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Original Article

Halophytic hosts imprint their parasites – the case of *Plicosepalus acaciae* and their hosts in the Arava Valley (Southern Negev, Israel)

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Running titel: Adaptation of *Plicosepalus acaciae* to salt stress

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ABSTRACT

- **Background and Aims** The mistletoe *Plicosepalus acaciae* (Zucc.) Wiens & Polhill (syn: *Loranthus acacia* Zucc.; Loranthaceae) with an east-sudanian distribution is a common parasite along the Arava-Valley and occurs north to the Dead Sea area and the Jordan Valley. In the southern Arava-Valley (Israel) it occurs on five halophytic and at least ten non-halophytic hosts. From the whole area in the Middle east more than 40 host species are known. Adaptation of *Plicosepalus* growing on halophytic hosts were investigated in comparison with non-halophytic hosts.
- **Methods** Anions pattern of different host-parasite association were investigated with an , while Cl was determined titrimetrically with micro-chlorocounter. The development of leaf succulence were determined of different growth stages.
- **Key Results** *Plicosepalus acaciae* can develop morphological adaptations when growing on halophytic hosts as other halophytes on saline soils. Formation of succulent leaves is a typical morphological adaptation in halophytes. Water content and succulence of the mistletoe increased on halophytic hosts especially on *Tamarix* species. Leaf water content was 3 times higher on halophytic hosts and the leaf volume increased 4 – 5 times. However, halophytic hosts differ considerably in their influence on ion pattern and on leaf structure of their parasites.
- **Conclusions** Like saline soils the hosts are to some extent imprinting their specific site-conditions onto the parasites. *Plicosepalus* shows a high morphological and ecophysiological plasticity to cope with salt stress and can be classified as a facultative eu-halophyte, which increases its halo-succulence according to the host which is in this respect comparable to soil

substrates. Basically this host-parasite-association is a perfect model system for adaptation to salt stress.

Keywords: Loranthaceae, mistletoe, parasite, ion pattern, salt stress, sodium, chloride succulence, physiological adaptations, plasticity

INTRODUCTION

Halophytes developing various physiological and morphological adaptations to cope with high salt concentration in soil and water (Waisel, 1972; Breckle, 2002; Flowers and Colmer, 2008).

Especially the regulation of Na^+ , K^+ , and Cl^- ions uptake, transportation and storage in the plant organs are in this context key issues to understand their life strategies (Breckle, 1990).

Hereby, the ions pattern and chemical composition of such terrestrial halophytes are often characteristic for the specific species and plant family and only partly influenced by the soil conditions ('physiotype concept', Albert, 1982). For example some desert halophytic Aizoaceae

and Chenopodiaceae are able to increase the Na^+ and Cl^- content in the succulent leaves also under low salinity conditions (e.g. Veste and Breckle, 2000; Veste et al, 2004). These emphasize the important of active ions regulation and selective transportation already in the root system.

On the other hand, xylem-trapping mistletoes depending for their nutrient and water uptake from their hosts (Glatzel and Geils, 2009) and lacking a typical root-shoot system for selective ions uptake. The haustorium connects the parasite with its host and allows the transportation of water, inorganic and organic compounds directly into the parasite with the transpiration stream.

A high accumulation of potassium and phosphate in mistletoes are reported (Lamont, 1983; Glatzel and Balasubramaniam, 1987; Popp 1987, Veste and Breckle, 1995; Todt et al., 2000), while both elements accompany sugars in the phloem sap (Glatzel and Geils, 2009). In this context, only few attention is given to the mistletoe adaptations when growing on halophytic hosts and the influence of the high saline conditions. Popp et al. 1995 showed the increase of ion

content and the development of leaf succulence in *Tapinanthus oleifolius* when growing on *Tamarix usneoides* and on *Euphorbia virosa* in Namibia. Another example is *Plicosepalus acaciae* (Zucc.) Wiens & Polhill (syn: *Loranthus acaciae* Zucc.; Loranthaceae) with an east-sudanian distribution. The mistletoe occurs all along the Arava-Valley and north to the Jordan Valley and in some regions in Jordan. The most common hosts are Acacia trees because of their wide distribution (Munzbergova and Ward, 2002; Bowie and Ward, 2004), while in the southern Arava-valley *Plicosepalus acaciae* occurs on halophytic host trees and shrubs (*Atriplex*, *Nitraria*, *Tamarix*) (Todt et al, 2000). Even though *Plicosepalus acaciae* grows preferentially on Acacia trees, the parasite needs to develop a high morphological and physiological plasticity to grow under such different salt conditions. These high flexibility makes the different host-parasite association of *Plicosepalus acaciae* to an interesting model system to understand their adaptation to salt stress. Up till now, several papers are dealing with the inhibitory or antimicrobial activity of plant extracts of mistletoes against bacteria, mainly because of their flavonoid content (see e.g. Waly et al., 2012). Here we investigated the ecological adaptation of the parasite and its halophytic and non-halophytic hosts in the Arava-Valley. A special focus is given on the ions uptake and its link to the development of leaf succulence in different growth stages and on different hosts. Furthermore, we compiled an updated check list of the known host-parasite association in the relation to salt stress.

MATERIALS AND METHODS

Plant collections were made in May and in September 1997 in the southern Arava-Valley at Yotvata (29° 53' N 35° 3' E, 40 km north of Eilat, Israel) and surroundings. The area is characterized by natural *Acacia* – *Tamarix* vegetation (Veste, 2004), influenced by groundwater, partly mobile sand dunes, agricultural fields, date palm plantations and the nearby settlement Yotvata. Surrounding hills are hamada desert with scattered *Haloxylon salicornicum*. The site

receives in average about 34 mm annual rain, which falls very irregularly but predominantly in the winter season from November to March (Fig. 1). However, the area is all over the year arid. All samples were taken in the close surroundings of Yotvata. Herbarium material from the recorded mistletoe-hosts associations were kept in the Herbarium of the Department of Ecology, University of Bielefeld (BIEL) and in 2005 transferred to the Herbarium of Göttingen (GOET).

For the determination leaves of 5 - 10 mistletoes were collected and after checking fresh weight they were oven-dried (105°C) for further analysis. Leaf area and leaf thickness were measured from young, middle aged and old leaves, in total 100 – 750 leaves. Old leaves were those just before wilting or yellowing at the older branches, they are about 2 years old.

Ash content was determined after burning by 600°C in an oven.

Succulence S is based on the organic dry matter (after Breckle 1976) and was calculated as follows:

$$S = g \text{ H}_2\text{O} / g \text{ organic d.m.} = fw - d.m. / d.m. - ash$$

Ion content was determined in hot water extracts with an atomic absorption spectrometer (AAS 2280, Perkin-Elmer, Waltham, Massachusetts, USA) in the C₂H₂ flame. Cl was determined titrimetrically with Micro-Chlorocounter (Marius, Utrecht, NL). In all analytic determinations 3 repetitions were made, unless the relative standard deviation was not below 2%, then additional checks were made.

