The effect of nitrogen supply on growth and water-use efficiency of xylem-tapping mistletoes*

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Abstract. Xylem-tapping mistletoes are known to have normally a higher rate of transpiration and lower water-use efficiency than their hosts. The relationships between water relations, nutrients and growth were investigated for *Phoradendron juniperinum* growing on *Juniperus osteosperma* (a non-nitrogen-fixing tree) and for *Phoradendron californicum* growing on *Acacia greggii* (a nitrogen-fixing tree). Xylem sap nitrogen contents were approximately 3.5 times higher in the nitrogen-fixing host than in the non-nitrogen-fixing host. The results of the present study show that mistletoe growth rates were sevenfold greater on a nitrogen-fixing host. At the same time, however, the differences in water-use efficiency between mistletoes and their hosts, which were observed on the non-nitrogen-fixing host did not exist when mistletoes were grown on hosts with higher nitrogen contents in their xylem sap. Growth rates and the accumulation of N, P, K, and Ca as well as values for carbon-isotope ratios of mistletoe tissues support the hypothesis that the higher transpiration rates of mistletoes represent a nitrogen-gathering mechanism.

Key words: Host parasite interactions – Mistletoe – Nutrient relations (mistletoes) – *Phoradendron* – Water relations (mistletoes).

Introduction

It has been hypothesized by Schulze et al. (1984) that xylem-tapping mistletoes have higher transpiration rates than their host as a mechanism to

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gather sufficient amounts of required nutrients from the host xylem sap. The observation that mistletoes have higher transpiration rates than their host has been made by numerous investigators (Kamerling 1910; Härtel 1937; Glatzel 1983; Schulze et al. 1984). Even earlier, Wolfe (1880) observed that mistletoes accumulated unusually high levels of potassium. Glatzel (1983) investigated the concentrations of other plant nutrients. These data indicate that N was the only element not accumulated by mistletoes to levels beyond those of their host. Measurements of transpiration rates and N contents in xylem water led to the hypothesis that since xylem parasites depend on the xylem sap as their sole source of N (they have no connection to the host phloem), high transpiration rates serve as a mechanism to gather N for growth of the mistletoes (Schulze et al. 1984). In contrast, the host also receives N via the phloem.

It is quite difficult to prove such a hypothesis, since i) mistletoes cannot be cultivated independently of their host, ii) establishment is difficult, and iii) growth is slow, not readily allowing growth-chamber studies. In order to investigate further this hypothesis, field studies were conducted on mistletoes growing in naturally different nutrient-supply regimes, where the rate of N supply to the mistletoes differed between hosts. If high transpiration rates are indeed a mechanism to gather limiting nutrients such as N, one could perturb such a system by adding N to the xylem. This is most conveniently made possible by using N_2-fixing species as hosts.

There are two possible mistletoe responses to be expected under increased N supply: i) the mistletoe could grow faster without changing its rate of water use or water-use efficiency. In this case, mistletoes could be regarded as water parasites which gather nutrients at a passive rate and use

them for their respective growth or ii) if nutrients are supplied in higher concentrations, the mistletoe could reduce its rate of transpiration and improve water-use efficiency. In this latter case, one could regard the increased transpiration rate under conditions of low N supply as a nutrient-gathering mechanism which is under mistletoe control. Both possible responses were investigated using *Phoradendron*, a common xylem mistletoe of western North America, growing on *Juniperus* (a non-nitrogen-fixing tree) and *Acacia* (a nitrogen-fixing tree).

Materials and methods

Plant materials. Phoradendron juniperinum Engelm. and *P. californicum* Nutt. are very closely related dioecious evergreen species of western North America (Munz 1959). In contrast to other *Phoradendron* species, both species are characterized by reduced scaly leaves and green photosynthetic stems. Both *Phoradendron* species obtain water and solutes through direct xylem connections from the host. Studies with ^{14}C have shown that there is no phloem connection between *Phoradendron* and host (Leonard and Hull 1965). *P. californicum* grows on a number of woody species, but preferentially on leguminous trees. In contrast, *P. juniperinum* grows only on conifers, especially species of *Juniperus*.

