Mistletoes and mutant albino shoots on woody plants as mineral nutrient traps

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Abstract

INTRODUCTION

It has long been known that mistletoes have significantly higher potassium contents in their foliage than their hosts (Glatzel, 1983; Lamont, 1985; Karunaichamy et al., 1999). One hypothesis to explain the difference is based on the cycling of potassium in tree photosynthate transport from the foliage to the roots in the phloem and back up into the canopy in the xylem (Lamont and Southall, 1982; Glatzel, 1983; Lamont, 1985). If mistletoes do not feed their hosts with sugars, elements which are involved in sugar loading and co-transported with sugars in the phloem are trapped in the parasite.

There is a remarkable physiological similarity between hemiparasitic plants, such as mistletoes, and albino shoots originating from somatic mutations. Both may be considered parasites; therefore, citrus farmers will usually remove such shoots as soon as they find them. Both grow, feed and are sheltered on a plant, while contributing nothing to its survival. The latter fact differentiates albino shoots from otherwise physiologically comparable fruits, which obviously are functional to species survival. Albino shoots import mineral nutrients both via the phloem during their growth and via the xylem when they transpire. Stomatal closure during the hottest part of the day was incomplete in albino leaves which lack chloroplasts in their guard cells. Therefore, the transpiration rate was higher than in green leaves (Lo Gullo et al., 2007), a peculiarity also found in mistletoes in relation to their hosts (Glatzel, 1983). Based on physiological similarities we hypothesize that mistletoes and albino shoots should display similar nutrient relationships to their host tissues and act as nutrient traps.

Development of the nutrient trap hypothesis was based on the mistletoe Loranthus europaeus, a rather atypical, dioecious, deciduous Loranth of temperate forests growing mainly on deciduous oaks. The species-rich, semi-deciduous mountain forests of the Nepal Himalayas (UMH, upper mixed hardwood forests in Nepal zonation; Shrestha, 2011) allowed us to expand the work to a variety of evergreen and deciduous hosts in three families parasitized by the more typical, evergreen, hemiparasitic Scurrula elata (Loranthaceae), which develops a complex haustorial system of abundant epicortical runners (Devkota and Glatzel, 2005). All parasitic plants receive mineral nutrients through the haustorium, a complex organ linking the vascular system of

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the parasite to that of the host (Kuijt and Toth, 1976; Kuijt, 1977; Bell and Adams, 2011). Whereas holoparasites import minerals via both xylem and phloem, hemiparasitic mistletoes seem to get most minerals with the xylem sap diverted from the host by tapping its xylem in the haustorium (Glatzel, 1983; Bell and Adams, 2011). Most hemiparasites have no efficient phloem connectivity with the host plant or do not leak substantial amounts of solutes back to the host (Bell and Adams, 2011). Thus, phloem–xylem recycling is restricted to within the mistletoe. This means that even phloem-mobile chemical elements will stay in the mistletoe, while additional amounts will enter the hemiparasite from the xylem when it transpires. The outcome is a net accumulation of potassium, sulphur and phosphorus as well as zinc, sodium and copper in the leaves of the mistletoe, which contain higher amounts of these elements than the host leaves. Potentially dangerous accumulation of solutes is avoided by restriction of water uptake, succulence, or export by shedding of leaves or fruits (Glatzel, 1983, 1996; Bell and Adams, 2011). Dangerous accumulation of solutes is particularly pronounced in holoparasites (Hibberd and Jeschke, 2001; Bolin et al., 2010) because they import solutes via both the xylem and the phloem pathways (Olson and Kuijt, 1985; Press et al., 1991).