For the statistical tests SPSS 7.5.1 was used. Correlations were checked with Spearman's correlation coefficient rs (Köhler et al., 1996; Lozan and Kausch, 1998). Box-Whisker-Plots were used to demonstrate the values in non-normal distributed values, indicating median and inter-quartile values as well as total variation.

RESULTS

In the Arava-Valley the highest density of *Plicosepalus acaciae* can be found in the close surroundings of Yotvata in the southern part of the Arava-Valley. Most of the trees in an area of $3 \times 3 \text{ km}^2$ are parasitized by *Plicosepalus acaciae*. The number of parasites decreases only in a few kilometers distance north and south of Yotvata. Only very few observations of *Plicosepalus acaciae* outside the Arava-Valley could be made by the authors. Wadis with high mistletoe infection rates can be found adjacent to those containing no infections. The movement pattern of bulbul (*Pycnonotus xanthopygos*) can explain the current distribution of *Plicosepalus acaciae* in the Arava valley as being the main disperser of the red berries with the sticky seeds after swallowing and defacation (Green et al., 2009). *Plicosepalus acaciae* is growing in Yotvata very commonly on *Acacia raddiana* and *A. tortilis*. A list of the hosts at the study site Yotvata, in the Arava-Valley and some other areas of the Middle East is given in Table 1.

It is obvious that a high proportion of wild host species has reduced leaves and photosynthesis is mainly in stems. The hosts *Haloxylon persicum* and *Calligonum comosum* are growing on the sand dunes in Yotvata and other sandy areas in the Arava-Valley. *Albizzia*, *Casuarina* and *Delonix* are introduced species and are growing within the Yotvata settlement, whereas *Tamarix aphylla* is natural for the northern Negev, but is planted in Yotvata as windbreaker around the fields and date-palms. Previously published informations on hosts of *Plicosepalus acaciae* (Zohary, 1966; Feinbrun-Dothan et al., 1991; Shmida et al., 1992) mention *Atriplex* and *Tamarix* but no particular species. Qasem (2009, 2011) has updated the list of hosts of *Plicosepalus acaciae* and mentions 26 species from 12 families (Table 1) in Jordan. In total there are now 37 non- and 6 halophytic hosts known.

The size of the mistletoe varies between the different hosts. The largest and many individuals of *Plicosepalus acaciae* grow on *Acacia* and *Tamarix* while on *Atriplex* and *Haloxylon* only few and smaller individuals occur. The highest density of *Plicosepalus acaciae* in the area could be found

on *Acacia tortilis* and *A. raddiana* as well as on *Tamarix nilotica*. No differences in density and preferences of *Plicosepalus acaciae* to non-halophytic or halophytic hosts could be observed.

For the xylem-trapping mistletoes the halophytic host may function like a salt rich substrate. With the transpiration stream ions are transported into the leaves of the parasite. The Na^+ and Cl^- content in mistletoe leaves is up to ten times higher when growing on *Tamarix* in comparision to *Acacia* (Veste and Breckle, 1995). When *Plicosepalus acaciae* was parasitic on halophytic hosts the leaf area (Fig. 2), the leaf thickness (Fig.3) and thus leaf volume (Fig. 4) of old leaves increased considerably, up to 3 fold in comparison to non-halophytic hosts, but rather differing on the various hosts. All values increased very significantly for *Plicosepalus acaciae* on all *Tamarix* species (Fig. 2 - 4). The maximum leaf area of *Plicosepalus acaciae* on *Tamarix nilotica* was 49.8 cm^2 (mean $15.1 \pm 6.2 \text{ cm}^2$) and on *Acacia tortilis* 25.8 cm^2 (mean $6.6 \pm 3.5 \text{ cm}^2$). The leaf thickness increased on *Acacia tortilis* from 2.5 (mean 1.2 ± 0.4) to 3.75 mm (mean 2.4 ± 0.4) on *Tamarix nilotica*. No significant differences in the leaf area, thickness and leaf volume could be found between *Plicosepalus acaciae* growing on the halophyte *Nitraria retusa* and on non-halophytes. Similar to other halophytes the increasing succulence is a morphological adaptation for the mistletoe to the increasing salt stress on halophytic hosts.

Succulence, expressed as water content related to organic dry matter (Fig. 5) exhibited the same trends. The reason for increased succulence is the higher ion-concentration and thus osmotic adjustment by Na^+ - and Cl^- ions (see below) and additional here not proven compatible solutes. This can also deducted from the higher Na/K-ratio on halophytic hosts (see Table 2), a very general rule for many other non-parasitic halophytes, too.

The sum of the analyzed cations is not equal to Cl^- -anions, other anions (SO_4^{2-} , but also organic acid anions) play often a role.

The data given here for Ca and Mg are the hot water fraction, which is approximately the portion of those cations which is osmotic relevant. It differs considerably between host species as

well as in the parasite samples, since Ca is often found in great quantities as precipitated Ca-Oxalate crystals (druses or raphides).

The ash content similarly to the ion sum exhibits much higher values in the parasites growing on halophytic hosts (Fig. 6). Uptake of NaCl under high salt input is rather stoichiometric, this means balanced, as is seen in the relation between Na and Cl (Fig. 7) at higher concentrations. At lower concentrations uptake of sodium can be very low and seems to be better controlled than chloride uptake (Fig. 7). The uptake of sodium and potassium is not strongly but still definitely antagonistic (Fig. 8). Therefore it follows that K-uptake is also antagonistic to chloride (Fig. 9).

Succulence of parasitic leaves increases significantly with higher sodium content in leaves (Fig. 10), this increase is even more significant to the sum of ions taken up (Fig. 11).

The interesting question is if the ionic pattern between host and parasite is to some extent mirrored. This can be checked only partly by the ion ratios of both. Table 4 shows the analyzed ion-ratios and Fig. 12 indicates the rather low correlation of ion concentrations between hosts and parasite.

DISCUSSION

The results indicate that host's concentrations of osmotic active ions are not strongly correlated with parasite's ion concentration of respective ions. This may easily be explained by the fact that the samples of leaves and of corresponding young host stems or host leaves are not compellingly osmotically dependant. Xylem-sap certainly has a lower ion-concentration than leaves, thus osmotic adjustment of the parasite is certainly kept, which is not reflected in the data of Fig. 12. Also the Na/K-ratios are misleading (Tables 2 and 4), since here again the typical high salt-

content of the bladders on leaf surface is not really relevant for the salt concentration subject to the xylem sucking parasite roots.

As in many *Atriplex* species also in *Atriplex halimus* the leaves are covered by salt bladder hairs. Their concentration may be very high up to saturated NaCl-solution; those bladders are means of desalinization of the leaves (Breckle, 1974; Schirmer and Breckle, 1982; Freitas and Breckle, 1992). It is not easily possible to analyze only the leaf content of ions in *Atriplex halimus*, thus the total values used here are very high and indicate the distinctive role of those bladders. However, also the salt content on the leaves of *Plicosepalus acaciae* growing on *Atriplex halimus* have an enriched salt content and exhibit a high succulence (Fig. 5).