P. californicum was studied in northwest Arizona, 15 km south of Oatman (latitude 34°57′N, longitude 114°25′W, 540 m elevation), where it grows abundantly on *Acacia greggii* in dry valleys.

The vegetation in this area is typical of the Colorado Desert subdivision of the Sonoran Desert. Mistletoe establishment appears to be most successful on current-year twigs of *Acacia*. In the first year, a single 1- to 2-cm-long sprout was formed, the seed coat was still visible, and there was no inflation on the host branch. In the second year, an inflation on the host branch was visible and the sprout showed initial secondary branching. Male plants may flower for the first time after the second year. In the third year, extensive twig elongation takes place and the first female flowers are formed. The first fruits mature in the fourth year and additional main branches develop from axiliary buds. From this point on, the current-year stems form flowers, which will then mature in the following year. Beginning in the fourth and fifth years, many side branches are produced, which fill in the spaces between main branches, resulting in a plant which is ball-shaped. In all successive years, the plant structure can be reconstructed since flowering always occurs on current-year twigs and fruits always develop on one-year-older twigs. Older annual growth increments can be recognized by i) the branching pattern, side branches are formed from buds at the apex of current year twigs, ii) the color and length of the internodes, which are short during the dormant dry or cold season and which show secondary bark and thickening with age, and iii) the leaf scales which carry fruit scars in their axils. Old plants have a very dense appearance due to the numerous side branches.

P. juniperinum was studied in Skull Valley, Utah (latitude 40°21′N, longitude 112°36′W, 1 740 m elevation) (west of Salt Lake City), where they heavily infect *Juniperus osteosperma* on a dry, sand-dune habitat. The vegetation of this area is characterized as intermountain pinyon-juniper scrub. The rate of development by *Phoradendron* on *Juniperus* is slower than on *Acacia*. Establishment in the first year appears to be most successful on green, current-year host twigs. At this stage a single stem is formed and no haustorial thickening is visible on the host. In the second year, side branches are produced by the mistletoe, and haustorial thickening occurs on second-year-old non-green twigs of the host. The haustorium migrates laterally between bark and xylem. In the third year, a large haustorium develops, the host twig thickens, and numerous secondary mistletoe buds develop preferentially in apical direction along the host twig axis. Male plants flower for the first time in the third year, whereas female plants flower for the first time in the fourth year and the first fruits are formed in the fifth year. Further development is similar to that described previously for *P. californicum*. Again, these patterns can be reconstructed from the branching pattern, the internode length, the color of the bud, and the fruit scars in the leaf axil scales.

Measurements. At each site, 1- to 10-year-old plants (one to six specimens per age class) were dissected into pieces of different age. For the purpose of this study, large plants were selected which did not show any obviously visible damage or previous branch loss. Therefore, the data represent the maximum growth with very little or no biomass loss between years. For each age class, average and total twig length, biomass and nutrient composition were determined. Amino N was assessed by micro-kjeldahl analysis (Lillivek 1970). Potassium, Ca and K were determined by inductively coupled argon plasma spectrometry (analyses were performed by the Department of Forestry, University of Montana, USA).

Xylem sap was extracted with a Scholander-type pressure chamber, with special care to ensure that air did not move through the xylem during extraction. The bark was stripped prior to xylem sap extraction. It was not possible to collect xylem water from *Acacia greggii* stems because of its large pith, but xylem water could be collected from another N_2-fixing legume, *Cercidium floridum*, which was also frequently parasitized by *Phoradendron* in the same habitat. Growth of mistletoes on *Cercidium* followed the same growth responses as *Phoradendron* on *Acacia*.

Leaf conductance to water vapor was measured using a steady-state porometer. The carbon-isotope ratio (δ^{13}C) was determined on current-year tissues by mass spectrometry (Tieszen et al. 1979).

