

Ecophysiology of the holoparasitic angiosperm *Cistanche phelypaea* (Orobanchaceae) in a coastal salt marsh

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Abstract: *Cistanche phelypaea* (L.) Cout. (Orobanchaceae) was found parasitising the roots of the succulent shrublets *Arthrocnemum macrostachyum* (Moric.) K.Koch (Chenopodiaceae) in a coastal salt marsh in Qatar. Measurements were conducted to identify soil properties, host, and noninfected plants by soil excavations to expose the haustoria of the parasite attached to the host roots. The water potential, osmotic potential, pressure potential, and chemical analyses were determined in parasite, host, and noninfected plants. Crown diameter and dry mass of the host plants were smaller than in the noninfected plants. A gradient of water potential existed between the host root and the underground tuberous body of the parasite. Potassium was the major cation found in the parasite, while sodium was dominant in the host and noninfected plants. The nitrogen, soluble sugars, total amino acids, and starch contents of the parasite were higher than those of the host and noninfected plants. The high ratio of K^+ to Ca^{2+} in the parasite indicates that it is phloem-feeding. The high nutrient element contents and metabolic products in the parasite are possibly related to the creation of osmotic and water potential gradients between the host and *C. phelypaea*.

Key words: *Cistanche phelypaea*, *Arthrocnemum macrostachyum*, water potential, osmotic potential, salt marsh, Qatar

1. Introduction

About 1% of the flowering plants, approximately 4000 species in total, are parasitic (Press and Phoenix, 2005). These plants form a close connection with the conducting system of the host plant(s) through specialised structures known as haustoria. The site of attachment to the host classifies the parasite as either root or shoot parasite, whereas the presence or absence of functional chloroplasts further defines the parasite as hemiparasitic or holoparasitic, respectively (Musselman and Press, 1995; Shavvon et al., 2012; Zare and Dönmez, 2013).

In the Arabian Desert, extensive studies were carried out on the flora, vegetation, and ecology of desert plants (Batanouny, 1981; Migahid, 1989; Zahran and Willis, 1992; Abulfatih et al., 2001). However, little work has been published on the angiosperm parasites as a group of plants infecting desert vegetation hosts (Mubarek, 1985; El-Husseini, 1988; Fahmy et al., 1996; Hegazy and Fahmy, 1999; Fahmy, 2008). This group of plants has received little attention since it represents a low percentage of life forms in arid regions of the Middle East and North Africa (Hassib, 1951; Boulos, 2002; Abd El-Ghani et al., 2013).

Cistanche phelypaea (L.) Cout. is an obligate root holoparasite of the family Orobanchaceae. Fahmy et al. (1996) found that *Cistanche phelypaea* was parasitising 6 perennial hosts belonging to different families of desert plants. The mature body of *Cistanche phelypaea* consists of an underground perennial fleshy tuberous rhizome from which 1–7 thick, flowering stalks emerge above the ground surface during springtime (Fahmy et al., 1996; Boulos, 2002).

There have been few studies on the biology and ecology of *Cistanche phelypaea*. Most works were concerned with the distribution, biomass, and host range (Batanouny, 1981; Farah, 1987; Fahmy et al., 1996) and the allelopathic potential (Hegazy and Fahmy, 1999). This study examines some ecophysiological interactions between *Cistanche phelypaea* and its host, *Arthrocnemum macrostachyum* (Moric.) K.Koch (Chenopodiaceae), in a coastal salt marsh in Qatar. The parasite and host species grow under a wide range of stresses: saline soil, high osmotic pressure of soil solution, dry atmosphere, heat, etc. (Fahmy et al., 1996; Hegazy and Fahmy, 1999; Fahmy and Al-Thani, 2006). In such an arid habitat, the success of this biotic interaction reflects a major challenge, not only for the host, which is

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adapted to salt stress because it is a succulent halophyte, but also to the parasite, which must cope with the salt-tolerant nature of the host as well as the abiotic conditions in the salt marsh.