Experiments with mistletoes are difficult due to the fact that they grow only on live hosts, are often not readily planted on hosts and are quite inaccessible for repeated sampling. The question of potential selective mineral nutrient uptake from the xylem is therefore still not conclusively resolved (Bell and Adams, 2011). Thus, phloem–xylem recycling is restricted to within the mistletoe. This means that even phloem-mobile chemical elements will stay in the mistletoe, while additional amounts will enter the hemiparasite from the xylem when it transpires. The outcome is a net accumulation of potassium, sulphur and phosphorus as well as zinc, sodium and copper in the leaves of the mistletoe, which contain higher amounts of these elements than the host leaves. Potentially dangerous accumulation of solutes is avoided by restriction of water uptake, succulence, or export by shedding of leaves or fruits (Glatzel, 1983, 1996; Bell and Adams, 2011). Dangerous accumulation of solutes is particularly pronounced in holoparasites (Hibberd and Jeschke, 2001; Bolin et al., 2010) because they import solutes via both the xylem and the phloem pathways (Olson and Kuijt, 1985; Press et al., 1991).

MATERIALS AND METHODS

Mistletoe studies

Mistletoe and host leaves came from the Annapurna Conservation Area of Nepal. Samples were collected between 1999 and 2002 in the Bhalache forest, a moderately steep, SE-facing slope west of the village of Ghandruk (28° 25’30”N, 83° 48’59”E), between 2100 and 2350 m elevation. Vegetation is an open, broadleaved semi-deciduous upper montane forest (Chaudhary, 2000; Shrestha, 2011) that has been degraded by heavy pastoral use. The dominant, common mistletoe species in this area is Scurrula elata (Loranthaceae).

We investigated chemical element contents in mistletoe and host leaves (study 1), we compared the element contents of host leaves on infected and uninfected branches (study 2), and we studied the effects of experimentally manipulated haustorium–shoot ratios on biometric and chemical variables (study 3). In study 1 the contents of a range of chemical elements in Scurrula leaves were compared with the contents in the leaves of four host species: Rhododendron arboreum Sm. (Ericaceae), a medium-sized, often multi-stemmed, evergreen tree; Lyonia ovalifolia (Wall.) Drude (Ericaceae), a deciduous shrub; Lindera pulcherrima (Nees) Benth. ex Hook.f. (Lauraceae), an evergreen shrub; and Viburnum erubescens Wall. (Caprifoliaceae), a deciduous shrub. In study 2, the element contents of host leaves, collected from mistletoe-infected host branches distal to the attachment point of the mistletoe, were compared with element contents in leaves on uninfected host branches. In study 3, we experimentally manipulated haustorium–shoot ratios in mistletoes by removing half of the foliage in spring and analysing the newly formed leaves in autumn.

To study the element contents in leaves of Scurrula and its hosts Rhododendron, Lyonia, Lindera and Viburnum we sampled 20 mistletoe specimens on each host species along with host leaves at similar positions in the crowns. Twenty leaves were collected from each mistletoe and host branch to ensure a representative sample and a sufficient amount for chemical analysis. For the study of the effects of mistletoe infection on the chemical composition of host leaves, 20 host leaves were collected from the apical parts of 20 branches with and 20 without mistletoe infection. The mistletoes had a foliage mass roughly matching by visual judgement the foliage mass on the terminal part of the host branch. We selected and marked infected and uninfected branches of, by visual judgement, comparable diameter. We then measured the diameter of the host branches, 5 cm distal from their attachment. We included only branches in the study with diameters not deviating more than 20% from the mean of all pre-selected branches. For the experimental manipulation of haustorium–shoot ratios in mistletoes, 40 individuals of the mistletoe Sc. elata of visually comparable size and an age of 4–6 years (determined by counting the dichotomous bifurcations) were marked on Rhododendron arboreum hosts. In May, prior to the flushing of the host trees, half of the branches with live leaves were snapped off at the dichotomous bifurcation points from 20 randomly selected mistletoe plants. In September, 20 leaves each on the newly formed branches of untreated and treated mistletoes were collected for analysis. Fresh mass of the leaves and leaf area were determined immediately after collection. The samples were then dried in a household fruit drier at the guest house in Ghandruk to prevent spoilage during transport.

In the laboratory (Institute of Forest Ecology, BOKU Vienna) the samples were re-dried at 80°C, cooled and weighed. After grinding, the element content was determined on randomly drawn subsamples. Total nitrogen was analysed using a semi-micro-Kjeldahl procedure after digesting samples with H2SO4 and Kjeltab catalyst (Fisher Chemicals) at 400°C. For analysis of the other elements, milled samples were digested...
with a mixture of HNO₃ and HClO₄ at 200 °C with reflux cooling. The digested samples were analysed by ICP-OES (inductively coupled plasma optical emission spectrometry; Perkin-Elmer Optima 3000 XL). Measurements were made after linear calibration ($r^2$ at least 0.999) with matrix-adapted standard solution (Spectronex).

