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A COMPARISON OF THE MINERAL RELATIONS OF A HALOPHYTIC HEMIPARASITE AND HOLOPARASITE

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The mineral relations of the halophytic root hemiparasite *Odontites verna* ssp. *serotina* and stem holoparasite *Cuscuta salina* var. *major* were compared. The xylem hemiparasite *Odontites* occurs on the upper parts of Dutch Wadden salt marshes attached to the roots of salt excluding monocotyledonous plant species. *Cuscuta* was sampled in San Francisco Bay (U.S.A.) salt marshes parasitizing *Salicornia pacifica* of the lower marsh zones. Despite salt accumulation in the host plant *Salicornia,* the phloem feeder *Cuscuta* maintains a relatively low Na concentration and a high potassium/calcium (125) ratio. In contrast, the xylem-xylem contact between the strongly transpiring hemiparasite *Odontites* and its host leads to a 5 to 7-fold increase of the sodium as well as calcium and magnesium content in the hemiparasite shoot tissue. The K/Ca ratio in the attached hemiparasite (8.2) was much lower than in the halophytic holoparasite *Cuscuta.* The ecological consequences of the differences between the hemi and holoparasite are discussed.

In both holoparasites and hemiparasites contact organs on the shoot and the stem enable the transfer of nutrients from the host to the parasite. In this paper a comparison is made between the mineral relations of a hemiparasite and a holoparasite occurring in salt marshes.

Odontites verna ssp. *serotina* is an annual, facultative hemiparasite and member of the Scrophulariaceae occurring in salt marshes and beach plains (Rozema *et al.* 1985a). In July 1984, studies were made of populations of *Odontites verna* ssp. *serotina* on the Westerkwelder and Beach Plain salt marsh of the Frisian Island Schiermonnikoog (53°29′ N, 6°12′ E). Using a Scholander's pressure bomb, the total water potential of the plant ψ_T was measured at midday (12.00–15.00) and aerial parts of hemiparasite and host plant were collected for mineral analysis (see Rozema *et al.* 1982). On Schiermonnikoog measurements were made on upper marsh sites where individuals of *Odontites* were present amidst one dominant host species (*table 1*) making up at least 60% of the total plant cover. By observation of haustoria on root systems *Odontites* was found

Table 1. Mineral composition (mmol or μmol/g DW) of the shoot tissue and total water potential of the plant ψ_T (MPa) of two host plant species parasitized and non-parasitized by the hemiparasite *Odontites verna* ssp. *serotina* in the Westerkwelder salt-marsh of Schiermonnikoog, July 1984. Average values of four replications.

Species	Mineral element: mmol/g DW		Mineral element: μmol/g DW		ψ_T	Na host / Na paras.	K / Ca
	K	Na	Ca	Mg			
Host *Festuca rubra* ssp. *litoralis*	.540	.140	19.1	26.7	−2.20	0.211	
Hemiparasite *Odontites verna*	.416	.665	50.5	105.3	−2.75		8.2
Host *Festuca rubra* ssp. *litoralis* non parasitized	.443	.090	17.9	31.4	−2.04		
Host *Juncus gerardii*	.580	.175	10.3	23.0	−2.10	0.136	
Hemiparasite *Odontites verna*	1.138	1.1287	137.2	325.8	−2.84		8.3
Host *Juncus gerardii* non parasitized	.325	.178	14.1	32.8	−2.17		
L.S.D. $\alpha = 0.05$	.214	.085	11.3	19.9	−.20		

to have xylem-xylem contact with at least the following host plant species *Festuca rubra* spp. *litoralis*. *Juncus gerardii*, *Agrostis stolonifera* and occasionally with *Elymus pycnanthus* and *Trifolium repens*.

In July 1983 the holoparasite *Cuscuta salina* var. *major* (MUNZ & KECK 1959) in a salt marsh of the San Francisco Bay near Palo Alto, (37° 45′N, 122°30′W) San Francisco, was found massively attached to the stem of *Salicornia pacifica* and to a minor extent to other halophytic species (*table 2*). Similar midday pressure bomb readings were done as above. Unlike *Salicornia* the very weak tissue of *Cuscuta* allowed no proper pressure bomb measurements. The root hemiparasite *Odontites* absorbs xylem sap with dissolved nutrients from its host by maintaining a significantly more negative water potential than that of its host (*table 1*, cf KLAREN 1975). This low water potential of the hemiparasite and the continuous flow of xylem water and dissolved nutrients is also related to a high transpiration rate of *Odontites* even during the dark period to some extent (ROZEMA *et al.* 1985b). The above monocotyledonous host plants for *Odontites* were found to be salt-excluding (ROZEMA *et al.* 1981) halophytes with relatively low Na-levels in the xylem sap. After growth in sand culture with 50 mM NaCl in the soil moisture the sodium content (mM) of the xylem sap in the hosts, obtained by the pressure bomb technique (ROZEMA *et al.* 1985b) was 10.0 (*Festuca rubra* ssp. *litoralis*), 6.1 (*Juncus gerardii*) and 2.5 (*Elymus pycnanthus*) respectively. The potassium content of the xylem sap of all three host species was about 3.5 mM. Nevertheless, the Na-concentration found in the shoot tissue of the hemiparasite exceeds that of the host species by a factor of 5 (*Festuca*) – 7.5 (*Juncus*). For the ions Ca and Mg a similar high accumulation factor exists, which is in agreement with findings of KLAREN (1975). Potassium concentrations in the hemiparasite were found even lower than that of the host plant species and never more than a factor of 1.5 higher than that of the host plant.