2. Materials and methods

2.1. Study site

The peninsula of Qatar is located between 24°27'N and 26°10'N, 50°45'E and 51°40'E (Figure 1). It is 180 km long, 85 km wide (Abulfatih et al., 2001), and covers an area of 11,437 km² within the vast desert belt extending from North Africa to Central Asia. Rainfall is scanty (54.6–76.1 mm year⁻¹), erratic, and variable in time and place (Babikir and Kürschner, 1992). More rainfall is expected between December and March. Qatar has a hot desert climate, with mild winters and very hot summers (Batanouny, 1981). The land elevation ranges between -6 m and 103 m from gulf level. Most of the land is only a few meters above the gulf level. The landscape is generally flat to undulating, with rocky hills and sand dunes situated in the south-west parts of the country (Abulfatih et al., 2001). The high landform types of the rocky and conglomerate hamada occupy most of the peninsula, whereas the maritime salt marshes occupy a narrow fringe bordering on these raised areas (Abdel-Razik and Ismail, 1990). The study site is a littoral salt marsh in the Al-Dhakhira region (Figure 1) on the north-eastern coast of the country (25°45'N, 51°30'E). The land seems to be at sea level and, accordingly, is periodically affected by tidal change (Abulfatih et al., 2001).

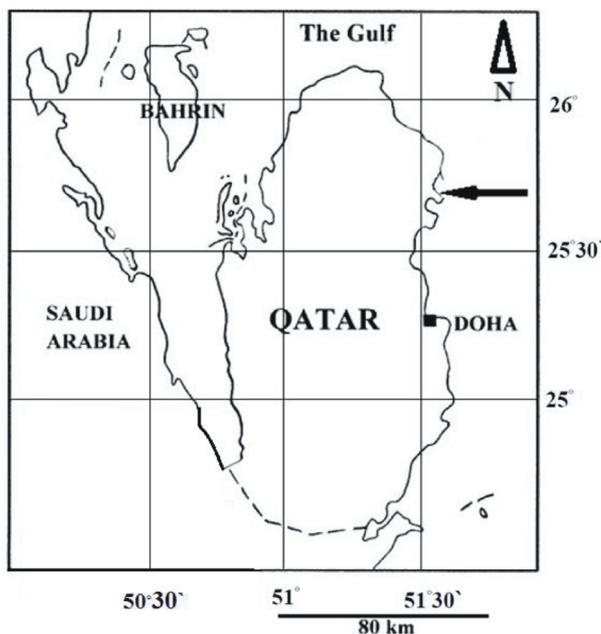


Figure 1. Location map of the State of Qatar and study area in the Al-Dhakhira region (solid arrow).

Plants living in the coastal marsh are subjected to periodic inundation and drainage. The study area was a coastal part of the marsh located above the high tide level, inland from a coastal mangrove zone dominated by *Avicennia marina* (Forssk.) Vierh. (Fahmy and Al-Thani, 2006).

This study was conducted during the springtime, in March and April, when *Cistanche phelypaea* was at its peak flowering stage. Field measurements and collections were conducted in 6 plots of 10 m × 10 m in the study area, which is part of the coastal low salt marsh zone located above the high tide level and dominated by the succulent halophyte *Arthrocnemum macrostachyum*. Species identification followed Batanouny (1981). The method of simple random sampling was carried out to study and collect the parasite–host association and noninfected plants within plots. From each plot, 10 sample points were investigated. The method of random number tables was applied to give the x and y coordinates of each sample (Williams, 1991). Confirmation of the hosts and the percentage infection were based on above-ground inspection followed by soil excavations to expose the attachments of the parasites to the host roots. One parasite–host association and 1 noninfected plant were sampled from 10 random points in each plot of the study area.

Soil samples were collected from the root zone of the parasite–host association (at about 30 cm of depth). The soil matric potential (Ψ_m) was determined with a soil tensiometer (Soil Moisture Equipment Company, Santa Barbara, CA, USA). The ceramic tip of the tensiometer was installed at the required depth (30 cm) using a steel pipe, which was pushed in vertically to make a pilot hole in the soil. The soil moisture content was determined gravimetrically. The oven-dried soils (105 °C) were analysed for mechanical properties and total carbonates (Jackson, 1958). Subsamples of oven-dried soils were used to prepare a soil–water extract after the water content of each sample had been raised to saturation. The extract was used for the determination of pH, osmotic potential (Ψ_s), and nutrient elements. The Ψ_s value was determined by measuring the freezing point depression of the soil extract using an automatic osmometer (Osmette S, Precision Systems, Inc., Natick, MA, USA). Sodium, potassium, and calcium were determined by inductively coupled mass spectrometer (Agilent Model ICP-MS Series 7500, Santa Clara, CA, USA). Chloride was estimated by titration with silver nitrate (Jackson, 1958), and sulphate was determined by the rapid turbidimetric procedure (Swaminathan and Sud, 1977). The total soil water potential (Ψ_{soil}) was calculated from the sum of $\Psi_m + \Psi_s$ (Larcher, 2003).