**Albino shoot studies**

Study objects were shoots of orange trees (*Citrus sinensis*) and oleander bushes (*Nerium oleander*). About 15-year-old *Citrus* plants were sampled between May and early September 2009 in an orchard in Roccavaldina, Messina, Italy (38°10′54″N, 15°22′22″E), while *Nerium* plants, about 8 years old, were sampled in an open field at the campus of the University of Messina (38°15′47″N, 15°35′37″E) at a south-west exposure. Three plants of both species were selected bearing green and at least two unpigmented albino shoots. All measurements were taken during the summer.

Maximum transpiration rate ($E_t$), photosynthesis rate ($P_N$) and leaf water potential ($\Psi_L$) were recorded hourly on five leaves between 1200 and 1500 h. This period was chosen because in a previous study (Lo Gullo et al., 2007) the stomatal conductance to water vapour as well as the transpiration rate in albino *Citrus* leaves were quite constant except during the hottest part of the day. The temperature during the daylight hours ranged from about 23 °C to about 28 °C with a relative humidity of 45–55 %. Plants were well irrigated the evening before experiments. At least eight green and eight albino, fully expanded leaves per plant were randomly selected for the determination of transpiration rate and photosynthesis rate with a portable photosynthesis system (LCi Biosystems, ADC Bioscientific Ltd, Hoddesdon, UK), equipped with the standard broadleaf cuvette for *Citrus* and a narrower cuvette (LCi 013/N) more suitable for the shape of *Nerium* leaves. At the same time, leaf water potential was determined on at least five green and five albino leaves in a pressure chamber (Soilmoisture 3500, Soilmoisture Equipment Corp., Santa Barbara, CA, USA).

At the end of field measurements, 50 green and 50 albino leaves were randomly sampled from six albino and six green branches. The leaves were immediately wrapped in thin plastic foil to prevent water loss. Fresh mass was measured with a digital precision balance (OHAUS Explorer, Switzerland, accuracy ±0.1 mg), leaf surface area with a portable Leaf Area Meter (LICOR LI-3000A, Lincoln, NB, USA). The leaves were marked, numbered and kept in a lab oven at 80 °C for 3 d to obtain single leaf dry mass. Dry mass per unit leaf area could then be calculated for each leaf. The dry samples were sent to the laboratory of the Institute of Forest Ecology, BOKU Vienna, for mineral analysis as described above.

To analyse phloem structure, at least five white and five green leaves from different stems of *Citrus* and *Nerium* were fixed in FAA (formalin–acetic acid–ethanol 1:1:1, v/v) and then post-fixed in 2 % osmium tetroxide in phosphate buffer, pH 7.2, for 2 h to demonstrate the protein and nucleic acid content of companion cells. After fixation the material was rinsed in tap water for 2 h and hand-sectioned. Transverse sections showing the midrib were alcohol-dehydrated, mounted in Surgipath Micromount resin and observed with a Leitz Diaplan light microscope with an immersion objective. Images were recorded through a Leica DC 300F camera connected to a PC.

Data were analysed with Excel (Microsoft Office) and SPSS as well as SigmaStat version 3.1 (SPSS, Chicago, IL, USA) to test for statistical differences of the treatment means (Student’s $t$-test).