In *Tamarix* the recreted salt crystals by salt glands normally are not kept on the surface but are blown away; analysis of young stems thus better reflects salt concentration within the stems. The ion sum in stem- and leaf-succulent eu-halophytes normally reflects the majority of osmotic active ions (Waisel, 1972) but already Walter (1968) pointed to the fact that some halophytes contain few inorganic anions compared with their cation pattern and their ash is rather alkaline (by carbonates from organic acid anions), he termed those alkali-halophytes in contrast to chloride- or sulphate-halophytes. Additionally osmotic adjustment is completed in many halophytes by free amino acids (prolin etc.) and saccharides and other sugars (Yancey, 1994).

Additional Ca (bound in Oxalat) or Mg (bound in chlorophyll) is not relevant for osmotic adjustment. Especially the total amount of Ca (as Ca-Oxalat) in some species can be very high (Williams 1960). Our samples exhibit that the soluble fraction of Ca is also very different between species (Table 3). This is due also for the ratio between hosts and parasite (Table 4) where the 2 chenopodiaceous species "cause" relatively much higher Ca-concentration in the parasite than in the other species .

Other mistletoes are also able to grow on halophytic hosts. In South Africa and Namibia of 19 mistletoes only *Tapinanthus oleifolius* (Loranthaceae) occurs on *Tamarix usneoides* and

Salvadora persica (Visser, 1981; Popp et al., 1995). Similar to *Plicosepalus acaciae* *Tapinanthus oleifolius* did show no preferences between non-halophytic *Acacia* and the halophyte *Tamarix usnoides* in the Ugab Rivier (Namibia) (Veste, pers. observation). On the other hand *Tamarix ramosissima* is an uncommon host for *Phoradendron californicum* (Loranthaceae), but the mistletoe is able to grow on the halophyte (Haigh 1996). On several mangrove species several mistletoes are reported. *Phthirusa maritima* (Loranthaceae) parasites on *Conocarpus erectus* and *Coccoloba uvifera* in Venezuela (Goldstein, et al. 1989), *Lysiana subfalcata* on *Ceriops tagal* in Australia (Ullmann, et al. 1985) and *Loranthus rhamnifolius* on *Sonneratia alba* and *Loranthus sansibarensis* and *L. dregei* on *Lumnitzera racemosa* (Walter and Steiner, 1936). They reported osmotic potentials of *Lumnitzera* host plant leaves with 2.9-3.6 MPa and 2.9-3.2 MPa in the various *Loranthus* parasite leaves. They included those hemi-parasitic species to the list of halophytic mangrove-species in contrast to the independant epiphytes in mangroves. Already in 1907 Holtermann reported *Loranthus capitellatus* from Ceylon (Sri Lanka) being common on Mangrove trees and being anatomically a halophytic mangrove species.

The Chenopodiaceae are known as distinct family with many halophytic species. A few are growing on sand, such a typical psammophyte is *Haloxylon persicum*. However, it can be concluded from the Na/K-ratios (Table 2) that also in this chenopod the physiotypic behaviour of Chenopodiaceae (Albert 1982) is exhibited.

Plicosepalus acaciae is able to develop succulence as a modificative adaptation under salt stress on hosts similar to the *Tapinanthus oleifolius*. But *Plicosepalus acaciae* showed a wider halophytic host spectrum in comparsion to *T. oleifolius*, where only *Tamarix usnoides* and *Salvadora persica* was reported (Visser, 1981; Popp et al., 1995). Various definitions and classifications of halophytes were proposed in the last decades. After the classification for halophytes by Breckle (1990; 2000; 2002), which includes the mechanisms for controlling the NaCl concentration in plants, *Plicosepalus acaciae* is a facultative eu-halophyte, which increases its halo-succulence according to the host which is in this respect comparable to soil substrates. In

any case the water-and nutrient-status of the host plants, especially under desert conditions has strong influence on the equilibrium of host and parasite and thus may mutually influence mortality (Bowie and Ward; 2004). Surface structure, size and indirectly host origin are influencing success of germination and of seedling establishment of parasite on host twigs (Rödl and Ward; 2002). If during these early stages of development halophytic character of the host plant and salinity of site plays a role is still unclear. Host-specificity seems to be rather low in mistletoes (Norton and Carpenter, 1998; Norton and de Lange, 1999) since seeds germinate readily in almost all situations whereas other parasitic plants germinate only in response to chemical signals from the host plants. Thus, a rather long list of host plants is now known (Table 1).

In future a more detailed analysis of xylem-concentrations and ion pattern of host and parasite is a strong desideratum for a better understanding of ecophysiological behaviour and the differing infestation rates of the parasite. Basically this host-parasite-association is a perfect model system and should be used for future experimental sets for ecophysiological research on halophytes.

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Table 1: Checklist of non-halophytic and halophytic hosts of *Plicosepalus acaciae* in the Arava-Valley (Israel and Jordan). Hosts in Yotvata (Israel) are marked with YOT. W: species growing in natural habitats. Cv: cultivated species. Data-source: 1) Post, 1932, 2) Zohary, 1966, 3) Täckholm, 1974, 4) Feinbrun-Dothan et al., 1991, 5) Shmida and Darom, 1992, 6) Veste and Breckle, 1995; Todt, 1999; Todt et al., 2000, 7) Vakin et al., 1996, 8) Kotschy, 1861, 9) Qasem, 2009; 2011

Host species	Family		Reference / Comments
Non-halophytic hosts			
<i>Acacia asak</i> (Forssk.) Willd.	Mimosaceae	Cv	9
<i>Acacia farnesiana</i> (L.) Willd.	Mimosaceae	Cv	9
<i>Acacia nilotica</i> (L.) Delile (= <i>A.arabica</i> (Lam. Willd.))	Mimosaceae	W	8, 9
<i>Acacia raddiana</i> Savi	Mimosaceae	W,YOT	1, 2, 3, 4, 5 (only <i>Acacia</i>), 7
<i>Acacia saligna</i> (Labill.) Wendl. (= <i>A.cyanophylla</i> L.)	Mimosaceae	Cv	9
<i>Acacia tortilis</i> (Forsk.) Hayne	Mimosaceae	W,YOT	1, 2, 3, 4, 5 (only <i>Acacia</i>), 6, 7
<i>Albizia lebbeck</i> Bentham	Caesalpiniaceae	Cv	6
<i>Anagyris foetida</i> L.	Fabaceae	W	9
<i>Balanites aegyptiaca</i> (L.) Delile	Zygophyllaceae	Cv	4
<i>Calligonum comosum</i> L'Her.	Polygonaceae	W,YOT	6
<i>Capparis spinosa</i> L.	Capparidaceae	W	6,9
<i>Casuarina cunninghamiana</i> Miq.	Casuarinaceae	Cv	6
<i>Casuarina equisetifolia</i> L.	Casuarinaceae	Cv	9
<i>Ceratonia siliqua</i> L.	Caesalpiniaceae	W	9
<i>Delonix regia</i> (Boyer ex. Hook) Rauf	Caesalpiniaceae	Cv	6
<i>Elaeagnus angustifolius</i> L.	Elaeagnaceae	W	8
<i>Ficus carica</i> L.	Moraceae	Cv	9
<i>Haloxylon persicum</i> Bunge	Chenopodiaceae	W,YOT	8
<i>Juglans regia</i> L.	Juglandaceae	Cv	9
<i>Melia azedarach</i> L.	Meliaceae	Cv	9
<i>Nerium oleander</i> L.	Apocynaceae	W	9
<i>Parkinsonia aculeata</i> L.	Caesalpiniaceae	Cv	9
<i>Pistacia atlantica</i> Desf.	Anacardiaceae	W	9
<i>Pistacia vera</i> L.	Anacardiaceae	Cv	9
<i>Poinciania gilliesii</i> Wall. ex Hook.	Caesalpiniaceae	Cv	9

