing with mistletoe water relations and has shown that stomata of the deciduous mistletoe *Loranthus europaeus* close at a more negative water potential than those of its host *Quercus robur*.

Our knowledge of the photosynthetic capacities of hemiparasitic plants also remains limited. Freeland (1943) demonstrated net CO₂ uptake by an American mistletoe while Seledzhana and Galan-Fabian (1961) showed with ¹⁴CO₂ feeding experiments that *Viscum* also fixes carbon. They noted that the mistletoe translocates little photosynthate to its host, suggesting that the *Viscum* infection is not mutualistic. Hull and Leonard (1964) used the same technique to show that photosynthetic capacity in several species of *Phoradendron* was greater than in several species of the dwarf mistletoe *Arceuthobium*. *Phoradendron* apparently did not utilize host photosynthate while *Arceuthobium* did.

In a more comprehensive study, Hellmuth (1971) showed that the Australian stem hemiparasite *Amyema nes-*

Methods

Phoradendron villosum occurs on *Quercus lobata* and other species of oak throughout California (Munz 1959). Work described here was carried out at the Jasper Ridge Biological Preserve of Stanford University. Jasper Ridge is located in the foothills of the Santa Cruz mountains 12 km west of Palo Alto, California, U.S.A. The mediterranean-type climate consists of hot, dry summers and cool, wet winters.

CO₂ and water vapor exchange measurements of host and hemiparasite were carried out in the field in July and August of 1982 with a portable steady-state gas exchange system described by Field et al. (1982). This system consists of a temperature-controlled cuvette, infrared gas analyzer and water-filtered light source. Humidity is added to the cuvette by leaf transpiration and controlled by varying the flow rate of dry air containing an ambient (~320 µl/l) concentration of CO₂. Ambient levels of CO₂ are maintained by adding a stream of 1% CO₂ in nitrogen to the cuvette to replace carbon dioxide assimilated by the leaf. Replicate measurements were made on several leaves of each species for each experimental manipulation of light, temperature or vapor concentration gradient. Typical response curves are shown in the figures.

Transpiration (*E*), net photosynthesis (*A*), stomatal conductance (*g*) and other gas exchange parameters were calculated as described in Field et al. (1982).

Stomatal pore lengths and densities were measured from acetate negatives (clear nail polish) of silicone impressions (Xantopren blue, Unitek Corporation, Monrovia, Ca.) of fresh leaf material.

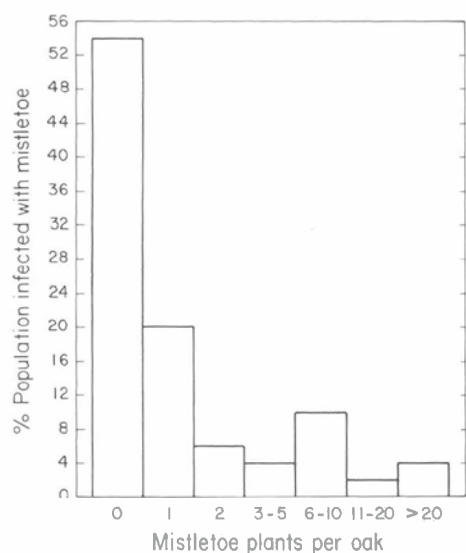


Fig. 1. Distribution of *Phoradendron* on 50 *Quercus lobata* individuals

Results and discussion

Frequency of infection

Parasitism of *Q. lobata* and other species by *Phoradendron* is common at Jasper Ridge. Although I report only on *Phoradendron* utilizing *Q. lobata* as a host, its occurrence was noted on *Q. douglassii*, *Q. agrifolia* and *Q. durata* as well.

Fifty *Q. lobata* trees at Jasper Ridge were surveyed for the presence of *P. villosum* infections in February of 1982 by running transects through the oak savanna until the requisite number of individuals were encountered. The evergreen *Phoradendron* is easily visible among the bare branches of its deciduous host at this time of year. Just under one-half of the *Q. lobata* trees surveyed contained at least one *Phoradendron* plant, while 16% of the oaks were host to 6 or more mistletoe plants (Fig. 1). The occurrence of *Phoradendron* on the *Quercus* hosts was not random (Poisson), $P < 0.05$, Kolmogorov-Smirnov test. Instead, the distribution of *Phoradendron* was clumped, with two of the *Quercus* plants host to 49% of all the mistletoe plants encountered. These hosts were not otherwise distinctive in size or habitat, suggesting that dispersal or host susceptibility factors are important in mistletoe distribution.

Gas exchange measurements

Photosynthetic and transpiration rates of the host plant and hemiparasite were determined as functions of light, leaf temperature and vapor concentration gradient (ΔW). Each of these responses is discussed in turn.