**RESULTS**

The presence of mistletoes on host branches of statistically non-significantly different diameter led to highly significant differences in total leaf area and total dry mass of host

| Table 1. Biometric variables of parasitized (Scurrula elata) and non-parasitized branches and leaves of Rhododendron arboreum, and element contents of dry leaves |
|----------------------|--|----------------------|--|
| Variable             | Non-parasitized *R. arboreum* | Parasitized *R. arboreum* | Mistletoe *S. elata* |
| Host branch diameter (cm) | 1.44 ± 0.13 | 1.51 ± 0.35 | – |
| Total leaf area (cm²) | 3554 ± 377 | 1985 ± 32.4*** | 741 ± 133*** |
| Total dry mass of leaves (g) | 83.1 ± 8.9 | 47.4 ± 34.8*** | 40.2 ± 4.3*** |
| Mean fresh mass of a leaf (g) | 1.32 ± 0.28 | 0.97 ± 0.28* | 0.98 ± 0.15* |
| Mean dry mass of a leaf (g) | 0.64 ± 0.15 | 0.50 ± 0.13* | 0.35 ± 0.07*** |
| N (mg g⁻¹) | 9.13 ± 1.37 | 8.19 ± 1.64** | 10.0 ± 1.98*** |
| P (mg g⁻¹) | 0.47 ± 0.08 | 0.43 ± 0.08 | 0.93 ± 0.21*** |
| S (mg g⁻¹) | 0.90 ± 0.11 | 0.81 ± 0.12** | 1.29 ± 0.41*** |
| K (mg g⁻¹) | 4.22 ± 1.08 | 3.98 ± 1.07 | 20.4 ± 5.29** |
| Ca (mg g⁻¹) | 7.35 ± 1.47 | 7.46 ± 1.39 | 5.85 ± 2.40* |
| Mg (mg g⁻¹) | 1.40 ± 0.31 | 1.33 ± 0.32 | 1.81 ± 0.33*** |
| Na (µg g⁻¹) | 1148 ± 32.3 | 1518 ± 71.0 | 151 ± 84 |
| Mn (µg g⁻¹) | 385 ± 163 | 374 ± 141 | 314 ± 178 |
| Fe (µg g⁻¹) | 79.4 ± 19.9 | 79.8 ± 22.9 | 57.4 ± 20.0* |
| Cu (µg g⁻¹) | 0.42 ± 0.34 | 0.21 ± 0.27 | 6.48 ± 0.90** |
| Zn (µg g⁻¹) | 14.1 ± 7.10 | 13.8 ± 16.0 | 15.9 ± 9.3 |

Statistically significant differences ($t$-test) compared with non-parasitized *Rhododendron arboreum* are indicated as follows: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. 
leaves (Table 1). The fresh and dry mass of individual host leaves was less influenced but was nevertheless statistically significantly reduced on branches infected with mistletoes. Element contents of host leaves on parasitized and non-parasitized branches were not significantly different except for nitrogen and sulfur (Table 1). Compared with the element contents of host leaves the mistletoe leaves had highly significant increases in nitrogen, phosphorus, potassium, calcium, iron and copper contents (Table 1).

Table 2 shows that a 50% reduction of potentially competing foliage of S. elata arising from an existing haustorial system on Rhododendron arboresum branches had no effect on biometric leaf variables and did not change element contents with the exception of a statistically significant but moderate increase in calcium and zinc levels.

Table 2. Effects of removal of half of the mistletoe branches in May on biometric data and nutrient contents of current year’s leaves of Scurrula elata, sampled in September 2002

| Variable | Control | 50% of the branches removed |
|----------|---------|----------------------------|
| Mean fresh mass of a new leaf (g) | 1.17 ± 0.26 | 1.25 ± 0.28 |
| Mean dry mass of a new leaf (g) | 0.37 ± 0.083 | 0.39 ± 0.083 |
| Mean leaf area of new leaves (cm²) | 25.7 ± 2.54 | 26.1 ± 2.81 |
| Specific leaf area of new leaves (cm² g⁻¹) | 69.6 ± 5.11 | 67.5 ± 6.02 |
| N (mg g⁻¹) | 10.0 ± 1.66 | 10.6 ± 1.48 |
| P (mg g⁻¹) | 1.20 ± 0.078 | 1.22 ± 0.084 |
| S (mg g⁻¹) | 1.30 ± 0.146 | 1.36 ± 0.112 |
| K (mg g⁻¹) | 20.0 ± 1.12 | 18.9 ± 1.27 |
| Ca (mg g⁻¹) | 6.77 ± 1.09 | 7.80 ± 1.41* |
| Mg (mg g⁻¹) | 2.05 ± 0.24 | 2.10 ± 0.24 |
| Na (mg g⁻¹) | 204 ± 23.3 | 187 ± 26.4 |
| Mn (µg g⁻¹) | 407 ± 132 | 480 ± 149 |
| Fe (µg g⁻¹) | 51.0 ± 23.1 | 53.3 ± 19.9 |
| Cu (µg g⁻¹) | 8.62 ± 1.32 | 9.37 ± 1.99 |
| Zn (µg g⁻¹) | 22.5 ± 8.33 | 34.0 ± 9.89* |

