Oecologia (Berlin) (1986) 68:279–284

Oecologia

Comparative water use and nitrogen relationships in a mistletoe and its host *

James R. Ehleringer [1], Craig S. Cook [1], and Larry L. Tieszen [2]

[1] Department of Biology, University of Utah, Salt Lake City, UT 84112, USA
[2] Department of Biology, Augustana College, Sioux Falls, SD 57197, USA

Summary. The impact of the xylem-tapping mistletoe *Phoradendron juniperinum* on the nitrogen and water relations of its host *Juniperus osteosperma* was investigated under natural field conditions. Leaf conductance, leaf water potential, and leaf Kjeldahl nitrogen contents were followed through the growing season on mistletoes, infected junipers (separating infected from uninfected stems) and uninfected junipers. Infected trees experienced lower leaf water potentials than uninfected trees and also had lower leaf conductances and lower leaf nitrogen contents. Infected juniper stems had higher conductances than uninfected stems. Mistletoes had higher leaf nitrogen contents than their hosts and much of this nitrogen appeared as arginine, a potential nitrogen storage compound. Photosynthetic rates (per unit leaf area) were significantly higher in junipers than in the mistletoe, and higher in the uninfected than infected junipers. Water use efficiencies as estimated by carbon isotope ratios were significantly lower in mistletoes than in their hosts. Increased mistletoe infestation appeared to increase absolute water use efficiency of both host and mistletoe.

Mistletoes are obligate parasites of higher plants (Kuijt 1969; Calder and Bernhardt 1983). Most mistletoes tap only the xylem of their hosts and obtain access to only water and mineral nutrients within the xylem fluids (Leonard and Hull 1965; Raven 1983).

Early measurements indicated that mistletoes transpiration rates were higher than those of the host (Kamerling 1910, Härtel 1937). Associated with this was the observation that a number of mineral elements accumulated in mistletoes leaf tissues to much higher concentrations than observed within host tissues (Wolff 1880; Glatzel 1983; Lamont 1983; Schulze and Ehleringer 1984). This results from the lack of any translocation of minerals from the parasite back to its host (Leonard and Hull 1965) in contrast to the retranslocation possible within the host. The extent of this mineral accumulation becomes especially apparent in autoparasitic systems where mistletoes parasitize other mistletoes (Ehleringer and Schulze 1985).

It has been suggested by Schulze, Turner and Glatzel (1984) that the higher transpiration rates are a means to acquire nitrogen, the macronutrient most limiting mistletoes growth. Additional supporting evidence has been provided by Schulze and Ehleringer (1984) and Ehleringer et al. (1985), although none of these studies included growth analyses in conjunction with complete plant water and nitrogen balances.

The purpose of this study was to explore interactions at the leaf level between water relations and nitrogen of the xylem-tapping mistletoe *Phoradendron juniperinum* and one of its principal hosts *Juniperus osteosperma*. Specifically, this study addresses the questions of 1) how do water relations and nitrogen contents of host and parasite differ through a growing season, 2) how does water use efficiency differ between host and parasite and does the infestation rate affect these interactions, and 3) how does host performance in terms of water and nitrogen differ between infected and unifected host trees?

Materials and methods

Phoradendron juniperinum Engelm. is a xylem-tapping mistletoe commonly parasitic on *Juniperus osteosperma* (Torr.) Little. The host-mistletoe system was studied in Skull Valley, Utah (lat. 40°21′N, long. 112°36′W, 1,740 m elevation), where mistletoes are heavily infecting junipers on a dry, sandy soil. The vegetation of this area is characterized as intermountain pinyon-juniper scrub. Juniper is the predominant tree in this area and the mistletoes infections occur most commonly on the deeper sandy soils and are rare to few on nonsandy soils.

The junipers sampled were mature trees ranging in height from 4–6 m. The mistletoes can be readily aged (Schulze and Ehleringer 1984) and those plants sampled fell into two distinct categories: young (2–3 years old and in a prereproductive stage) and mature (6–10 years old and reproductive). The juniper trees included individuals without any mistletoes (control trees) and individuals with mistletoes (infected trees). Within the infected trees, subdivisions were made to separate uninfected stems from infected stems. The uninfected stems were stems without any mistletoes on the stem all the way back to the principal stem connection. Infected stems had mistletoes on the main secondary branch: the juniper tissues sampled on infected stems were all distal to the point of mistletoes attachment to the host branch.