<i>Prosopis chilensis</i> (Mol.) Stuntz.	Mimosaceae	Cv	9
<i>Prosopis farcta</i> Macbride	Mimosaceae	W, Hazeva	Y. Vaknin pers. comm. in 6 , 9
<i>Punica granatum</i> L.	Punicaceae	Cv	2
<i>Retama raetam</i> Webb.&Berth	Fabaceae	W	9
<i>Rhamnus</i> spec. L.	Rhamnaceae	W	1
<i>Rhus tripartita</i> Grande	Anacardiaceae	W, YOT	4 (only <i>Rhus</i>), 9
<i>Ochradenus baccatus</i> Delile	Resedaceae	W	4, 5 (only <i>Ochradenus</i>), 6
<i>Pistacia atlantica</i> Desf.	Anacardiaceae	W	9
<i>Salix alba</i> L.	Salicaceae	W	9
<i>Ziziphus jujuba</i> Mill.	Rhamnaceae	Cv	9
<i>Ziziphus lotus</i> Lam.	Rhamnaceae	W, YOT	9
<i>Ziziphus spina-christi</i> (L.) Desf.	Rhamnaceae	W	1, 2, 3, 4, 5 (only <i>Ziziphus</i>), 7, 9
Halophytic hosts			
<i>Atriplex halimus</i> L.	Chenopodiaceae	W, YOT	2,4 (only <i>Atriplex</i>)
<i>Nitraria retusa</i> Forsk.	Zygophyllaceae	W, YOT	4 (only <i>Nitraria</i>), 6
<i>Tamarix aphylla</i> (L.) Karsten	Tamaricaceae	Cv, W, YOT	2, 4, 5 (only <i>Tamarix</i>)
<i>Tamarix jordanis</i> Boiss.	Tamaricaceae	Cv, YOT	2, 4, 5 (only <i>Tamarix</i>)
<i>Tamarix nilotica</i> Bunge	Tamaricaceae	W, YOT	2, 4, 5 (only <i>Tamarix</i>), 6
<i>Tamarix pentandra</i> Pallas	Tamaricaceae	Cv	9

Table 2: Sodium-potassium ratio [derived from mmol/kg H₂O values] in leaves of the non-halophytic hosts *Acacia tortilis*, *Calligonum comosum* and *Haloxylon persicum* the halophytic hosts *Tamarix nilotica*, *Atriplex halimus* and *Nitraria retusa* and the respective *Plicosepalus acaciae* hemi-parasites on them.

Non-halophytic	Na / K	Halophytic	Na / K
<i>Acacia tortilis</i> Leaves	0.37	<i>Tamarix nilotica</i> Young shoots	0.65
<i>Plicosepalus acaciae</i> Old leaves	0.069	<i>Plicosepalus acaciae</i> Old leaves	2.46
Middle age leaves	0.056	Middle age leaves	1.81
Young leaves	0.056	Young leaves	1.06
<i>Calligonum comosum</i> shoots	0.77	<i>Atriplex halimus</i> Leaves	5.90
<i>Plicosepalus acaciae</i> Old leaves	0.41	<i>Plicosepalus acaciae</i> Old leaves	4.31
Middle age leaves	0.40	Middle age leaves	2.26
Young leaves	0.37	Young leaves	1.75
<i>Haloxylon persicum</i> shoots	1.36	<i>Nitraria retusa</i> Leaves	3.30
<i>Plicosepalus acaciae</i> Old leaves	1.10	<i>Plicosepalus acaciae</i> Old leaves	2.45
Middle age leaves	0.92	Middle age leaves	1.54
Young leaves	0.68	Young leaves	0.82

Table 3: Ion contents of old leaves of *Plicosepalus acaciae* on various hosts (\pm = standard deviation) and corresponding ionic contents of host plants (white: non-halophytic hosts, grey: halophytic hosts) [in each cell: upper figure = mmol/kg d.m.; lower figure = mmol/kg H₂O]

Taxon: Parasite and relevant Host	Na ⁺	K ⁺	Ca ²⁺	Mg ²⁺	Cl ⁻
<i>Plicosepalus acaciae</i> (N=12)	45,9 ± 12,6 26,6 ± 7,67	668 ± 201 375 ± 63,9	307 ± 104 181 ± 72,9	86,4 ± 19,7 49,5 ± 8,01	220 ± 88,9 126 ± 46,7
<i>Acacia raddiana</i> (N=12)	55,7 ± 14,1 44,7 ± 16,8	161 ± 89,4 115 ± 35,7	519 ± 243 440 ± 217	94,3 ± 24,9 78,4 ± 31,3	82,3 ± 28,7 63,6 ± 24,2
<i>Plicosepalus acaciae</i> (N=10)	38,0 ± 8,56 23,2 ± 6,63	596 ± 296 334 ± 125	454 ± 128 274 ± 84,6	111 ± 32,2 65,6 ± 15,2	248 ± 80,5 144 ± 29,7
<i>Acacia tortilis</i> (N=10)	47,6 ± 10,0 40,3 ± 8,23	127 ± 53,3 105 ± 37,2	607 ± 272 528 ± 242	162 ± 51,5 140 ± 49,8	82,5 ± 21,6 70,7 ± 20,9
<i>Plicosepalus acaciae</i> (N=2)	35,9 ± 4,46 14,4 ± 2,73	864 ± 199 334 ± 27,5	283 ± 50,3 111 ± 15,1	259 ± 46,1 102 ± 13,9	140 ± 10,5 56,9 ± 13,6
<i>Albizia lebbeck</i> (N=2)	33,1 ± 1,06 14,5 ± 2,52	269 ± 83,9 112 ± 12,8	141 ± 77,9 69,5 ± 47,2	149 ± 53,4 70,8 ± 37,1	49,9 ± 13,0 20,9 ± 1,24
<i>Plicosepalus acaciae</i> (N=10)	399 ± 176 142 ± 59,2	997 ± 313 350 ± 76,8	83,6 ± 60,4 31,9 ± 25,3	312 ± 94,3 112 ± 36,8	399 ± 190 141 ± 65,8
<i>Calligonum comosum</i> (N=10)	108 ± 56,0 70,1 ± 33,1	156 ± 98,4 91,4 ± 44,3	51,9 ± 102 60,0 ± 147	283 ± 92,0 204 ± 109	79,0 ± 25,5 52,9 ± 19,2
<i>Plicosepalus acaciae</i> (N=2)	822 ± 293 247 ± 14,0	688 ± 139 222 ± 48,9	41,0 ± 3,07 13,9 ± 4,74	128 ± 21,1 41,9 ± 10,7	789 ± 273 238 ± 16,2
<i>Casuarina cunninghamiana</i> (N=2)	98,7 ± 15,5 71,0 ± 21,6	255 ± 16,3 181 ± 38,9	267 ± 2,04 188 ± 27,3	195 ± 14,1 135 ± 11,1	317 ± 106 234 ± 108
<i>Plicosepalus acaciae</i> (N=7)	556 ± 126 327 ± 59,6	496 ± 52,4 295 ± 38,3	127 ± 38,9 75,0 ± 23,6	265 ± 57,0 160 ± 46,4	387 ± 173 223 ± 86,0
<i>Haloxylon persicum</i> (N=8)	941 ± 165 572 ± 110	698 ± 113 420 ± 43,8	7,23 ± 2,74 4,44 ± 1,87	295 ± 39,4 181 ± 37,5	479 ± 202 290 ± 127
<i>Plicosepalus acaciae</i> (N=10)	329 ± 208 145 ± 76,2	862 ± 184 397 ± 61,4	111 ± 35,9 52,6 ± 19,0	133 ± 28,6 61,8 ± 13,7	166 ± 121 73,4 ± 42,1