Results

The daily courses of leaf conductance to water vapor by mistletoes and their hosts showed smaller differences in the *Phoradendron-Acacia* system than in the *Phoradendron-Juniperus* system (Fig. 1). The absolute leaf conductance values were quite different between the two systems. This was probably due to other factors, since it is known that conifers have a lower leaf conductance and CO_2 assimilation rates than broad-leaf trees (Körner et al. 1979; Schulze and Hall 1982). The daily courses were measured at the end of the dry season and, therefore, represented the time of lowest soil water supply. Under these conditions, *P. californicum* showed similar daily rates of water loss as its N_2-fixing host, but *P. juniperinum* transpiration rates were twice as high on its non-N_2-fixing host. Although it is not possible to extrapo-
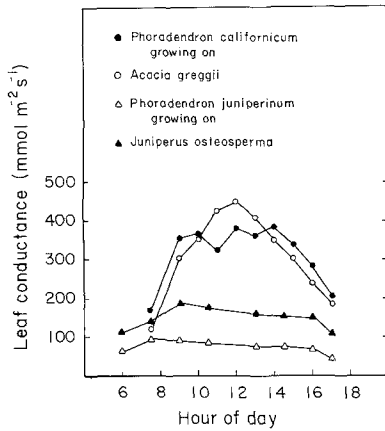
Fig. 1. Daily courses of leaf conductances to water vapor for mistletoes and their hosts. *Closed circles* are *Phoradendron californicum* growing on *Acacia greggii* (*open circles*) at Oatman, Arizona on November 7, 1983. *Open triangles* are *Phoradendron juniperinum* growing on *Juniperus osteosperma* (*closed triangles*) at Skull Valley, Utah on September 1, 1983
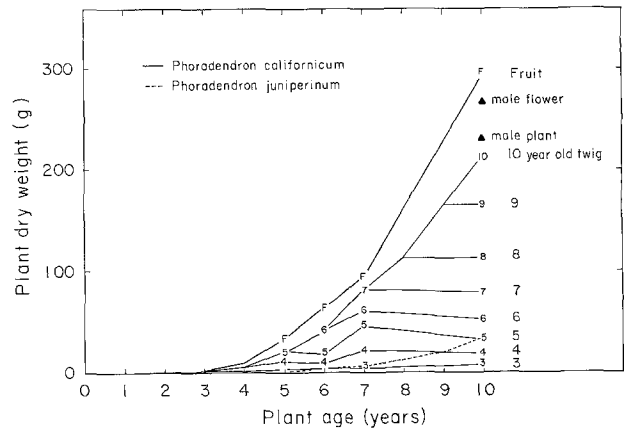

Fig. 2. The relationships between mistletoe dry weight and age for *Phoradendron californicum* and *P. juniperinum*. Small numbers indicate the age of the respective tissue, *F* indicates fruits. The growth rate is represented by the slope of the lines. The biomass of a certain age class is indicated by the difference from that of the previous younger tissue. Only total biomass is shown for *P. juniperinum*

late from these data to the response patterns during other seasons, the data available indicated that the transpiration rate was more similar to that of the host when the mistletoe was growing on a N_2-fixing host. This is a first indication that the mistletoes might regulate the rate of water loss depending on the rate of nutrient supply in the xylem. The N supply is different in both host species. In *Juniperus osteosperma* at the end of the dry season the xylem concentration of N was $35 \text{ mg} \cdot l^{-1}$, but $127 \text{ mg} \cdot l^{-1}$ in *Cercidium floridium*.

Growth rates of mistletoe increase with N supply. After 10 years of growth, the twig biomass of *P. californicum* was about seven times greater than in *P. juniperinum,* and ten times larger if fruit biomass was included in the comparison (Fig. 2). The data, derived from an analysis of mistletoes of different age, indicated a very consistent growth pattern. Each year, a new generation of current-year twigs was produced, which increased slightly in mass during the following year, but thereafter biomass remained nearly constant. Some branch loss undoubtedly occurred in old specimens (i.e. the six-year-old specimens).