Diurnal courses of water relations parameters were measured at several times through the growing season. Leaf

Offprint requests to: J. Ehleringer

* Dedicated to Professors D. Wiens (Salt Lake City) and H. Ziegler (München) for initiating our curiosity in mistletoes

conductance to water vapor was measured with a null balance porometer and leaf water potentials with a Scholander-type pressure chamber (model 1,000, PMS Instruments, Corvallis, OR). Leaf temperatures were measured with 36 gauge copper-constantan thermocouples and relative humidity with a Vaisala sensor; both were coupled to a datalogger (CR21, Campbell Scientific, Logan, UT), which averaged 1 min readings over a 15-min period. Sample size for all measurements was ten readings from five different trees.

Photosynthetic measurements were made using an open gas exchange system described previously by Ehleringer (1983). The gas exchange measurements were collected on stems that had been collected in the field the previous evening. Near sunset the entire brach (2–3 m long) was first cut near the junction with the main trunk; a second distal cut was then made under water and this branch with its base in water was transported back to the laboratory for gas exchange measurements the following morning. The sample size for each treatment was 3–4 sets of leaves (reduced to scales) on different plants. These measurements were collected during late May and early June.

Carbon isotope ratios were determined on current year leaf tissues using a rationing mass spectrometer (Tieszen et al. 1979). All carbon isotope values are expressed relative to the PDB standard.

Leaf Kjeldahl nitrogen contents were measured on current year leaf tissues using an autoanalyzer. Amino acid composition of current year leaf tissues was measured using a Durrum amino acid analyzer by the Department of Biochemistry at the University of California, Davis CA. Samples for both carbon isotope ratio and amino acid analyses were collected at midday in late spring.

Results

Throughout the course of the day in the spring, leaf conductances to water vapor were consistently higher in the mistletoes leaves than in either the infected or uninfected leaf tissues on mistletoes-infected junipers (Fig. 1). Leaf conductances of both mistletoe and juniper leaves were very close to zero before dawn and gradually increased with morning irradiances attaining maximum values on May 24 of 0.074, 0.066, and 0.055 mol m^{-2} s^{-1} for the mistletoe, infected juniper and uninfected juniper leaf tissues, respectively. Leaf conductances of both mistletoe and host decreased gradually through the day as the Δw gradient increased. In both juniper and mistletoe leaf tissues the midday decreases in leaf conductance were highly correlated with increased Δw. There was no afternoon recovery of leaf conductance in either the mistletoe or juniper leaf tissues.

Within the different juniper leaf tissues, the uninfected control trees had higher leaf conductances than the infected trees and maintained these higher leaf conductances throughout the day (Fig. 1). There was an unexpected difference in leaf conductance between juniper leaf tissues from infected and uninfected stems. Juniper leaves on infected stems maintained consistently higher leaf conductances than did those leaves on uninfected stems. In all cases the leaf temperatures of both sets of juniper tissues were similar so that the leaf conductance differences were also indicative of proportional differences in transpiration rate.

Leaf water potentials of mistletoe tissues reached a minimum value of −2.9 MPa on May 24 and were much more negative than juniper tissues from either infected stems (minimum value of −1.9 MPa) or uninfected stems (minimum value of −1.8 MPa). There were no consistent differences in juniper leaf water potentials between the uninfected stems and the infected stems on the mistletoe-infected trees; throughout much of the day the water potential was lower on the infected stems, but at other times during the day there was no difference in the two values. On this sample date, there was a small but constant difference in leaf water potentials of approximately 0.3 MPa between the mistletoe-infected and the uninfected, control juniper trees.