2.2. Plant size and water content

The crown diameters (cm) of the host and noninfected plants were determined by measuring tape. The parasite body was divided into underground tuberous part and

aboveground inflorescence. The plant bodies of the host and noninfected individuals were separated into roots and shoots. The dry mass of the plant parts was measured after oven-drying at 70 °C until constant mass was obtained. Water content of the different parts was calculated and expressed as percentage of fresh mass.

2.3. Water potential (Ψ_w) and its components

The Ψ_w of the target plants was determined following the dye method (Knipling, 1967). Samples were obtained at midday from the different parts of the plants. Samples from the tuberous parts and the inflorescence axis of the parasite were obtained with a cork borer as discs (0.5 cm in diameter \times 0.5 cm in thickness). The discs of the tuberous body were obtained from the part nearest to the point of contact to the host root. Samples from the roots of noninfected plants were comparable to those from the host with regards to order of root origin and distance from the apical portion of the lateral root. Segments of roots were obtained as discs (0.5 cm thick \times 0.25 cm in length). Segments from the shoots of the host and the noninfected plants (0.5 cm thick \times 0.25 in length) were obtained from the uppermost fully expanded parts. Segments from each organ of the target plants were equilibrated in mannitol solutions of known molality. The osmotic potentials (MPa) of the different concentrations of mannitol solutions were calculated from the van't Hoff equation (Hopkins and Hüner, 2004):

$$\Psi = -C\gamma RT,$$

where C is the molar concentration, γ is the activity coefficient, R is the universal gas constant (0.00831 kg MPa mol⁻¹ K⁻¹), and T is the absolute temperature (K = °C + 273). The water potential of the tissue was estimated as equivalent to the osmotic potential of the mannitol solution, in which there was no net water exchange between the tissue and the solution.

For the determination of osmotic potential (Y_s) of tissues, comparable to those used for Y_w , the samples from different parts were collected, kept in well-stoppered tubes, and rapidly transported to the laboratory in an ice box. The samples were stored at -25 °C. The Y_s of the pressed sap was determined using an osmometer (Osmette S, Precision Systems, Inc.). It was not possible to obtain sap from roots by pressing; therefore, an aqueous extract of oven-dried ground material was prepared by mixing 100 mg of plant powder with 2 mL of water (Köhl, 1996). The Y_s of the root extract was measured with an osmometer. Application of the latter method to oven-dried leaves gave 95% reproducible values of Y_s of those obtained directly by osmolality of the pressed sap. The values of the osmotic potential (mOsm kg⁻¹) were converted to MPa from a standard curve of different molar concentrations of NaCl solutions (prepared under laboratory conditions at 25 °C), and the corresponding osmotic potential values

were measured by osmometer (Lang, 1967). The pressure potential (Y_p) was calculated indirectly by subtracting Y_w from Y_s (Hopkins and Hüner, 2004).

2.4. Chemical analyses of plants

The shoots and roots of host and noninfected plants, as well as the tuberous body and inflorescence of the parasite, were harvested at midday. The samples were briefly rinsed in deionised water and blotted dry. The flowers of the parasite were split longitudinally in order to expose their floral nectaries (at the base of the ovary) to washing by water to remove nectar. The plant materials were stored in well-stoppered tubes and transferred to the laboratory in an ice box. The samples were freeze-dried, ground to fine powder, and stored in a desiccator. Next, 500 mg of dry mass from each sample was ashed at 450 °C in a muffle furnace for 24 h. The resulting ash was weighed, and the ash content was expressed as percentage of oven-dried mass. Five millilitres of 0.1 M nitric acid was added to the ashed material, and dilutions with distilled water were made. Sodium, potassium, calcium, and sulphate were analysed in the nitric acid-soluble extracts. Chloride was determined after extraction of the dry mass in deionised water (see soil analyses for methods of analysis of minerals, chloride, and sulphate).