Growth rates were exponential, but the rate of increase was higher for mistletoes growing on N_2-fixing hosts than on non-N_2-fixing hosts (Fig. 3). The log-linear increase in biomass with time indicated that after parasite establishment, growth rate was constant and independent of major climatic events over many years. This is surprising, given that these parasites were growing in desert environments which had experienced both extremely wet and dry seasons in the last decade (U.S. Weather
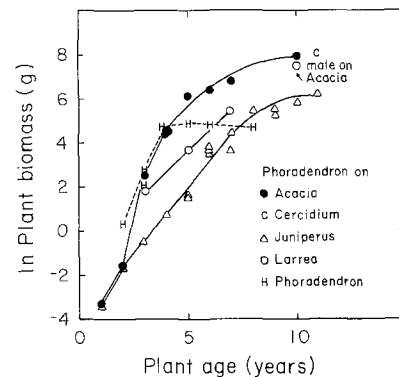
Fig. 3. Logarithm (*ln*) of mistletoe biomass versus age of *Phoradendron californicum* growing on *Acacia greggii* (*closed circles*), *Cercidium floridum* (*c*), *Larrea divaricata* (*open circles*), and on *Phoradendron californicum* (*H*) (hyperparasites), which is growing on the same plant which was studied as parasite on *Cercidium floridum*, and for *Phoradendron juniperinum* growing on *Juniperus osteosperma*

Bureau Records). The mistletoe growth curves leveled off after six years of growth on *Acacia,* but not until after nine years growth on *Juniperus.* The differences in growth of *Phoradendron* on *Juniperus* and *Acacia* could conceivably be partially the result of differences in environmental factors between the two habitats (winter versus winter-summer precipitation). However, that this was not the case was shown by investigating *P. californicum* growing on *Larrea divaricata* (a non-N_2-fixing shrub) which grows in the same habitats as *A. greggii.* These data clearly indicated that *Phoradendron* growth on non-N_2-fixing *Larrea* in the summer-rain climate was similar to that of *Phoradendron*

Table 1. Age-related changes in total twig length, twig number and average twig length of *Phoradendron juniperinum* on *Juniperus osteosperma* and *Phoradendron californicum* on *Acacia greggii*. n.d. = not determined

Plant age (years)	Total twig length (m)		Number of twigs		Average twig length of current-year-twig (cm)	
	Juniperus	*Acacia*	*Juniperus*	*Acacia*	*Juniperus*	*Acacia*
2	0.19	0.32	11	14	1.8	2.0
3	0.46	6.36	27	75	1.7	11.4
4	1.59	21.89	98	328	1.6	8.1
5	3.63	97.69	198	1835	1.8	5.0
6	17.07	324.98	730	2958	2.1	12.5
7	25.19	289.02	2037	3448	1.5	6.7
8	37.18	n.d.	2762	n.d.	2.1	n.d.
9	77.24	n.d.	5090	n.d.	1.5	n.d.
10	119.14	691.67	6861	6454	1.5	10.7

Fig. 4. The relationship between dry-weight biomass of *Phoradendron juniperinum* and the sapwood area of the host branch at the point of infection

growing on *Juniperus* in a predominatly winter-rain habitat.

The growth rate of hyperparasites, i.e. *P. californicum* growing on *P. californicum* in the *Phoradendron-Acacia* system, was the same as for *P. californicum* growing on *Acacia* (the host of the parent *Phoradendron*), but growth leveled off at a much younger stage (Fig. 3). This was because the hyperparasite was generally overgrown by the parent *Phoradendron* plant. The growth rate of male plants was similar to that of female plants (Fig. 3), because the investment in male flowers was very large (Table 2). *Phoradendron* growing on *Cercidium floridium* (another N_2-fixing tree growing adjacent to *Acacia*) showed the same rate of development as when growing on *Acacia* (Fig. 3).