<i>Ochradenus baccatus</i> (N=10)	129 ± 53,1 109 ± 39,7	209 ± 60,5 178 ± 36,6	117 ± 23,0 102 ± 22,7	71,5 ± 14,8 62,7 ± 15,7	85,4 ± 59,2 69,6 ± 40,7
<i>Plicosepalus acaciae</i> (N=2)	74,1± 17,0 25,6± 0,86	961 ± 253 330 ± 0,69	249 ± 14,8 90,3 ± 18,5	208 ± 33,0 73,3± 7,84	745 ± 76,6 267 ± 43,5
<i>Ziziphus spina-christi</i> (N=2)	67,2± 2,87 36,1± 12,3	102 ± 52,9 45,5± 11,7	258 ± 131 116 ± 28,3	196 ± 32,3 98,7± 14,3	385 ±14,2 207 ± 69,3
<i>Plicosepalus acaciae</i> (N=3)	2603± 231 479 ± 22,4	609 ± 193 111 ± 30,1	160 ± 74,0 30,1 ± 14,4	271 ± 67,1 50,6 ± 14,1	3006± 373 552 ± 42,8
<i>Atriplex halimus</i> (N=3)	3267± 400 1955± 801	594 ± 171 331 ± 86,1	11,2 ± 4,10 6,28 ± 2,13	268 ± 46,0 179 ± 122	3458± 430 2084± 902
<i>Plicosepalus acaciae</i> (N=10)	1481± 366 500 ± 77,4	572 ± 182 204 ± 81,0	344 ± 71,4 121 ± 36,0	281 ± 42,6 97,0 ± 15,9	1068± 302 362 ± 81,3
<i>Nitraria retusa</i> (N=10)	1586± 762 446 ± 154	457 ± 159 135 ± 48,9	611 ± 155 179 ± 45,0	513 ± 85,6 151 ± 27,0	1560± 724 442 ± 146
<i>Plicosepalus acaciae</i> (N=17)	1503± 531 300 ± 105	621 ± 145 126 ± 35,1	501 ± 105 102 ± 26,6	632 ± 62,6 128 ± 18,1	1382± 471 273 ± 72,8
<i>Tamarix aphylla</i> (N=15)	586 ± 196 306 ± 82,5	259 ± 58,6 139 ± 37,8	504 ± 127 274 ± 87,9	598 ± 166 326 ± 107	573 ± 217 299 ± 92,0
<i>Plicosepalus acaciae</i> (N=12)	2253± 466 402 ± 54,8	917 ± 219 169 ± 52,2	517 ± 67,9 94,2± 16,8	291 ± 45,9 53,0± 10,7	1621± 438 289 ± 60,1
<i>Tamarix nilotica</i> (N=12)	240 ± 99,9 169 ± 72,5	367 ± 67,1 259 ± 46,5	590 ± 112 417 ± 84,6	319 ± 52,1 226 ± 42,0	413 ± 544 287 ± 368

Table 4: Ion ratio [mmol-paras/mmol-host] calculated from mmol/kg H₂O values for the checked parasite/host pairs (white: non-halophytic hosts, grey: halophytic hosts)

Ion ratio: Parasite / Host for taxon	Ratio for Na ⁺	Ratio for K ⁺	Ratio for Ca ²⁺	Ratio for Mg ²⁺	Ratio for Cl ⁻
<i>Acacia raddiana</i> (N=12)	0.60	3.26	0.41	0.63	1.98
<i>Acacia tortilis</i> (N=10)	0.58	3.18	0.52	0.47	2.04
<i>Albizia lebbeck</i> (N=2)	0.99	2.98	1.60	1.44	2.72

<i>Calligonum comosum</i> (N=10)	2.03	3.82	0.53	0.55	2.66
<i>Casuarina cunninghamiana</i> (N=2)	3.48	1.23	0.074	0.31	1.02
<i>Haloxylon persicum</i> (N=8)	0.57	0.70	16.9	0.88	0.77
<i>Ochradenus baccatus</i> (N=10)	1.33	2.23	0.52	0.99	1.05
<i>Ziziphus spina-christi</i> (N=2)	0.71	7.25	0.78	0.74	1.29
<i>Atriplex halimus</i> (N=3)	0.24	0.34	4.79	0.28	0.26
<i>Nitraria retusa</i> (N=10)	1.12	1.51	0.68	0.64	0.82
<i>Tamarix aphylla</i> (N=15)	0.98	0.91	2.91	0.39	0.91
<i>Tamarix nilotica</i> (N=12)	2.37	0.65	0.23	0.23	1.01

Figure-Legends:

Fig. 1: Ecological Climatic diagramm of Yotvata (Southern Arava, Israel) indicating 12 month of arid season

Fig. 2: Leaf area (cm^2) of young and old leaves of *Plicosepalus acaciae* parasitic on non-halophytic (light grey) and halophytic (dark grey) hosts. Box-Plots indicate interquartile range, median (thick line) and total variation

Fig. 3: Leaf thickness (mm) of young and old leaves of *Plicosepalus acaciae* parasitic on non-halophytic (light grey) and halophytic (dark grey) hosts. Box-Plots indicate interquartile range, median (thick line) and total variation

Fig. 4: Volume (cm^3) of young and old leaves of *Plicosepalus acaciae* parasitic on non-halophytic (light grey) and halophytic (dark grey) hosts. Box-Plots indicate interquartile range, median (thick line) and total variation

Fig. 5: Succulence (g H_2O g⁻¹ d.m.org.) of young and old leaves of *Plicosepalus acaciae* parasitic on non-halophytic (light grey) and halophytic (dark grey) hosts, with standard-deviation