The preference of the target plants for overall uptake of K over Na can be proven with calculation of the K:Na selectivity ratio ($S_{K:Na}$), according to the method of Pitman (1976). This was calculated as follows:

$$S_{K:Na} = \text{K:Na in plant tissue} / \text{K:Na in the soil}.$$

Total carbon and nitrogen contents of the freeze dried samples were analysed by combusting a known mass in an oxygen gas stream at 1925 °C using a PerkinElmer 2400 CHN elemental analyser.

The dried plant samples were extracted with 80% ethanol. The total soluble sugars in the extract were determined with anthrone reagent using glucose as a standard, while the total free amino acids were estimated as glycine following the ninhydrin method (Allen et al., 1974). Starch was estimated according to the method of Ashraf (1994).

2.5. Statistical analysis

Data from soil and plant measurements were means of 6 replicates obtained from 6 comparable soil sites of the study area and from 6 individuals of parasite, host, and noninfected plants. Student's t-test (Williams, 1991) was used to compare the mean values of the measurement variable (crown diameter in centimetres) of the noninfected and host plants. Minitab statistical software was used to assess the significance of variation among the means of plant parameters using one-way analysis of variance. The least significant difference was calculated to verify the significance of the difference between the means of each parameter analysed in different parts of the parasite, host,

and noninfected plants. Multiple comparisons between means were carried out to argue significant differences between the values of each measured parameter in different parts of the parasite, host, and noninfected plants.

3. Results

3.1. Study site, species composition, and soil analyses

Field observations revealed that *Cistanche phelypaea* was parasitising the roots of the succulent shrublets *Arthrocnemum macrostachyum* (Moric.) K.Koch (family Chenopodiaceae) and that infection reached 68%. The hosts and the noninfected plants of *Arthrocnemum macrostachyum* constituted a vegetation zone that was located about 110 m from the coast of the gulf. The width of the *Arthrocnemum macrostachyum* zone was about 39 m, and its cover percentage reached 20.8%. Species associated with *Arthrocnemum macrostachyum* in its zone were *Salsola soda* L., *Salicornia europaea* L., and *Halocnemum strobilaceum* (Pall.) M.Bieb. (all from family Chenopodiaceae). The soil of the root zone was classified as sandy loam (Table 1), and the soil reaction was alkaline (pH 8.4). According to Abrol et al. (1988), the soil was

Table 1. Analyses of soil in the root zone (g 100 g⁻¹ of the dry soil; 25–50 cm depth) supporting the angiosperm root parasite *Cistanche phelypaea*, its host, and the noninfected plants growing under natural conditions in the coastal salt marsh, Al-Dhakhira, Qatar. Each value is an average of 6 determinations ± standard deviation. The values are expressed as percentage of oven-dried soil, except pH, electric conductivity, soil matric, and osmotic potentials.

Parameters	Values
Sand	65.0 ± 5.30
Silt	22.6 ± 1.40
Clay	12.0 ± 1.80
Soil moisture	19.0 ± 1.58
pH	8.40 ± 0.80
Electric conductivity (mS cm ⁻¹)	4.17 ± 0.92
Soil matric potential (ψ_m in MPa)	-0.10 ± 0.02
Soil osmotic potential (ψ_s in MPa)	-0.15 ± 0.03
Total carbonates	36.5 ± 4.10
Sodium	0.65 ± 0.10
Potassium	0.14 ± 0.02
Calcium	0.23 ± 0.04
Chloride	0.78 ± 0.21
Sulphate	0.68 ± 0.15

classified as moderately saline (EC = 4.17 mS cm⁻¹) with a total carbonate content of 36.5% oven-dried soil. The osmotic component of the soil water potential (Ψ_s = -0.15 MPa) was lower than the matric component (Ψ_m = -0.10 MPa) due to the presence of soluble salts, especially sodium, chloride, and sulphate.