Values are mean ± s.d.; t-test: *P < 0.05.

Leaf biometry, photosynthesis, transpiration and element contents of green and albino leaves of Citrus and Nerium were summarized in Table 3. Statistically significant differences in leaf specific dry mass (LMD) were recorded in both species (P < 0.001). Compared with green leaves, the leaf-specific dry mass was 25% less (99.8 ± 27.6 vs. 131.5 ± 14.0 g m⁻²) in albino Citrus and 38% less (82.0 ± 16.0 vs. 132.7 ± 35.9 g m⁻²) in albino Nerium (Table 2). Albino Citrus and Nerium leaves had a surface area about 60% smaller than green leaves. The absence of pigments in albino leaves of both species prevented photosynthesis (Pₐ) (Table 3). Differences in element contents of green and albino leaves were highly significant for N, P and K as well as for Ca in both species.

Figure 1 compares the nitrogen, phosphorus and potassium contents in host and mistletoe leaves as well as in green and white leaves of Citrus and Nerium plants with mutant albino shoots. Phosphorus and potassium contents were significantly higher in mistletoes than in host species (P < 0.001). In Scurrula, leaf P content was about 50% higher than in Lindera, Lyonia and Viburnum and more than 100% higher than in Rhododendron. A similar trend, but with higher increase, was found for leaf potassium in mistletoe, which was about two times higher than in Lindera, Lyonia and Viburnum, while a slight but significant increase of about 19% was recorded in the hemiparasite compared with Rhododendron. Figure 1 shows also that the nitrogen, phosphorus and potassium contents in albino as well as in control (green) leaves of Citrus and Nerium were statistically higher in albino than in green leaves in both species. However, while P and K contents increased two- to three-fold in albino leaves, nitrogen content was only about 13% higher in albino Citrus and 47% higher in albino Nerium.

When element contents are related to N content (Fig. 2), the K/N and P/N ratios are statistically highly significantly more variable in mistletoe and albino leaves than in host and green leaves, respectively, with the exception of a non-significantly different P/N ratio in Nerium. In other words,
an enrichment of P and K in relation to the protein content was
evident in the mistletoe as well as in albino leaves, with N
serving as a proxy for protein. In leaves of Scurrula parasitizing
Lindera and Lyonia, S/N as well as Mg/N ratios were signif-
ificantly more variable. Ca/N ratios in leaves of Scurrula parasitizing
Rhododendron and in albino leaves of Citrus
and Nerium were significantly narrower.

Microscopic observation of phloem structure showed an
obvious reduction in the number of companion cells in
albino leaves in both species. Companion cells were smaller
in albino leaves and sometimes absent (Fig. 3).

DISCUSSION

Our data extend the evidence for a functional correspondence
between mistletoes and albino leaves. Albino leaves of Citrus
as well as Nerium show a higher evapotranspiration rate
compared with green leaves during the hottest part of the day,
despite a similar decline in leaf water potential (Table 3).
Hydraulic conductance (K) of albino shoots was thus higher
than in green shoots because it depends directly on transpiration
rate (E_l) and inversely on the drop of water potential (∆Ψ)
(K = E_l/∆Ψ). These data, together with those in a previous study (Lo
Gullo et al., 2007), support the idea that albino leaves as well as
mistletoes change the water balance of a green plant (Glatzel,
1983; Lamont, 1985; Lo Gullo et al., 2007). Both leaf size
and leaf mass of host leaves on mistletoe-infected branches
are reduced (Table 1). This is in accordance with the hypothesis
that hemiparasitic mistletoes have a competitive advantage in
diverting water and mineral elements dissolved in the xylem
sap from their host and thus restrict the growth of host leaves
(Glatzel, 1983; Glatzel and Geils, 2009).