Fig. 6: Ash-content of old leaves of *Plicosepalus acaciae* parasitic on non-halophytic (light grey) and halophytic (dark grey) hosts. Box-Plots indicate interquartile range, median (thick line) and total variation for N>2

Fig. 7: Correlation between Na^+ - and Cl^- -content (mmol kg⁻¹ H_2O) in leaves of *Plicosepalus acaciae*

Fig. 8: Correlation between Na^+ - and K^+ -content (mmol kg⁻¹ H_2O) in leaves of *Plicosepalus acaciae*

Fig. 9: Correlation between K^+ - and Cl^- -content (mmol kg⁻¹ H_2O) in leaves of *Plicosepalus acaciae*

Fig. 10: Correlation between succulence (g H_2O g⁻¹ d.m.org.) and Na^+ -concentration (dots: mmol kg⁻¹ d.m.; crosses: mmol kg⁻¹ H_2O) in leaves of *Plicosepalus acaciae*

Fig. 11: Correlation between succulence (g H_2O g⁻¹ d.m.org.) and the ion sum ($\text{Na}^+ + \text{K}^+ + \text{Ca}^{2+} + \text{Mg}^{2+} + \text{Cl}^-$, mmol kg⁻¹ d.m.) in leaves of *Plicosepalus acaciae*

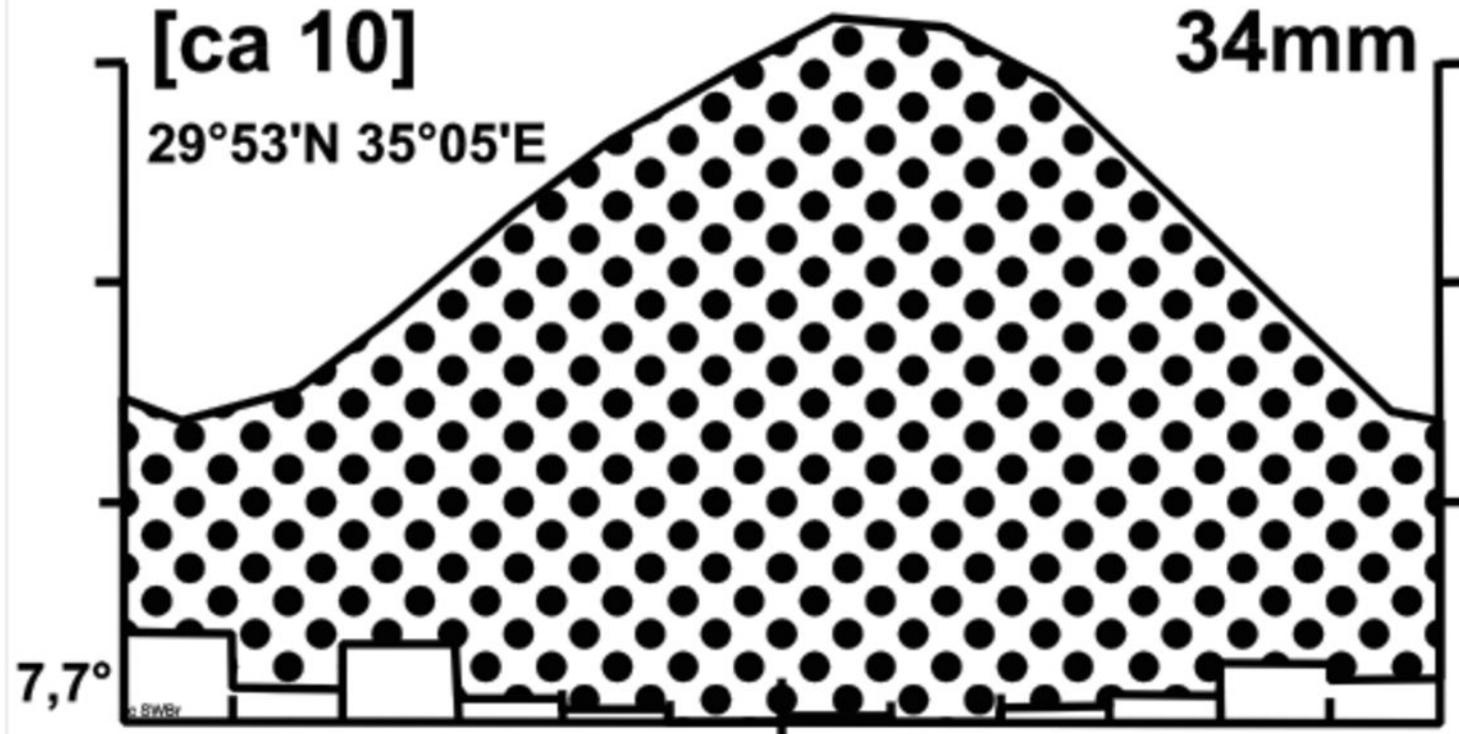
Fig. 12: Ratio of ion-concentration parasite/host for the 5 ions, calculated from the mmol per kg H_2O values. The values for *Atriplex halimus* are beyond the graph ($\text{Na}^+ = 479/1955$; $\text{Cl}^- = 552/2084$)

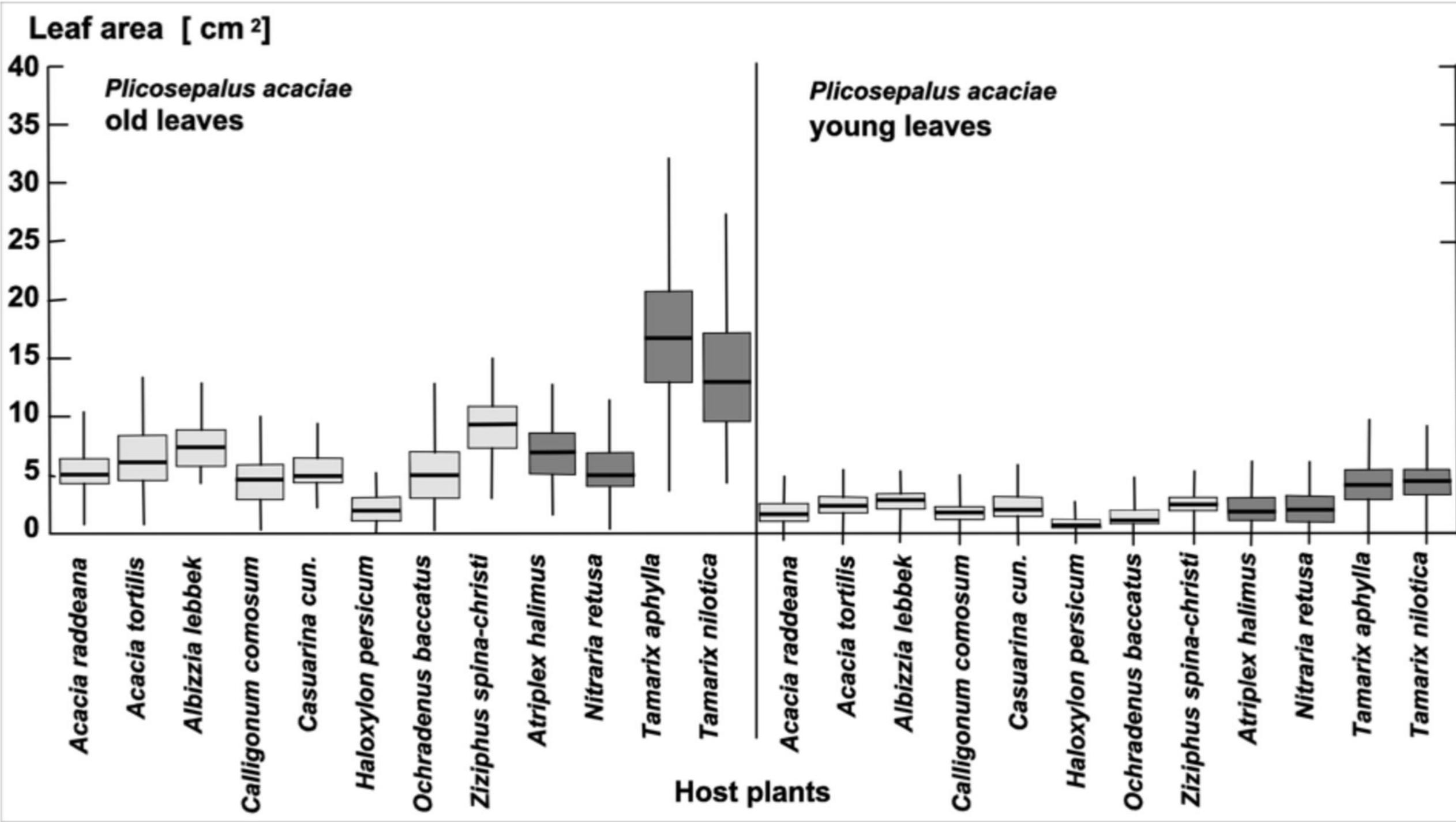
Yotvata (40m)