3.2. Plant size and water content

The crown diameter (df = 10, t = 3.93, P < 0.01; Table 2) and dry mass (df = 24, F = 2642, P = 0.000; Table 3) of the *Arthrocnemum macrostachyum* host were significantly lower than those of the noninfected plants. The dry mass of the parasite per individual host was significantly higher (1.3-fold) than the root mass of the host, and both were significantly lower than the root mass of the noninfected plants. The water content of the shoots and roots of noninfected *Arthrocnemum macrostachyum* plants was significantly higher than that of comparable organs in the host (df = 24, F = 337.1, P = 0.000; Table 3). The water content of the parasite parts was lower than that of the shoots of noninfected plants and was significantly higher than in the roots.

3.3. Water potential (Ψ_w) and its components

Midday Ψ_w in the plants studied could be classified into 2 main categories (df = 24, F = 2178.2, P = 0.000; Figure 2). The lowest values of Ψ_w (most negative) were observed in the shoots of the host, followed by the shoots of the noninfected plants, the tuberous parts of the parasite, and inflorescence of the parasite. The soil supporting the investigated species showed the highest Ψ_w (-0.25 MPa; Table 1). A gradient of Ψ_w existed between the host root (-0.76 MPa) and the tuberous body of the parasite (-2.95 MPa). Within the parasite, a gradient of Ψ_w also occurred between the tuberous body and the aboveground inflorescence. Osmotic potential (Ψ_s) exhibited the same trend as Ψ_w but at lower (more negative) values (df = 24, F = 3136.9, P = 0.000; Figure 2). The lowest Ψ_s occurred in the tuberous body of the parasite and the host shoot, while the highest values were detected in the soil (-0.15 MPa). The Ψ_s of the host shoots was significantly lower than that

Table 2. The crown diameter of noninfected and host plants parasitised by *Cistanche phelypaea* growing under natural conditions in the coastal salt marsh, Al-Dhakhira region, Qatar. Results are means ± standard deviation of 6 individual plants.

<i>Arthrocnemum macrostachyum</i> plants	Crown diameter (cm)
Noninfected plant	135.8* ± 22.7
Host plant	85.2 ± 17.8

*: Crown diameter of the noninfected plant is significantly different from that of the host plants at P < 0.01 according to Student's t-test.

Table 3. Dry mass (g) and water content (% fresh mass) of the different parts of the root parasite *Cistanche phelypaea*, its host, and noninfected *Arthrocnemum macrostachyum* plants growing under natural conditions in the coastal salt marsh, Al-Dhakhira region, Qatar. Values are means \pm standard deviations. Different letters within each column indicate significant differences between means at $P < 0.05$. HR = host root, HS = host shoot, INF = inflorescence of the parasite, NIR = root of the noninfected plant, NIS = shoot of the noninfected plant, TU = tuberous body of the parasite. For each parameter, degrees of freedom (df) = 24, while level of probability equals 0.000 in all analysed cases.

Species	Organ	Dry mass (g)	Water content (% fresh mass)
<i>Cistanche phelypaea</i>	INF	14.76 \pm 1.23e	71.42 \pm 1.11c
	TU	7.68 \pm 0.44f	74.80 \pm 2.17b
<i>Arthrocnemum macrostachyum</i>	NIS	99.52 \pm 1.71a	84.56 \pm 1.21a
	NIR	30.40 \pm 1.52c	61.40 \pm 0.89d
	HS	58.28 \pm 2.18b	72.00 \pm 1.00c
	HR	17.48 \pm 1.50d	46.60 \pm 2.07e
F-value of variance ratio by ANOVA test		2642.92	377.07