The differences in growth in *Phoradendron* growing on N_2-fixing versus non-N_2-fixing hosts can be further seen in the total twig length and the total twig numbers (Table 1). Total twig length of *Phoradendron* on *Acacia* was much larger than for *Phoradendron* on *Juniperus*, especially in the younger stages. The larger total twig length was mainly the result of a higher average twig length in the *Phoradendron* growing on *Acacia* when compared with growth of *Phoradendron* on *Juniperus*. The total twig number increased almost exponentially with age, and after 10 years of growth, the *Phoradendron* on *Juniperus* had reached about the same total twig number as *Phoradendron* on *Acacia*. At that age, both parasites had a very dense, ball-shaped appearance. Considering that there were about 7000 pieces of 1.5 cm length packed into the outer portion of the spherical structure, it is quite conceivable that self-shading was one
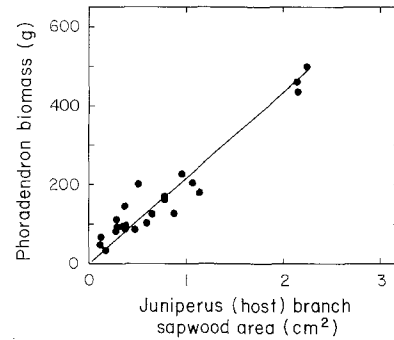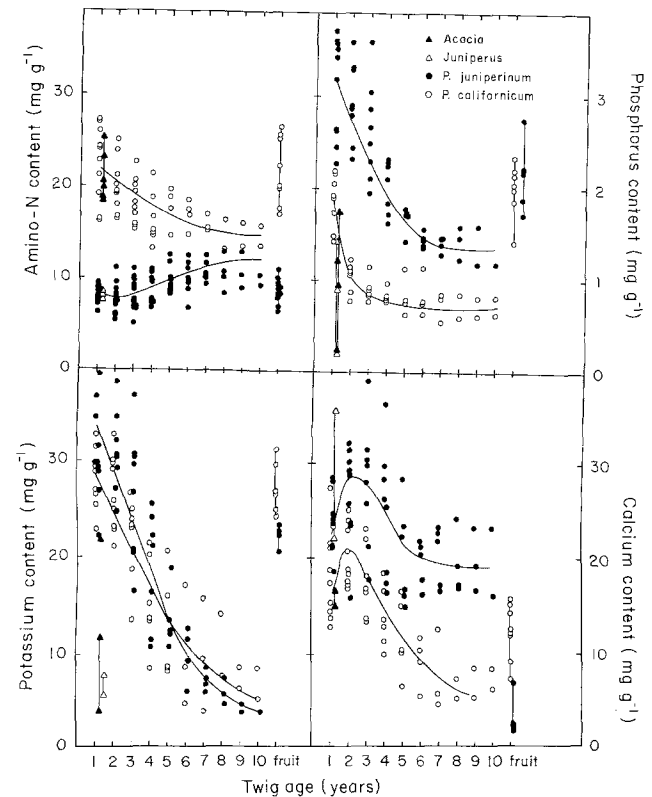

Fig. 5. The relationships between nitrogen, phosphorus, potassium and calcium contents with mistletoe tissue age, mistletoe fruits and host leaf tissues

major reason for the decline in growth rate at later ages.