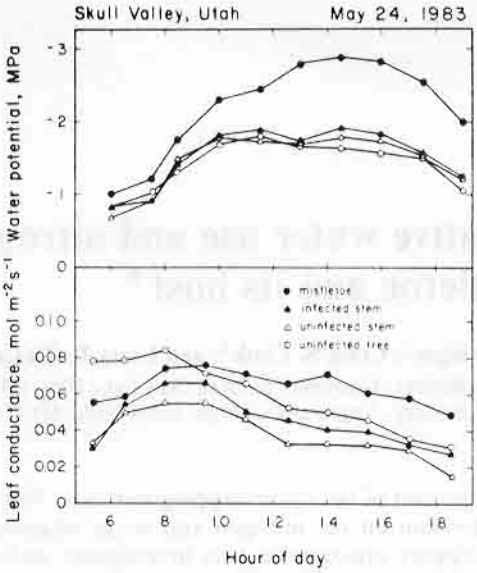

Fig. 1. Diurnal courses of leaf conductance to water vapor and leaf water potential on May 24, 1983. During the day skies were clear and air temperatures ranged 12–29° C; leaf temperatures of mistletoe and juniper were similar and ranged 11–27° C. The Δw gradient ranged from 12–41 mbar bar^{-1} over the course of the day. Plotted are average observations each hour for *Phoradendron juniperinum* (mistletoe), leaf tissues from infected stems and uninfected stems of the host *Juniperus osteosperma* (juniper) and from an adjacent uninfected control juniper tree

Near the end of the summer growing season, leaf conductances to water vapor in the mistletoes continued to greatly exceed those of the host leaf tissues (Fig. 2). Mistletoe leaf conductances peaked at approximately 0.183 mol m^{-2} s^{-1} at midmorning and declined as the Δw gradient increased. A similar diurnal pattern was seen in both the infected, uninfected and control juniper leaf tissues, but maximum values were lower than mistletoe leaf conductances at 0.102, 0.096 and 0.120 mol m^{-2} s^{-1}, respectively. Juniper leaf conductances also decreased after midmorning most likely in response to an increased Δw. From the limited field data available, it did not appear that the stomatal sensitivity to humidity ($\partial g / \partial w$) of mistletoe and juniper (from either infected or uninfected trees) differed from each other.

Just as in the spring diurnal observations, the mistletoes maintained lower water potentials than their hosts throughout the day in late summer (Fig. 2). Mistletoe leaf water potentials decreased rapidly in the morning on September 1 to a minimum of −3.4 MPa, which was maintained more or less throughout the remainder of the day. In contrast, leaf water potentials of infected and uninfected stems of

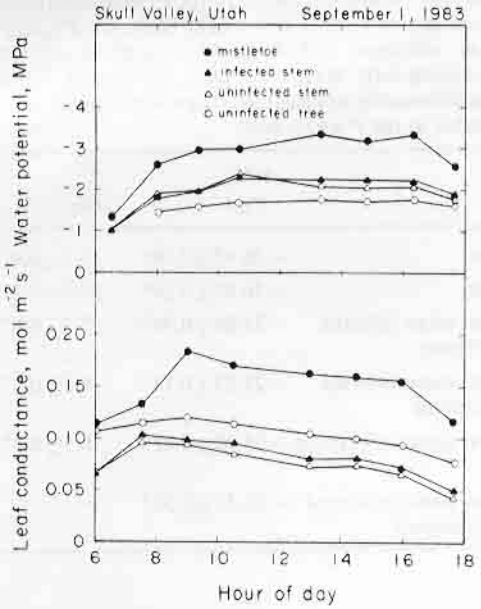

Fig. 2. Diurnal courses of leaf conductance to water vapor and leaf water potential on September 1, 1983. During the day skies were clear and air temperatures ranged 19–33° C; leaf temperatures of mistletoe and juniper were similar and ranged 18–32° C. The Δw gradient ranged from 23–51 mbar bar^{-1} over the course of the day. Plotted are average observations each hour for *Phoradendron juniperinum* (mistletoe), leaf tissues from infected stems and uninfected stems of the host *Juniperus osteosperma* (juniper) and from adjacent uninfected control juniper trees