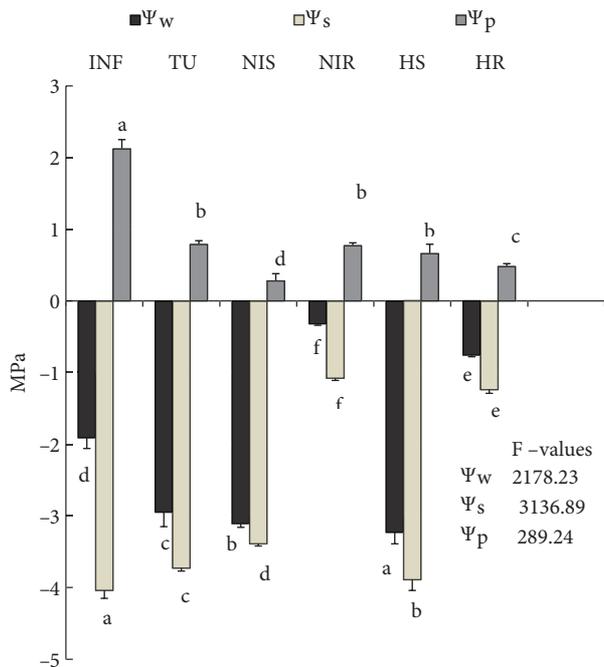


Figure 2. Middy water potential (Ψ_w), osmotic potential (Ψ_s), and pressure potential (Ψ_p) of the different parts of the root parasite *Cistanche phelypaea*, its host, and noninfected *Arthrocnemum macrostachyum* plants growing under natural conditions in the coastal salt marsh, Al-Dhakhira region, Qatar. Vertical line above each bar represents one standard deviation of the mean ($n = 6$). F represents the value of the variance ratio of the one-way analysis. Degrees of freedom (df) = 24, while level of probability equals 0.000 in all analysed cases. Bars topped by different letters within each component of water potential are significantly different. HR = host root, HS = host shoot, INF = inflorescence of the parasite, NIR = root of the noninfected plant, NIS = shoot of the noninfected plant, TU = tuberous body of the parasite.

of noninfected plants. The calculated pressure potential (Ψ_p) ranged from 2.12 in the inflorescence to 0.79 MPa in the tuberous part of the parasite (df = 24, F = 289.2, P = 0.000; Figure 2). The Ψ_p of the host root (0.48 \pm 0.04 MPa) was significantly lower than that of the noninfected plant, and both were significantly lower than that of the tuberous body of the parasite (0.79 \pm 0.04 MPa).

3.4. Chemical analyses of plants

The inflorescence and the tuberous body of the parasite contained significantly less sodium and more potassium than the shoots of the host and noninfected plants (Figure 3). The sodium content of the roots was significantly lower than in the shoots or in the parasite parts (df = 24, F = 2223.4, P = 0.000; Figure 3). The lowest sodium content was in host roots. The parasite had statistically significantly higher ratios of K:Na (df = 24, F = 1685.0, P = 0.000; Figure 3) and K:Na selectivity ratios ($S_{K:Na}$) than the host and the noninfected plants (df = 24, F = 1684.9, P = 0.000; Figure 4).

Calcium content was 30.2% lower than potassium and 14% lower than sodium, especially in the roots. The contents of calcium in the parasite and in *Arthrocnemum macrostachyum* shoots were significantly higher than in the roots of the host and noninfected plants (df = 24, F = 162.39, P = 0.000; Figure 3).

The ratio of potassium to calcium was higher in the parasite parts than in the hosts and the noninfected plants (df = 24, F = 162.39, P = 0.000; Figure 3). For example, in the parasite K:Ca ranged from 5.19 in the inflorescence to 5.24 in the tuberous parts. The ratios in the organs of the host and the noninfected plants were lower than in the parasite, especially in the roots (3.13 and 3.33 in noninfected and host roots, respectively).