Light

CO_2 exchange and stomatal conductance of *Q. lobata* and *Phoradendron* on a unit area basis are shown as a function of photosynthetically active photon flux in Figs. 2A and B. The relatively high light intensity required for saturation

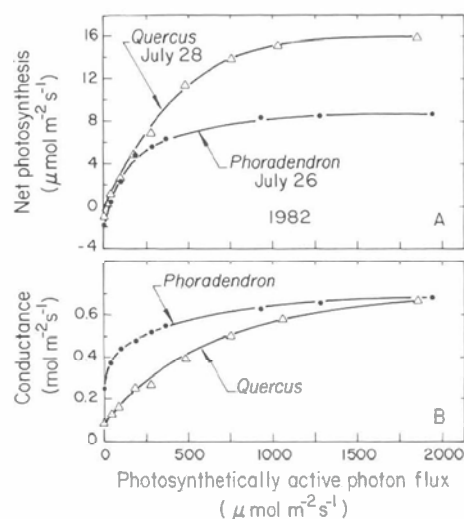


Fig. 2. Leaf photosynthesis and conductance of *Phoradendron* and *Quercus* as a function of photosynthetically active photon flux. $\Delta W = 10 \text{ mmol H}_2\text{O mol}^{-1} \text{ air}$, leaf temperature = 25 degrees C

Table 1. Photosynthetic characteristics of *Phoradendron* and *Quercus*

	<i>Phoradendron</i>	<i>Quercus</i>
Maximum Rate ^a ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	8.46 $\pm$ 1.30 leaves 8.4 stem	16.76 $\pm$ 1.73
Dark Respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$ at 25 C)	-1.84 $\pm$ 0.19	-1.05 $\pm$ 0.10
Photosynthetically active photon flux for one-half maximum rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	180 $\pm$ 20	420 $\pm$ 80

(Values $\pm$ one std. dev., $n=8$ for maximum rate and dark respiration figures, $n=3$ for one-half maximum rate photon flux.)

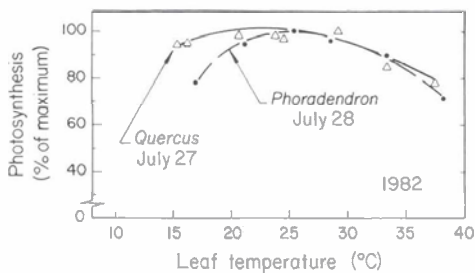
^a PAPF = 1,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $\Delta W = 10 \text{ mmol H}_2\text{O mol}^{-1} \text{ air}$, leaf temperature = 25 degrees C

and high rate of net CO_2 uptake observed in *Quercus* (Table 1) are typical of leaves adapted to sunny conditions, while the much lower maximum rate and lower light intensity necessary for saturation of the photosynthetic apparatus in *Phoradendron* are more typical of species adapted to shade (Björkman 1981). The leaves in *Phoradendron*, however, unlike those in most shade plants have a high tissue weight per unit area (Table 2). The leaf specific weight (weight per unit area) of mistletoe is almost 3 times that of *Q. lobata*. This means that the photosynthetic rate of *Phoradendron* on a weight basis is extremely low (only 1/5 that of its *Quercus* host). This very high leaf specific weight also accounts for the relatively high rate of dark respiration of *Phoradendron* (Fig. 2A) on a unit area basis. A consequence of the high leaf specific weight and low maximum rate of photosynthesis is that the daily leaf carbon balance per unit area is considerably lower in the mistletoe than in its host. The green stems of *Phoradendron* are capable of net photosynthesis (Table 1), partially compensating for the less favorable carbon balance of the leaves.

Table 2. Leaf characteristics of *Phoradendron* and *Quercus*

	<i>Phoradendron</i>	<i>Quercus</i>
Leaf Size (cm ²) <i>n</i> = 18	4.03 ± 1.52	25.48 ± 10.29
Specific wt. (g m ⁻²) <i>n</i> = 18	411 ± 64	144 ± 12
Stomatal Density (stoma mm ⁻²) ^a	58.4 ± 14.5 (leaf) 6.4 ± 4.2 (stem)	389 ± 46
Stomatal Pore Length (μm) <i>n</i> = 360	28.8 ± 3.1	14.2 ± 2.3

(All values ± one std. dev.)