Studies on uptake and discrimination of elements by the
haustorium support the hypothesis that active uptake plays
only a minor or no role in *Scurrula elata*, despite the fact that this mistletoe has a complex system of epicortical runners and secondary haustorial sinkers. The presence of mistletoes with a leaf area comparable with that on the terminal section of the host branch had no effect on element levels in the host leaves when compared with host leaves on uninfected branches, with the exception of nitrogen and sulphur, both of which were moderately reduced (Table 1). This could be an effect of high levels of nitrogen and sulphur compounds in the xylem during flushing of the leaves, when mistletoe leaves transpire more than host leaves and thus divert more of these elements from the host. Some uptake of phloem solutes, however, cannot be excluded (Panvini and Eickmeier, 1993; Marschner *et al.*, 1995; Hibberd and Jeschke, 2001; Tešitel *et al.*, 2010).
The experiment on haustorium–shoot ratio manipulation, i.e. a 50% reduction of potentially competing foliage of *S. elata* arising from an existing, several-year-old haustorial system on *Rhododendron arboreum* branches, had no effect on biometric leaf variables and did not change element contents with the exception of a statistically significant but moderate increase in calcium and zinc levels (Table 2). In rooted plants, coppicing or shoot pruning generally leads to larger leaves that are better supplied with nutrients, as demonstrated by many experiments (Insley et al., 1981; Nuorteva and Kurkela, 1993; Lavigne et al., 2001). Higher calcium levels could be a result of the low mobility of calcium in plant tissues (Hanger, 1979; Marschner et al., 1995) which prevents translocation of these elements from the leaves to the fruits of mistletoes. Note that we could not include the fruits of the mistletoes in our study because birds had consumed most ripe fruits at the time of sampling. As new leaves emerge before flowering and fruiting, we think that the removal of 50% of competing branches would primarily affect new leaves.

Based on comparison of the element contents of leaves from parasitized and non-parasitized host branches (Table 1) and the results of the experiment on haustorium–shoot manipulation we conclude that the haustorium of the hemiparasitic mistletoe *Scurrula elata* is functionally not analogous to a root because apparently it has no or only a very limited capacity for selectively controlling the uptake of solutes from the host’s xylem water. This is probably a general feature of hemiparasitic mistletoes, which seem to lack an endodermis-like structure in their haustoria. An endodermic barrier is a prerequisite for nutrient discrimination and active uptake.

Elements that are recycled between photosynthetically active plant organs and photosynthe-tic-respiring tissues of rooted plants in an exchange between phloem and xylem (Marschner et al., 1995; Thompson and Zwieniecki, 2005; Pritchard, 2007; Gajdanowicz et al., 2011) are enriched in the hemiparasite (Fig. 1). This is in accordance with the hypothesis that sugars and associated ions or complex solutes in the phloem sap of mistletoes are retained in the parasite and not transferred to the phloem system of the host in significant amounts (Glatzel, 1983; Glatzel and Geils, 2009). As haustoria of parasitic plants are quite variable (Kuijt, 1977; Bell and Adams, 2011) it is not yet clear whether this is a consequence of the lack of a functional phloem interface in the haustorium of all hemiparasites or a more fundamental consequence of parasitism. Even parasitic plants with their own photosynthesis are functionally parasites and not just different ‘branches’ of the host contributing to its carbon gain.

The evidence thus supports the hypothesis that enrichment of phosphorus and potassium in mistletoe tissues as well as in albino leaves results from their role as traps for elements cycled between xylem and phloem. Even though hemiparasitic mistletoes have green leaves and are capable of photosynthesis, they do not exchange the products with their hosts but rather invest their photosynthetic gain in abundant fruiting, which is essential for successful dispersal. Because almost no phloem sap of the parasite finds its way into the host, the elements co-transported with the sugars in the phloem remain trapped in the mistletoe.