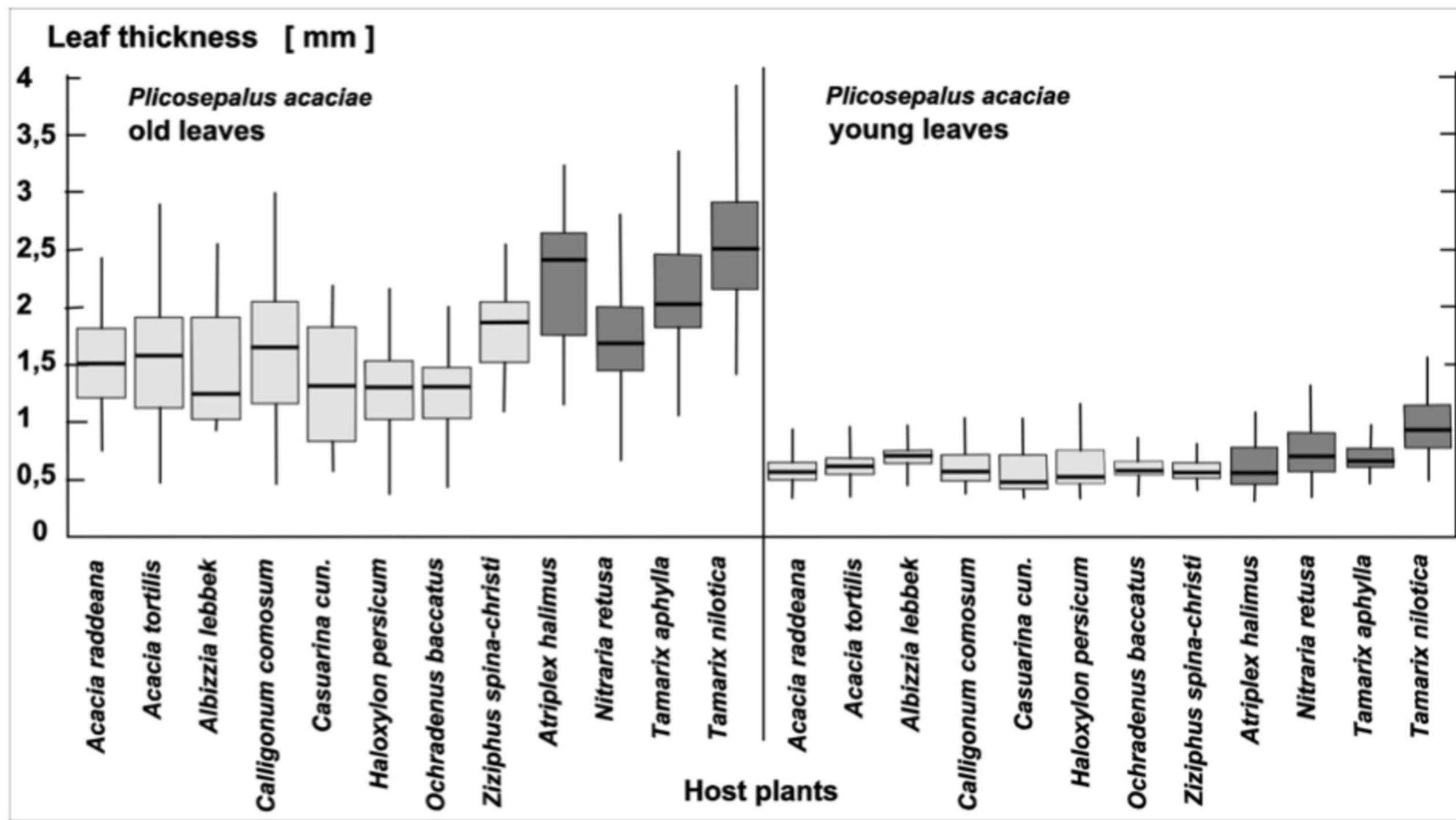
[ca 10]