^a Measured at 6 locations on 12 leaves**Fig. 3.** Normalized net photosynthesis as a function of temperature in *Phoradendron* and *Quercus*. PAF = 1,000 μmol m⁻² s⁻¹, ΔW = 5 mmol H₂O mol⁻¹ air

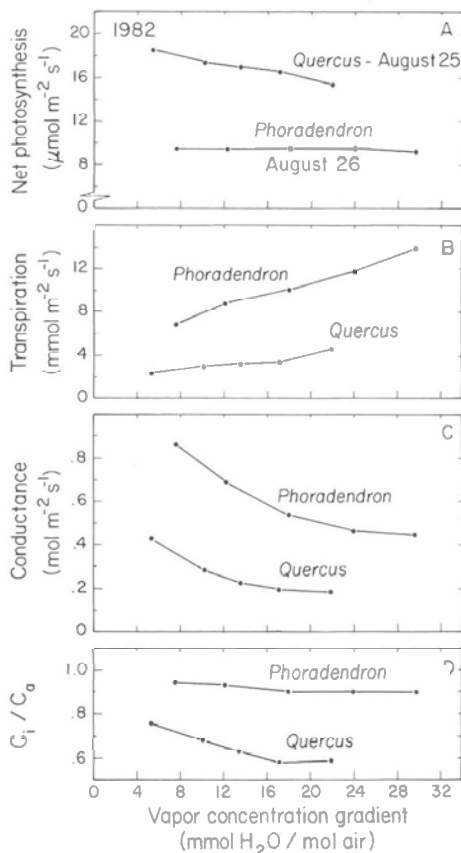
Despite the large differences in net CO₂ uptake between host and hemiparasite, stomatal conductances in both species are similar (Fig. 2B). Stomata are larger but less numerous in *Phoradendron* than *Quercus* (Table 2). Stomatal conductances are discussed in more detail below with reference to the water use efficiency of both species.

Temperature

The responses of net photosynthesis in *Phoradendron* and *Quercus* to temperature are qualitatively similar (Fig. 3). The optimum range of temperatures for maximum photosynthesis is apparently somewhat broader in the oak than in the mistletoe, however. Greater than 90% of the maximum rate of photosynthesis is observed in the oak with leaf temperatures ranging from 15 degrees C (the lowest leaf temperature measured) to approximately 32 degrees C. The temperature response of the mistletoe was similar although it appeared to drop off steeply below about 20 degrees C. Wagener (1957) has noted the sensitivity of *Phoradendron* to low temperatures.

Vapor concentration gradient

In contrast to *Quercus*, net CO₂ uptake in *Phoradendron* declines only slightly with an increasing leaf-air vapor concentration gradient (Fig. 4A). This is not because *Phoradendron* stomata fail to respond to an increasing ΔW, but because of the high conductance of this species relative to its photosynthetic capacity (Fig. 4C). At a light intensity of 1,000 μmol/m²s, the stomatal conductance of *Phoradendron* is approximately 2 and one-half times that of its host

**Fig. 4A-D.** Net photosynthesis, transpiration, stomatal conductance to water vapor and ratio of intercellular CO₂ to external CO₂ as functions of leaf-air vapor concentration gradient. PAF = 1,000 μmol m⁻² s⁻¹, leaf temperature = 30 degrees C

while the net rate of CO₂ uptake in the mistletoe is only one-half that of the oak. Because of the high conductance and low photosynthetic rate, even at a ΔW of greater than 30 mmol H₂O/mol air, the internal concentration of CO₂ in *Phoradendron* is over 90% of that existing outside of the leaf. This contrasts sharply with the internal concentrations of CO₂ in *Quercus* (Fig. 4D).

The very high rate of transpiration combined with the low rate of net photosynthesis in *Phoradendron* means that *E/A*, the instantaneous water-use efficiency, of this species is very low. As Figs. 5A and B show, compared to its host, *Phoradendron* is indeed a profligate user of water. At a light intensity of 1,000 μmol/m²s and depending on the vapor concentration gradient, *Phoradendron* transpires from 3 to 5 times as much water as its host at the same ΔW per equivalent unit of photosynthesis. Figure 5b shows instantaneous water use efficiency (*E/A*) for the two species as light varies but at a constant ΔW of 8.5 ± 1 mmol H₂O/mol air. There is a large difference in water use efficiency (mols water transpired per mol carbon assimilated) even at the low light intensities which *Phoradendron* often experiences.