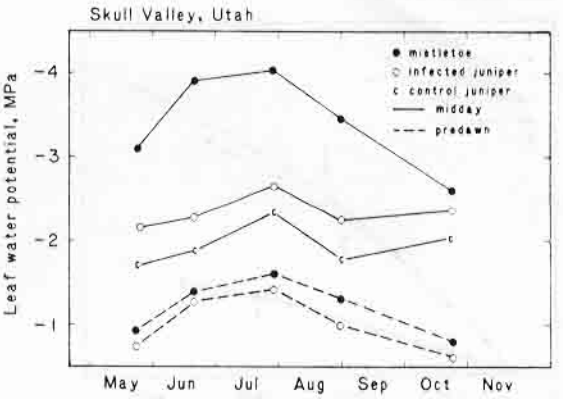

Fig. 3. Seasonal changes in the predawn and midday leaf water potentials for leaf tissues of *Phoradendron juniperinum* (mistletoe), of *Juniperus osteosperma* infected with mistletoes (infected juniper) and adjacent uninfected juniper trees (control)

Table 1. Gas exchange characteristics of mistletoe (*Phoradendron juniperinum*) and juniper (*Juniperus osteosperma*) leaves measured under an incident photon flux (400–700 nm) of 1.6 mmol m^{-2} s^{-1}, a leaf temperature of 20° C, an ambient CO_2 concentration of 335 µl l^{-1}, and a Δw of 11 mbar bar^{-1}. A_{max} is the maximum photosynthetic rate under these conditions, g is the leaf conductance to water vapor at A_{max}, and c_i is the intercellular CO_2 concentration at A_{max}. Data are $x \pm 1$ SE of 3–4 leaves on different plants

	A_{max} (µmol m^{-2} s^{-1})	g (mol m^{-2} s^{-1})	c_i (µl l^{-1})	c_i/c_a
uninfected juniper (control)	9.03 ±0.88	0.143 ±0.013	230 ±3	0.687 ±0.012
infected juniper	7.50 ±1.18	0.106 ±0.016	213 ±3	0.647 ±0.003
mistletoe	3.43 ±0.30	0.130 ±0.012	284 ±10	0.855 ±0.013

the infected juniper tree were approximately 1.1 MPa higher at −2.3 MPa. Leaf water potentials of the infected juniper tree on September 1 were clearly lower than leaf water potentials on the uninfected, control juniper tree, suggesting that the presence of mistletoes was imposing a significant water stress on juniper.

The impact of mistletoes on leaf water potentials in juniper over the course of the entire growing season is seen in Fig. 3, where mistletoe infected trees consistently have leaf water potentials 0.3–0.5 MPa lower than adjacent, uninfected trees.

It is possible that the higher leaf conductances and transpiration rates in mistletoes are associated with overall higher rates of gas exchange activity. To examine this possibility, photosynthetic activity was measured on infected/noninfected juniper leaves and mistletoe leaves in the spring. Specifically, we were interested in determining gas exchange characteristics under ambient conditions and the stomatal limitations to gas exchange under these conditions.

When measured under near optimal ambient conditions, photosynthetic rates of junipers exceeded those of the mistletoe by a factor of 2–3 (Table 1). Maximum photosynthetic rates (A_{max}) of mistletoe leaves averaged only 3.43 µmol m^{-2} s^{-1}, whereas those of uninfected juniper leaves were 9.03 µmol m^{-2} s^{-1} under the same conditions. Surprisingly, A_{max} of the infected juniper leaves was depressed by 17%, averaging only 7.50 µmol m^{-2} s^{-1}. Despite the lower photosynthetic rate by mistletoe leaves, mistletoe leaf conductances were still higher than those on the infected juniper leaf tissues, resulting in a much higher intercellular CO_2 concentration (c_i) in the mistletoe than in the juniper leaves. Leaf conductances in the infected juniper tissues were reduced sufficiently that c_i was lower than in the uninfected control juniper leaves. Consequently, the c_i/c_a ratios were greatest in the mistletoe (0.855), lowest in the infected juniper leaves (0.647) and intermediate in the uninfected juniper leaves (0.687).

A_{max} and c_i values, though, do not provide information on the stomatal limitations to photosynthesis. In order to evaluate the limitations on photosynthetic rate imposed by diffusion through the stomates (l_s), the photosynthetic dependence on c_i was determined for both juniper and mistletoe leaves. Net photosynthetic rate in mistletoe leaves was lower than observed for juniper leaves at all c_i values (Fig. 4). The photosynthetic dependence on c_i was similar between infected and uninfected, control juniper leaves, although photosynthetic rates at higher c_i values were generally lower in infected juniper leaves. Figure 4 also shows the differences in operational c_i values under ambient conditions (indicated by arrows). l_s was calculated using a c_i of 350 µl l^{-1} as an upper limit and the observed c_i. From these calculations, l_s was 16% for the mistletoes, 35% for the infected juniper leaves and 26% for the uninfected, control juniper leaves. Thus, mistletoe leaves not only had the lower photosynthetic rate, but that rate was also limited less by diffusional factors than it was for juniper leaves.