The abundance of phosphorus and potassium in mistletoe tissues is an indicator for substantial xylem–phloem–xylem cycling of these elements in trees. Root hemiparasites such as *Striga* (Smith and Stewart, 1990) and *Odontites* (Llugany et al., 2009) accumulate potassium from their herbaceous hosts just like mistletoes on above-ground tree branches. To quantify mineral cycling by the use of hemiparasites as probes, additional information on the dynamics of leaf turnover in host and parasite as well as export by flowering and fruiting would be needed.

In albino leaves of *Citrus* as well as *Nerium*, higher contents of nitrogen, phosphorus and potassium compared with green leaves were found, too (Fig. 1). Relating the element contents

**Fig. 3.** Phloem cross-section of albino (W) and green (G) *Citrus sinensis* and *Nerium oleander* leaves. Arrows indicate sieve elements with companion cells (CC/SE) as well as sieve elements without companion cells (SE). Scale bar = 10 μm.
of mistletoe and albino leaves to the nitrogen content (as a proxy for protein or ‘living matter’) of host leaves and green leaves, respectively, provides additional information (Fig. 2). The trapping of potassium is evident both in mistletoes and in albino shoots. With the exception of Nerium, phosphorous accumulates too. These observations are in agreement with the nutrient trap hypothesis proposed for Loranthus europaeus by Glatzel (1983). The significantly lower Ca levels in albino leaves as compared with mistletoe leaves could be the result of differences in development and sampling earlier in the growing season. Albino shoots are the result of flushing from buds and are formed over a relatively short time depending exclusively on organics supplied by the plant from which they sprout. Hemiparasitic mistletoes, by contrast, grow over the whole growing season on carbohydrates from their own photosynthesis.

Albino shoots, in contrast to mistletoes, have a functional connection with the phloem of the mother tree. They do not, however, photosynthesize and are therefore permanent sinks for carbohydrates, although the import is at very different rates during and after shoot and leaf development. Mass import of sugars ends at the same developmental stage as in green leaves (Turgeon, 1984), but is not followed by a period of export. The import must continue, although at a much reduced rate, to maintain cell metabolism. It has to be assumed that potassium entering this sink together with the sugars is not re-loaded into the phloem because of a lack of newly synthesized sucrose and will thus accumulate together with the ions imported via the xylem. In this respect albino shoots resemble holoparasites, which lack photosynthesis and are therefore permanent sinks exclusively on organics supplied by the plant from which they obtain their nutrition (Deeken et al., 2002). K⁺ might also keep the gradient in phloem sucrose small where a large gradient in phloem osmotic potential is needed to compensate for an opposite gradient in xylem water potential. A low-viscosity potassium solution could reduce osmotic potentials without increasing the concentrations of sucrose, which makes solutions viscous (Thompson and Zwieniecki, 2005).

Potassium is actively taken up into the phloem under ATP consumption in sucrose-loading sources. A recent paper (Gajdanowicz et al., 2011) suggests that the potassium could act as an ‘energy battery’ for the phloem membrane by producing ATP when released. This would solve a problem that is of importance for the release phloem: it is doubtful whether the few mitochondria in sieve elements of higher plants are functional at all, companion cells with their rich complement of mitochondria are rare in release phloem (van Bel, 2003), and oxygen is a scarce commodity in the phloem (van Dongen et al., 2003). On the other hand, phloem function depends on a steady local energy supply. The role of potassium proposed by Gajdanowicz et al. (2011) could be a supply of this energy via a ‘mobile battery’. The need for high phosphate concentrations in the phloem may be related to ATP-dependent phloem unloading.

Conclusions

Our hypothesis was that there should be strong similarities between mistletoes and albino shoots not only in water relationships (as had already been found) but also in the accumulation of some chemical elements, in particular potassium and phosphorous. This is indeed what we have found, and a common cause in the two systems is an inability to re-export these elements once they have entered the mistletoe or the albino shoot. As Marschner et al. (1995) have argued, there is a general tendency for potassium and phosphorus enrichment in plant parts importing large amounts of carbohydrates via the phloem without the functional role or the anatomical prerequisites for re-exporting these nutrients. Thus, mistletoes and albino shoots become traps for normally recycled chemical elements.

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