Cowan and Farquhar (1977) have suggested that the slope of the relationship between *E* and *A* (*dE/dA*) provides another test of the efficiency of water use in a plant. In their model, given a certain amount of water to be transpired throughout a day, carbon gain is maximized (water-use efficiency is optimized) if *dE/dA* is constant. *dE/dA* in *Phoradendron* and *Quercus* was evaluated by the method of Far-

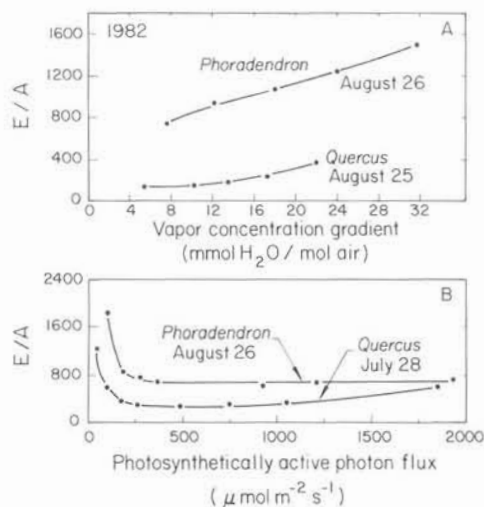


Fig. 5 A, B. Instantaneous water-use efficiency (E/A) of *Phoradendron* and *Quercus* as a function of ΔW and photosynthetically active photon flux.

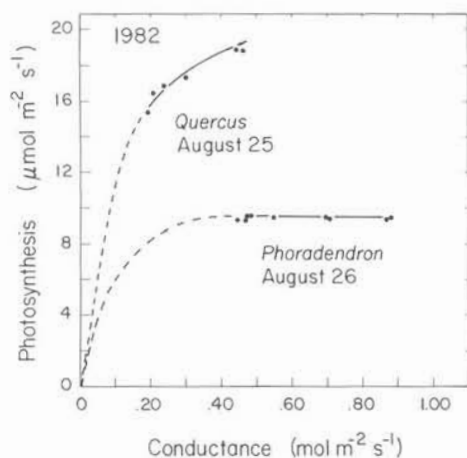


Fig. 6. Relationship between net photosynthesis and conductance in *Phoradendron* and *Quercus*. Values from ΔW curves.

quhar et al. (1980) and was fairly constant for these species. This is in agreement with the results of Farquhar et al. (1980), Hall and Schulze (1980), Williams (1981) and Field et al. (1982) who have shown that many plants control stomata to efficiently regulate water loss. The very small slope of the A/g relationship (Fig. 6) in *Phoradendron* means that the value of dE/dA is large but very sensitive to measurement error (if the slope was actually zero, dE/dA would be undefined). The actual value of dE/dA in *Phoradendron* ($\sim 30,000$) is far higher than that in *Quercus* (~ 500) and suggests that the mistletoe "sets" the amount of water to be used each day at a far higher value than its host. Why has *Phoradendron* set this value so high? Outside of the context of a host-parasite relationship, there are few reasons for this behavior. A plant that operates its stomata in such a manner would over the course of a season be out-competed by rivals with a greater absolute (E/A) water-use efficiency when water is limiting.

There may be several adaptive advantages, however, in a high and, as conventionally defined, inefficient rate of

transpiration in a hemiparasitic plant. First, of course, any increase in stomatal conductance will increase the concentration of CO_2 inside the leaf and thus carbon assimilation somewhat. The marginal gain of this strategy decreases, however, as conductance increases and its quite low at the conductances commonly observed in *Phoradendron* (Fig. 6). It appears unlikely that stomatal conductances are high in *Phoradendron* just to facilitate CO_2 exchange. Alternatively, with an apparently unlimited supply of water, *Phoradendron* could potentially modulate transpiration to control leaf temperature. With such control the leaves could remain closer to optimum temperatures for photosynthesis. *Phoradendron*, however, has a broad temperature optimum (Fig. 3) and a shady location within the host canopy. In addition, Field et al. (1982b) have shown that only a limited potential for transpirational cooling exists (~ 5 degrees C) even under the best of conditions. A final, perhaps more likely advantage of a high rate of transpiration, is that additional quantities of resources that are found in the host transpiration stream, such as mineral elements or hormones, are carried to the hemiparasite. Glatzel (1983) found that the mistletoe *Loranthus europaeus* accumulated on a leaf area basis more nutrients than its host, *Quercus petraea*. He attributed this accumulation to a higher rate of transpiration in the mistletoe than in the host and to the absence of phloem connections between the hemiparasite and host. Some mineral elements (specifically potassium) normally cycle back down the phloem but are prevented from doing so and thus accumulate for this reason as well. Mineral elements which accumulate in large quantities may be utilized in maintaining low osmotic potential so that total mistletoe leaf water potential remains more negative than that of the host.

The oak mistletoe, *Phoradendron villosum*, has a lower capacity to fix carbon than its host, the California valley oak, *Quercus lobata*. Maximum stomatal conductance of host and hemiparasite are similar, although under identical conditions, mistletoe conductance is usually greater. These parameters result in an unusually high ratio of intercellular CO_2 concentration to that occurring outside of the leaf in *Phoradendron* and to a less efficient use of water by this species in the production of photosynthate.

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