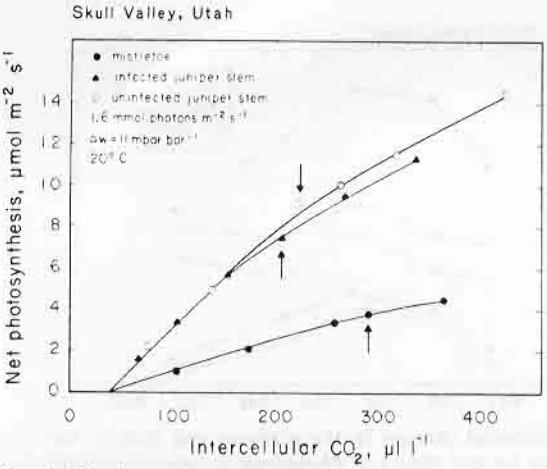

Fig. 4. The dependence of net photosynthesis on intercellular CO_2 concentration for leaves of *Phoradendron juniperinum* (mistletoe), of *Juniperus osteosperma* infected with mistletoes (infected juniper) and for uninfected stems on infected juniper trees (uninfected juniper)

The previous data sets strongly suggested that mistletoes had lower water use efficiencies (molar ratio of carbon dioxide fixed by photosynthesis to water loss by transpiration) than did any of the juniper leaves. Water use efficiency is related to c_i as

$$A/E=(c_a-c_i)/1.6\,\Delta w$$

where A is the net photosynthetic rate, E is transpiration rate, c_a and c_i the ambient and intercellular CO_2 concentrations, and Δw the leaf to air water vapor concentration gradient. Since leaf temperatures of the mistletoes and junipers were similar and both parasite and host were growing in the same microenvironment, it is fair to assume that water use efficiency was dependent primarily on the value of c_i. Further evaluation of the water use efficiencies of mistletoes and junipers were evaluated by measuring the carbon isotope ratio, which is known to be negatively related to c_i (Farquhar et al. 1982a; Farquhar et al. 1982b; Farquhar and Richards 1984).

Carbon isotope ratios were measured on both young and mature mistletoes growing on junipers and on the infected stem, uninfected stem and control tree juniper leaves in the late spring. These data show that the carbon isotope ratios of mistletoes were more negative than those of their host, implying that water use efficiency was indeed lower than in their juniper host (Table 2). The data were collected in a paired fashion and there is an indication that the difference in water use efficiency between mistletoe and host was slightly greater on younger than on mature mistletoes. There appear to be some small changes in the carbon isotope ratio of the junipers with juniper tissues infected by young mistletoes showing a decrease in water use efficiency and juniper tissues infected by mature mistletoes showing an increase in water use efficiency when both were compared to the performance of juniper leaves on an adjacent branch that was not infected. These data are limited by small sample sizes and a clearer indication of potential differences between young/mature mistletoes and infected/uninfected juniper must await more extensive sampling beyond the scope of this study.

Kjeldahl nitrogen values were measured on the same leaf tissues used for carbon isotope analyses. Leaf nitrogen contents were much higher in the young mistletoes than they were in the mature individuals and, overall, nitrogen contents were higher in the mistletoes than in the junipers.

The extent of mistletoe infestation on a tree appeared to have an effect on the carbon isotope composition, presumably reflecting changes in water use efficiency of the host and parasite (Table 3). On junipers that were heavily infested, there seemed to be an improvement in water use efficiency by young mistletoe and infected/uninfected juniper leaves. Carbon isotope ratios of mature mistletoes appeared not to change with the extent of infestation. Although sample sizes were again small, the differences in carbon isotope ratios between host and parasite with infestation suggest that host water use efficiency is more affected than is that of the parasite.