Collected in the lower parts of a San Francisco Bay salt marsh the sodium content of the *Salicornia pacifica* shoot tissue is much higher (2.96–4.90 mmol Na/g DW) than for the shoot tissue of *Festuca rubra* ssp. *litoralis* and *Juncus gerardii*, growing in Schiermonnikoog salt marshes (0.14–0.175 mmol Na/g DW, *table 2*). The Na concentration in the parasite *Cuscuta* tissue was 4–10 times less than that of the host plant tissue. The sodium levels in the stem holoparasite *Cuscuta salina* may even be lower than that of the root hemiparasite *Odontites verna* ssp. *serotina* (*tables 1* and *2*). There is no accumulation of K, Ca and Mg in *Cuscuta* relative to the host plant tissue (*table 2*) either. The content of Mg in *Cuscuta* tissue is lower than in the host plant, while the potassium content in *Cuscuta* varies significantly less than in the host. Of the micronutrients, only the Fe content of the holoparasite exceeded that of the host plant species and this is in agreement with data presented by WALLACE *et al.* 1978. Apparently, the manner of uptake of phloem fluid and dissolved substances by the holoparasite *Cuscuta* enables the maintenance of low Na concentrations. WALLACE *et al.* (1978) observed similarly low Na concentrations in the stem holoparasite *Cuscuta nevadensis* Johnston, parasitizing desert halophytes. This may confirm that the *Salicornia* phloem and not the xylem is the source of nutrients unlike the relationship between *Odontites* and its hosts.

According to WOLSWINKEL (1977) phloem feeding parasites have a relatively low Ca and a relatively high K content and consequently a relatively high K/Ca ratio. In accordance with this hypothesis the K/Ca ratio calculated for *Cuscuta* (38.8–218.8) always greatly exceeds the K/Ca ratio determined for *Odontites* (8.2). The data in *table 2* agree with figures presented by Ernst for the root holoparasite *Cistanche lutea* feeding on the halophyte *Halimione portulacoides* (BAUMEISTER & ERNST 1978). The shoot tissue concentration of Na,K Ca and Mg in *Cistanche* is lower than in the shoot of ist host.

Similar to the shoot hemiparasite *Phoradendron villosum*, a mistletoe on *Quercus lobata* (HOLLINGER 1983) and in *Rhinanthus* (KLAREN 1975), transpiration in *Odontites verna* ssp. *serotina* is high and exceeds that of the host plants (ROZEMA non published). This transpiration rate may contribute to the accumulation of ions in the hemiparasite. Alternatively, in the phloem feeding *Cuscuta* species, transpiration is low (TER BORG *et al* 1981). Hemiparasites of the Scrophulariaceae and holoparasites of the Cuscutaceae may be relatively host aspecific (TER BORG *et al.* 1981). In the particular case of salt marsh environment with different kinds of stress (ROZEMA *et al.* 1985a), xylem feeding halophytic hemiparasites like *Odontites* will have a more limited distribution along a gradient of soil salinity than the phloem feeding *Cuscuta*. Because of the negative waterpotential in the xylem of the host, *Odontites* must always develop and maintain a more negative water potential by solute uptake or synthesis accompanied by a high transpiration rate (cf *table 1*, KLAREN 1975). The accumulation of any inorganic ions including the potentially toxic Na^+ and Cl^- is a consequence that limits the distribution of *Odontites* of the salt marsh to the upper parts in salt-excluding

Table 2. Mineral composition (mmol or µmol/g DW shoot) of the shoot tissue and total water potential of the plant ψ_T (MPa) of four host plant species parasitized and non-parasitized by the holoparasite *Cuscuta salina* var. *major* in the San Francisco Bay Salt marsh, July 1983. Average values of four replications L.S.D. calculated at $\alpha = 0.05$ level.

	Mineral element										
	mmol/g DW			µmol/g DW					ψ_T	Na host / Na paras.	$\frac{K}{Ca}$
	K	Na	Cl	Ca	Mg	Fe	Mn	P			
Salicornia pacifica	.441	2.96	3.90	6.81	27.6	.152	.256	34.10	−4.21	6.3	
Parasite *Cuscuta salina*	.388	.47	.49	3.11	4.6	.792	.232	n.d.			124.7
Atriplex hastata	.228	4.39	5.61	1.90	34.1	.343	.264	18.06	−2.83	3.4	
Parasite *Cuscuta salina*	.300	1.31	1.68	7.74	5.6	1.130	.129	49.88			38.8
Frankenia grandiflora	.239	1.06	1.29	4.89	15.8	.196	.125	44.81	−2.42	7.1	
Parasite *Cuscuta salina*	.299	.119	.72	3.23	4.3	.363	.087	37.22			92.6
Kochia	.518	1.17	.841	.94	8.0	.241	.123	129.18	−2.83	9.0	
Parasite *Cuscuta salina*	.256	.13	.169	1.17	2.6	.210	.083	40.57			218.3
Kochia non parasitized	.586	.88	.81	1.19	5.9	.287	.099	25.91			
L.S.D. $\alpha = 0.05$	.102	.63	.65	.62	2.7	.084	.051	16.52	−.28		

monocots (*Festuca rubra* ssp. *litoralis, Juncus gerardii, Agrostis stolonifera, Elymus pycnanthus*). Phloem feeding halophytic holoparasites like *Cuscuta salina* and *Cistanche lutea* (BAUMEISTER & ERNST 1978) absorb only relatively small amounts of sodium and therefore may even occur in the lowest zones of salt marshes, on salt accumulating euhalophytes *Salicornia pacifica* and *Halimone portulacoides*. From this ecological point of view *Cuscuta salina* is expected to be more aspecific with regard to host plant species than *Odontites verna* ssp. *serotina*.

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