In order to obtain insight into the growth interaction of mistletoes with their hosts, the weights of mistletoes of different sizes were related to the sapwood area of the host branches (Fig. 4). The host branch tended to die beyond the point of mistletoe infection. Despite this, host vascular tissue development continued up to the point of infection, and the mistletoe biomass appeared to be linearly related to the sapwood area of the host branch. This meant that the host branch must have
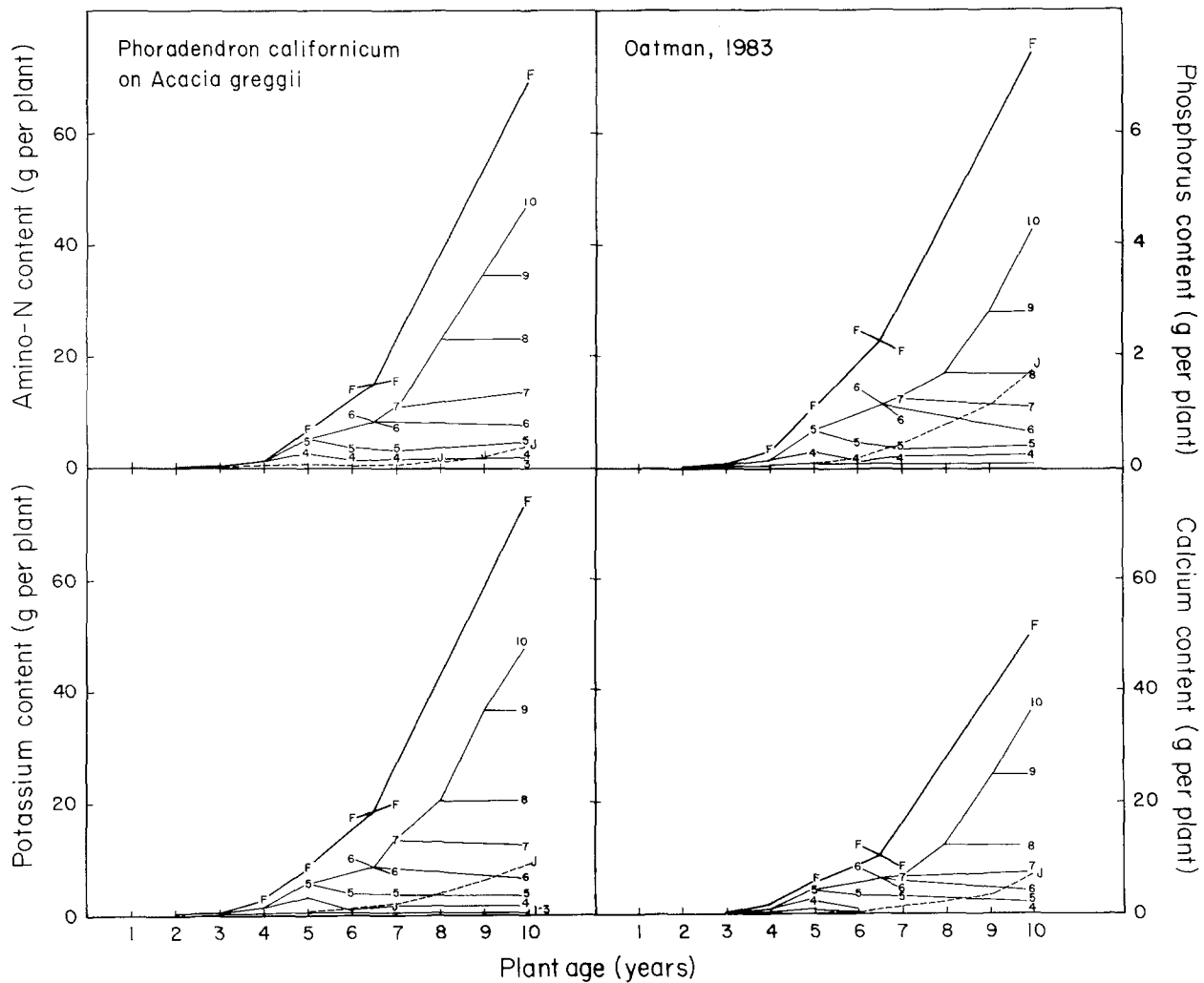
Fig. 6. The accumulation of amino nitrogen, phosphorus, potassium and calcium with plant age. *Small numbers* indicate the age of the respective tissue. *F* indicates fruits. The nutrient accumulation is the slope of these lines with age. The nutrient content of a certain age class is indicated by the difference from that of the previous younger tissue. Only the total amount of nutrients per plant of a certain age is shown for *P. juniperinum* (*J*)

continued to grow sapwood at a rate required by the water demand of the mistletoe, even though the host tissue was dead beyond the point of infection and even though there was no phloem connection between the mistletoe and its host.

The N, P, K and Ca levels in the xylem sap of mistletoes showed different changes with twig age (Fig. 5). When grown on *Acacia*, the N content of one-year-old *Phoradendron* shoots from plants of different ages reached about 22 mg g^{-1} and was similar to the N content of the host. With increasing twig age, the N content decreased to 15 mg g^{-1} in 10-year-old twigs. Fruits had the same N content as the young shoots. The N content of young shoots of *Phoradendron* growing on *Juniperus* was only about 9 mg g^{-1}, and was of similar magnitude to that of the host leaf tissue. However, in contrast to mistletoe growth on *Acacia*, the mis-

tletoe N contents increased with age to 12 mg g^{-1} in 10-year-old twigs. Whereas twigs lost N with age when grown on *Acacia*, an N enrichment was observed when grown on *Juniperus*, indicating a more nutrient-deprived status in this host plant. Phosphorus and K were accumulated in the mistletoe beyond the levels of the host and the accumulation was larger for *Phoradendron* growing on *Juniperus* than on *Acacia*. The P and K contents decrease with tissue age independent of the host. In contrast to growth on *Juniperus*, Ca is not accumulated beyond the level of the host when growth occurs on *Acacia*. P and K, Ca is further accumulated in the two-year-old tissue, but the Ca content declines with greater tissue age and this decline is stronger in mistletoes growing on *Acacia* than on *Juniperus*.