The Schulze et al. (1984) explanation for mistletoe parasitism suggested that the primary function of parasitism was to acquire nitrogen, the macronutrient most limiting mistletoe growth. The mistletoes do appear to affect the distribution of nitrogen within the host (Fig. 5). Leaf nitrogen contents of infected juniper trees were lower than uninfected trees throughout the season. At the same time, mistle-

Table 2. Carbon isotope ratios (relative to the PDB standard) and Kjeldahl nitrogen contents (on a dry weight basis) for *Phoradendron juniperinum* (mistletoe) and *Juniperus osteosperma* (juniper) leaves sampled during early May, 1983. Data are $x \pm 1$ SE. Values within a column followed by different letters are significantly different from each other at the $P<0.01$ level

Tissue	$\delta^{13}C$ (‰)	N (mg g^{-1})
young mistletoe	-26.83 ± 0.19^a	14.2 ± 0.9^a
mature mistletoe	-26.42 ± 0.24^a	10.0 ± 1.2^b
juniper leaves on stems infected by young mistletoe	-23.80 ± 0.39^b	7.7 ± 0.6^b
juniper leaves on stems infected by mature mistletoe	-23.25 ± 0.14^b	8.4 ± 0.8^b
juniper leaves on stems uninfected by mistletoe	-23.40 ± 0.31^b	8.5 ± 0.5^b
juniper leaves on trees uninfected by mistletoe (control)	-23.32 ± 0.31^b	–

Table 3. Carbon isotope ratios (relative to the PDB standard) of mistletoe (*Phoradendron juniperinum*) and juniper (*Juniperus osteosperma*) leaf tissues for mature host trees in Skull Valley, Utah that were lightly or heavily infected with mistletoes. Young mistletoes were 2–3 years old (preflowering) and mature mistletoes were 6–10 years old. Data are average values in parts per mil with the sample size in parentheses

	Mistletoe infestation	
	light	heavy
young mistletoe	−27.20 (2)	−26.45 (2)
mature mistletoe	−26.33 (4)	−26.60 (2)
uninfected juniper branch	−23.65 (4)	−22.75 (2)
infected juniper branch	−24.10 (2)	−23.03 (2)

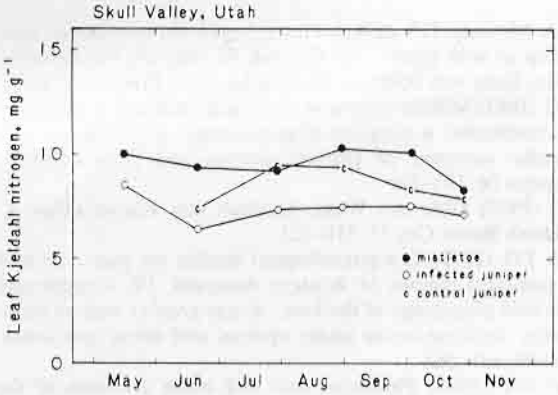

Fig. 5. Seasonal changes in the leaf Kjeldahl nitrogen content for leaf tissues of *Phoradendron juniperinum* (mistletoe), of *Juniperus osteosperma* infected with mistletoes (infected juniper) and adjacent uninfected juniper trees (control)

Table 4. Amino acid composition of leaves of *Juniperus osteosperma* and *Phoradendron juniperinum*. The composition data are presented as a percentage of the total

Amino acid	*Juniperus osteosperma*	*Phoradendron juniperinum*	Ratio of parasite/host
ASP	8.5	9.2	1.08
THR	4.6	4.8	1.04
SER	4.6	5.5	1.20
GLU	10.5	8.4	0.80
PRO	5.4	7.7	1.4
GLY	9.7	9.5	0.98
ALA	10.8	8.8	0.81
VAL	7.0	5.9	0.84
MET	1.5	0.7	0.47
ILE	5.2	4.4	0.87
LEU	8.6	7.3	0.85
TYR	2.9	4.0	1.38
PHE	4.2	3.3	0.79
ABU	1.1	1.5	1.36
LYS	5.7	7.0	1.23
HIS	2.0	2.9	1.45
ARG	3.9	9.2	2.36

toe leaves maintained 20–30% higher nitrogen contents than did their hosts (and higher even than in the control junipers) throughout the season.