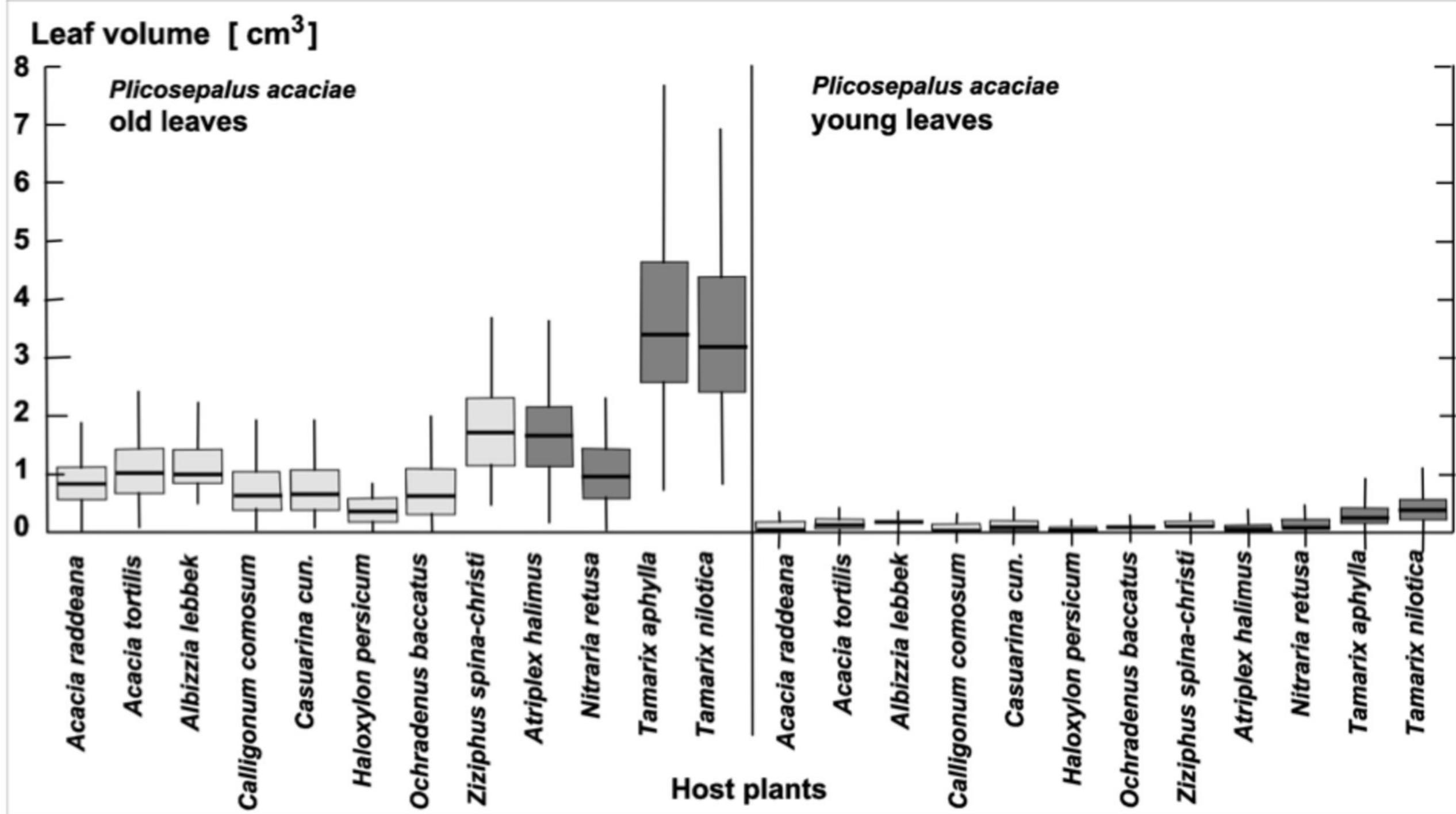
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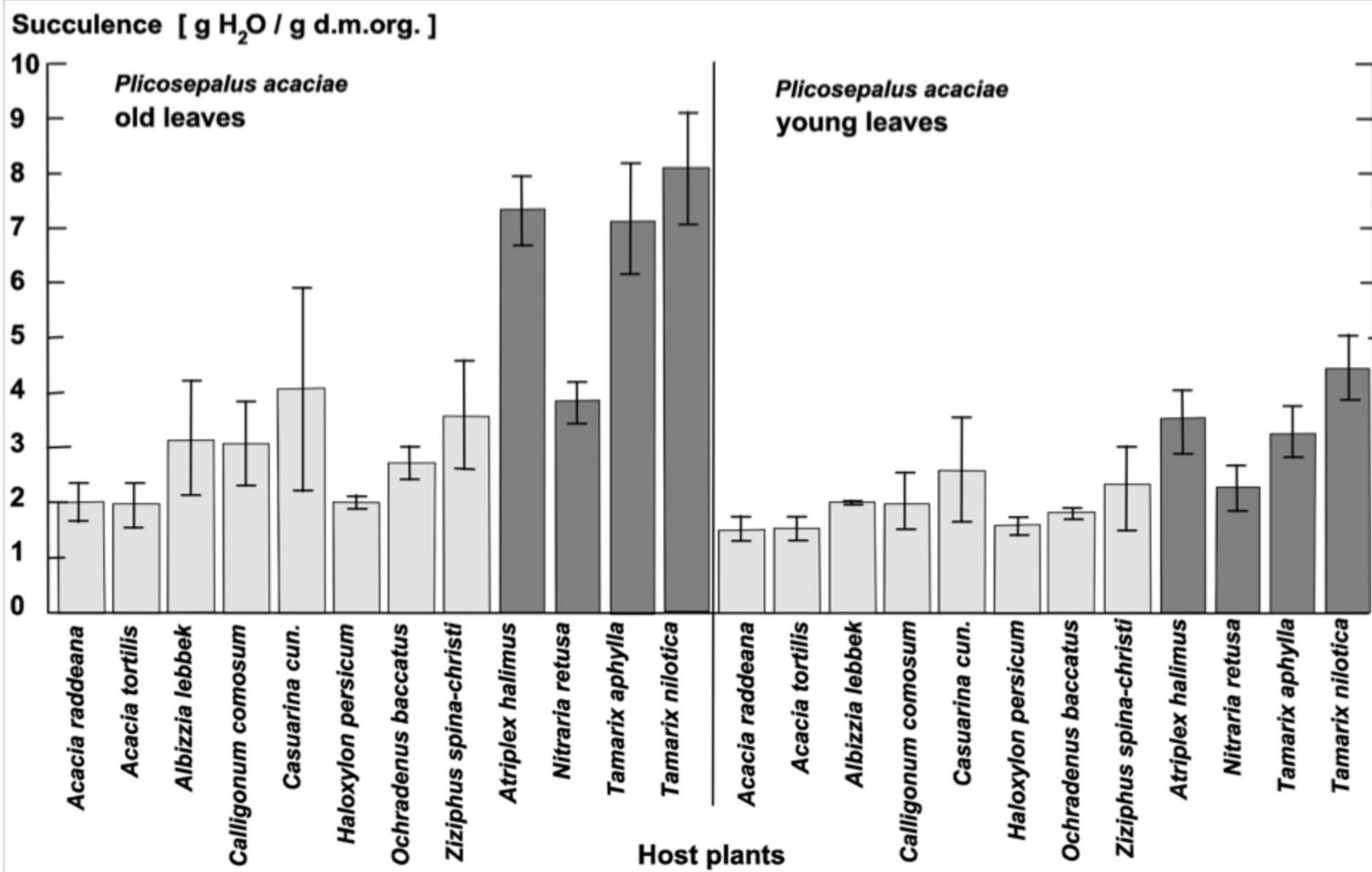
23,1°C
34mm











Ash content (% of d.m.)

40

30

20

10

0

Plicosepalus acaciae old leaves

N = 12

10

2

10

2

7

2

10

3

10

17

12

Acacia raddeana

Acacia tortilis

Albizia lebbek

Calligonum comosum

Casuarina cun.

Haloxylon persicum

Ochradenus baccatus

Ziziphus spina-christi

Atriplex halimus

Nitraria retusa

Tamarix aphylla

Tamarix nilotica

Host plants