The decrease in N, P, K and Ca with twig age

Table 2. Production of and nutrient requirement for mistletoe fruits of *Phoradendron juniperinum* growing on *Juniperus osteosperma* and *Phoradendron californicum* growing on *Acacia greggii*. n.d. = not determined

Plant age (years)	Fruit biomass (gDW)		Fruit biomass as percent of total growth (%)		Nutrient requirement for fruits as percent of total annual requirement							
					Nitrogen		Phosphorus		Potassium		Calcium	
	Juniperus	*Acacia*	*Juniperus*	*Acacia*	*Juniperus*	*Acacia*	*Juniperus*	*Acacia*	*Juniperus*	*Acacia*	*Juniperus*	*Acacia*
4	0.0	35.4	0	41	0	42	0	51	0	45	0	37
5	0.0	100.4	0	43	0	43	0	50	0	44	0	31
6	2.6	227.8	8	71	10	74	9	74	2	83	2	50
7	11.8	256.1	22	29	25	43	20	64	5	51	5	48
8	24.3	n.d.	39	n.d.	45	n.d.	28	n.d.	17	n.d.	17	n.d.
9	24.2	n.d.	24	n.d.	23	n.d.	30	n.d.	8	n.d.	8	n.d.
10	45.0	852.0	5	51	27	62	27	68	5	66	5	52
Male flowers	n.d.	322.2	n.d.	39	n.d.	22	n.d.	37	n.d.	32	n.d.	29

Table 3. Carbon-isotope ratios of *Phoradendron species growing on Acacia* and *Juniperus*. Data are mean ± 1 SD

		No. of determinations	$\delta^{13}C$ (‰)	$\delta^{13}C$ difference (‰)
Phoradendron californicum		4	−26.93 ± 0.14	−0.20 ± 0.51
Acacia greggii		4	−27.13 ± 0.52	
Phoradendron juniperinum		6	−26.42 ± 0.24	−3.02 ± 0.20
Juniperus osteosperma		6	−23.40 ± 0.31	
Phoradendron californicum[a]	Hyperparasite	2	−28.5	−0.60
Phoradendron californicum	Parent host and parasite	1	−27.9	−0.60
Acacia greggii	Host	1	−27.3	

[a] Hyperparasitic *Phoradendron* growing on its parent plant which is, in turn, parasitic on *Acacia*

of *Phoradendron* growing on *Acacia* could either be the result of a dilution effect with growth of a respective age class, or it could be caused by nutrient retranslocation. Both possible effects can be separated from the total accumulation of nutrients per plant (Fig. 6). Very little N was translocated from old to young tissues within the mistletoe. All the N which comes from the xylem of the host was directly transported to the youngest, newly grown twigs and to the fruits. The decreasing N content in old tissues (Fig. 5) of *Phoradendron* on *Acacia* appeared to be merely a dilution effect resulting from increases in growth of the respective twig age class. This seems also to be the case for P, K, and Ca, although some translocation may have occurred between two-year-old twigs and fruits (located on two-year-old twigs). *Phoradendron* on *Juniperus* showed similar patterns of nutrient accumulation as shown in Fig. 6, but at a much lower level. The enrichment of N (Fig. 5) was of minor importance when the nutrient accumulation of the whole plant was considered. For both types of hosts, the largest proportion of N

was invested by mistletoes in the current year's growth and into fruits.

Fruit production was a very important feature in *Phoradendron* (Table 2). When growing on *Acacia*, 40–70% of the annual growth was invested into fruits. This harvest index is higher than observed in most annual herbaceous species and higher than in any other woody plants (Schulze 1982). The harvest index was lower when *Phoradendron* was growing on *Juniperus*. Fruit production was also an important sink for nutrients. More than 70% of the annual N, P and K gain and even more than 50% of the Ca gain may be transported into fruits of *Phoradendron* on *Acacia*. This proportion is appreciably lower when growth occurs on *Juniperus*, partially because of a lower fruit production and because of substantial differences in the nutrient contents (Fig. 5). Especially N, but also K and Ca contents are lower when *Phoradendron* is growing on *Juniperus* than on *Acacia*.