Typically, there is a tight positive correlation between leaf photosynthetic rate and Kjeldahl nitrogen content (Field and Mooney 1985). Thus, it is unusual that mistletoes should have higher leaf nitrogen contents but lower photosynthetic capacities than junipers (Fig. 4, Fig. 5). It is possible that much of the leaf amino nitrogen in mistletoes is not used in daily metabolism (such as photosynthesis and respiration), but is instead stored as simpler polypeptides for later use in seed production, which is known to be extremely high in this mistletoe species (Schulze and Ehleringer 1984). Amino acid analyses of leaf tissues of both juniper and mistletoe supported this notion (Table 4). Mistletoe leaves had much higher concentrations of arginine, which contains four *N* per amino acid, and is known to frequently serve as a nitrogen storage compound. In addition, from other studies it is known that proline often serves as an osmoticum and the relatively higher concentrations of proline in mistletoe may have been important for achieving the lower water potentials observed.

Discussion

The leaf conductance observations on *Phoradendron juniperinum* and *Juniperus osteosperma* demonstrate that through the growing season the mistletoe maintains a higher transpiration rate than does its host. This host-parasite transpiration difference has been reported earlier by other investigators (Kamerling 1910; Härtel 1937; Vareschi and Pannier 1953; Hellmuth 1971; Glatzel 1983; Schulze et al. 1984; Schulze and Ehleringer 1984; Ullmann et al. 1985). However, this study extends earlier observations by showing that mistletoe infected host trees have a significantly lower rate of water loss than uninfected trees. Moreover, because of the higher rates of water loss associated with mistletoe parasitism, infected trees experience significantly lower leaf water potentials than do uninfected trees. Thus, it appears that several aspects of juniper water relations (leaf conductance, leaf water potential and water use efficiency) are worsened by the presence of these parasites. Increased infestation appears to aggravate this situation, but since whole plant water balances were not measured we cannot estimate the magnitude of this effect on host productivity.

Although there are several references to mistletoes being unregulated in their use of host xylem water (Härtel 1937; Vareschi and Pannier 1953), the results of this study suggest that mistletoes exercise some control over rates of water loss. Leaf conductances were near zero at night and also decreased during the day in response to an increased Δw. Stomatal sensitivity to Δw by mistletoe leaves has also been reported by Hollinger (1983) and Ullmann et al. (1985). If one explanation for mistletoe parasitism is to acquire nitrogen (discussed further below), then it is unclear why there should be any pronounced regulation of leaf conductance and transpiration rate as was observed unless there are threshold leaf water potentials that adversely affect mistletoe metabolism. Alternatively, the water wasting associated with a decreased water use efficiency may lead to reduced host longevity in these arid habitats and thus affect the total lifetime reproductive effort of the mistletoe.

The drain of the mistletoe parasitism on host performance is seen not only in decreased water potentials, but also in leaf Kjeldahl nitrogen contents. If photosynthesis is proportional to nitrogen content as expected (Field and Mooney 1985), then the decreased leaf nitrogen contents in infected trees would translate into lower rates of photosynthesis and carbon gain by the host. In turn, this should result in reduced growth and reproductive activity in the infected junipers, perhaps especially so in the infected stems. There appears to be an indication that initially juniper tissues distal to the point of mistletoe infection have increased leaf conductances and decreased water use efficiencies relative to uninfected juniper tissues. However, in older infections the performance of the infected host tissues seems to have deteriorated and these host tissues are usually dead after 5–8 years of infection. This infected host tissue behavior when mistletoes are still young, which somewhat mimics the mistletoe behavior, might be a method whereby infected tissues can obtain sufficient mineral nutrition to reproduce. If phloem translocation to infected areas is reduced and or

the nitrogen content of host xylem fluid distal to the parasite is reduced, there may be few other options for acquiring sufficient amounts of the minerals necessary for reproduction available to the infected host tissues.

Schulze et al. (1984) have proposed that the higher transpiration rates by mistletoes are necessary to acquire nitrogen, the macronutrient most limiting mistletoe growth. Studies by Schulze and Ehleringer (1984) on *Phoradendron juniperinum* growing on *Juniperus osteosperma* support this notion and have shown that all macronutrients except nitrogen are accumulated in large excess by the mistletoe leaf tissues. The high nitrogen requirement of *P. juniperinum* appears associated with an extremely high reproductive output and the production of seeds with relatively high nitrogen contents. In accordance with this, it is not surprising to find that there are such high concentrations of arginine, a nitrogen storage compound, in mistletoe leaves.