The previous data on biomass and nutrient accumulation showed that one primary response of mistletoes to an improved N supply was an in-

creased rate of growth. However, the question remaining unanswered so far is whether or not the improved rate of N supply also had an effect on the water-use efficiency. Only information on transpiration rates and water-use efficiency could indicate whether or not the mistletoes regulated the rates of water loss according to the nutrient supply rate. This question cannot be precisely answered without continuous porometer measurements. However, long-term estimates of water-use efficiency can be derived from the $\delta^{13}C$ value (Farquhar et al. 1982a, b). If the differences in $\delta^{13}C$ values between host and mistletoe were more similar when grown on a N_2-fixing host when compared with growth on a non-N_2-fixing host, this would be a very strong indication that water-use efficiency had improved with the rate of N supply. Table 3 shows that indeed the differences in $\delta^{13}C$ values between host and mistletoe were smaller when *Phoradendron* was grown on *Acacia* than when grown on *Juniperus*. These data indicated that *Phoradendron* not only grew faster with a higher rate of N supply, but also improved its water use, thus providing support for the initial hypothesis that mistletoe transpiration was regulated according to the rate of N supply.

Discussion

Mistletoes are known to have relatively high transpiration rates and unusually high K levels in their tissues (Wolfe 1880; Nicoloff 1923; Hartel 1937; Lamont and Southall 1982), but there has been no attempt to combine this information in order to gain an understanding of the underlying nutrient and water fluxes (Atsatt 1983). Recently Glatzel (1983) attempted to explain the Ca and K levels in mistletoes by the influx rates via the transpiration stream. It appears that both K and Ca are passively accumulated. The K enrichment is the consequence of a lack of a retranslocation link (i.e. phloem) between the mistletoe and its host. This enrichment should increase with transpiration rate. This is clearly the case for the accumulation of P, K, and Ca in *Phoradendron* growing on *Juniperus* when compared with their growth on *Acacia*.

The situation is different for N, which was not accumulated in mistletoes growing on oak (Glatzel 1983). In conjunction with measurements of xylem sap concentrations, Schulze et al. (1984) concluded that the high transpiration rates of mistletoes on oaks were a mechanism to obtain the required amount of nitrogen for growth. This again could be a passive process resulting from intrinsically

higher transpiration rates in mistletoes. Thus, the question still unanswered is whether or not mistletoes transpire at a rate closer to that of their host if nitrogen is more abundant in the xylem sap. Only under such a situation could mistletoes reduce the expenditure of host water reserves and supplies, which in arid climates may be important to host survival. The present observations of mistletoe growth on *Juniperus* under conditions of reduced N supply show that water-use efficiency is lower in an attempt to obtain sufficient N from the xylem sap. However, Schulze et al. (1984) showed that there is a limit to the extent that the mistletoe transpiration rate can exceed that of the host; this rate is determined by the conductivity and water-contents properties of the host tissues. Even though the host twig grows in proportion to the mistletoe biomass, the mistletoe can only maintain a constant but limited higher level of water loss than its host, and cannot transpire at a greatly elevated rate. The N content of young mistletoe tissues of *Juniperus* is at the low end of the spectrum when compared with that of other higher plants, but increases with leaf age indicating that even older tissues are capable of N uptake. This is opposite to the pattern observed under higher N-supply rates in *Acacia*.

Both growth rates and fruit production are increased under higher N-supply rates, but at the same time the differences in water-use efficiency between host and mistletoe disappear. The absolute rates of transpiration differ between the hosts, but this is consistent with general differences in water-loss patterns between gymnosperms and angiosperms (Schulze and Hall 1982). However, for the present comparison, it is only important to note that the proportional differences in growth of mistletoes on hosts with different xylem sap N contents do not correspond with proportional differences in transpiration rates. The similarity in transpiration rates of *Phoradendron* and *Acacia* are not the result of limited water supply to the *Acacia*. *Cercidium floridum* is a leguminous tree with water-storage capabilities occurring in the same habitats as *Acacia*, but still the water-use efficiency of the mistletoe on *Cercidium* is close to its host (unpublished observations). Thus, the present observations strengthen the support for the hypothesis that the high transpiration rates of xylem-tapping parasites are a parasitism to obtain nitrogen from their hosts.

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