Acknowledgments. This study has been supported by NSF Grant BSR 81-13136.

References

Calder M, Bernhardt P (eds) (1983) The biology of mistletoes. Academic Press, New York

Ehleringer JR (1983) Ecophysiology of *Amaranthus palmeri*, a Sonoran Desert summer annual. Oecologia 57:107–112

Ehleringer JR, Schulze E-D (1985) Mineral concentrations in an autoparasitic *Phoradendron californicum* growing on a parasitic *P. californicum* and its host, *Cercidium floridum*. Amer J Bot 72:568–571

Ehleringer JR, Schulze E-D, Ziegler H, Lange OL, Farquhar GD, Cowan IR (1985) Xylem mistletoes: water or nutrient parasites? Science 227:1479–1481

Farquhar GD, O'Leary MH, Berry JA (1982a) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Aust J Plant Physiol 9:121–137

Farquhar GD, Ball MC, von Caemmerer S, Roksandic Z (1982b) Effect of salinity and humidity on $\delta^{13}C$ value of halophytes – evidence for diffusional fractionation determined by the ratio of intercellular/atmospheric partial pressure of CO_2 under different environmental conditions. Oecologia (Berlin) 52:121–124

Field CB, Mooney HA (1985) The nitrogen-photosynthesis relationship in wild plants. In: Givnish TJ (ed) On the economy of plant form and function. Cambridge Univ Press (in press)

Glatzel G (1983) Mineral nutrition and water relations of hemiparasitic mistletoes: a question of partitioning. Experiments with *Loranthus europeus* on *Quercus petraea* and *Quercus robur*. Oecologia 56:193–201

Härtel O (1937) Über den Wasserhaushalt von *Viscum album* L. Ber Dtsch Botan Ges 55:310–321

Hellmuth EO (1971) Eco-physiological studies on plants in arid and semi-arid regions of Western Australia. IV. Comparison of the field physiology of the host, *Acacia grasbyi*, and its hemiparasite, *Amyema nestor* under optimal and stress conditions. J Ecol 59:351–363

Hollinger DY (1983) Photosynthesis and water relations of the mistletoe, *Phoradendron villosum*, and its host, the California valley oak, *Quercus lobata*. Oecologia 60:396–400

Kamerling Z (1910) Verdunstungsversuche mit tropischen Loranthaceen. Ber Dtsch Bot Ges 32:17–24

Kuijt J (1969) The biology of flowering parasitic plants. University of California Press Berkeley

Lamont B (1983) Mineral nutrition of mistletoes. In: Calder M, Bernhardt P (eds) The biology of mistletoes. Academic Press, New York, pp 185–204

Leonard OA, Hull RJ (1965) Translocation relationships in and between mistletoes and their hosts. Hilgardia 37:115–153

Raven JA (1983) Phytophages of xylem and phloem: a comparison of animal and plant sap-feeders. Adv Ecol Res 13:136–234

Schulze E-D, Ehleringer JR (1984) The effect of nitrogen supply and water-use efficiency of xylem-tapping mistletoes. Planta 162:268–275

Schulze E-D, Turner NC, Glatzel G (1984) Carbon, water and nutrient relations of two mistletoes and their hosts: a hypothesis. Plant Cell Environ 7:293–299

Tieszen LL, Hein D, Quortrup S, Troughton J, Imbamba S (1979) Use of $\delta^{13}C$ values to determine vegetation selectivity in East African herbivores. Oecologia 37:351–359

Ullmann I, Lange OL, Ziegler H, Ehleringer JR, Schulze E-D, Cowan IR (1985) Diurnal courses of leaf conductance and transpiration of mistletoes and their hosts in central Australia. Oecologia (in press)

Vareschi V, Pannier F (1953) Über den Wasserhaushalt tropischer Loranthaceen am natürlichen Standort. Phyton 5:140–152

Wolff EV (1880) Aschenanalysen von landwirtschaftlichen Produkten II. Teil. Weigant Hempel, Parey, Berlin

Received August 18, 1985