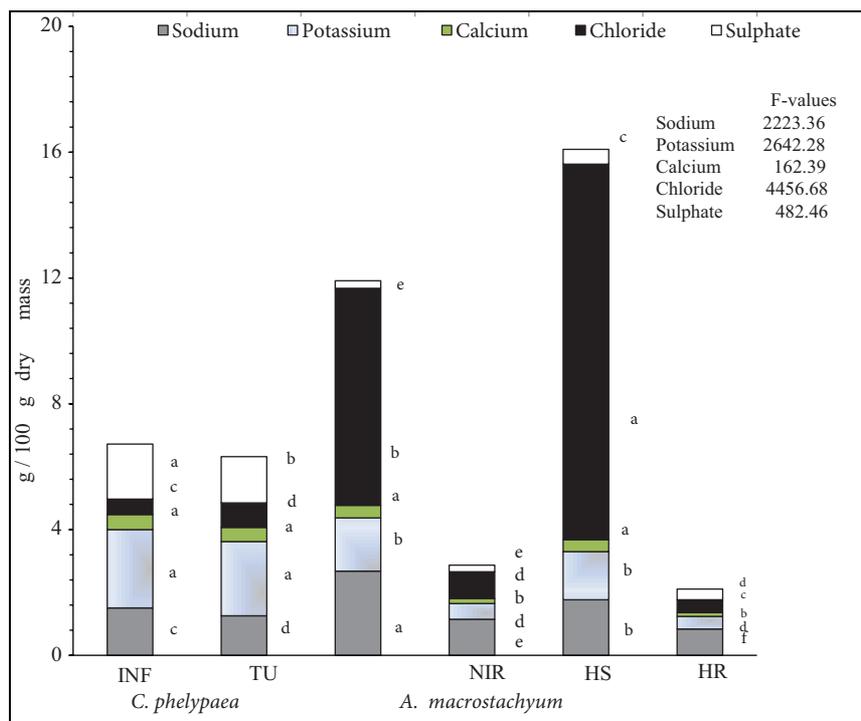


Figure 3. The contents of some nutrient elements (% oven-dried mass) in the different parts of the root parasite *Cistanche phelypaea*, its host, and the noninfected *Arthrocnemum macrostachyum* plants growing under natural conditions in the coastal salt marsh, Al-Dhakhira region, Qatar. Vertical line above each bar represents one standard deviation of the mean ($n = 6$). F represents the value of the variance ratio of one-way analysis. Degrees of freedom (df) = 24, while level of probability equals 0.000 in all analysed cases. Different letters to the right of bars indicate that values of each nutrient element in the different organs of the plants are significantly different. HR = host root, HS = host shoot, INF = inflorescence of the parasite, NIR = root of the noninfected plant, NIS = shoot of the noninfected plant, TU = tuberous body of the parasite.

The chloride content in the roots of noninfected and host plants, and in the parasite parts, were significantly lower than in the *Arthrocnemum macrostachyum* shoots ($df = 24$, $F = 4456.8$, $P = 0.000$; Figure 3). The highest chloride content occurred in the shoots of the host plants ($11.94 \text{ g } 100 \text{ g}^{-1}$ dry mass, ± 0.37). The sulphate contents in the parasite parts were much higher than chloride and were significantly higher than in the roots (5.15-fold) and shoots (3.72-fold) of host and noninfected plants ($df = 24$, $F = 482.46$, $P = 0.000$; Figure 3). The sulphate contents of host plants ($0.34\text{--}0.47 \text{ g } 100 \text{ g}^{-1}$ dry mass) were significantly higher than in noninfected plants ($0.21\text{--}0.24 \text{ g } 100 \text{ g}^{-1}$ dry mass; Figure 3).

Overall, nitrogen contents were 93.3%–97.6% lower than carbon in the tissues of the parasite, host, and noninfected plants (Table 4). The highest nitrogen content occurred in the inflorescence of the parasite. The average nitrogen content of the parasite ($2.12 \text{ g } 100 \text{ g}^{-1}$ dry mass) was higher than in the host and noninfected plants. In

the roots of host and noninfected plants, the contents of nitrogen were significantly lower than in the shoots ($df = 24$, $F = 214.76$, $P = 0.000$; Table 4).

The ash contents of the parasite parts (inflorescence and tuberous body) were significantly (72%) lower than in the shoots of the host and noninfected plants ($df = 24$, $F = 4237.81$, $P = 0.000$; Table 4). The roots and shoots of the host plants showed significantly lower ash contents than the comparable organs of the noninfected plants.

The contents of total soluble sugars were higher than the total free amino acids (1.5- to 13.9-fold of amino acids in the host shoot and tuberous part of the parasite, respectively; Table 4). The contents of soluble sugars ($df = 24$, $F = 663.88$, $P = 0.000$) and total free amino acids ($df = 24$, $F = 560$, $P = 0.000$; Table 4) in the parasite parts were significantly higher than in the host and noninfected plants. The total free amino acid and soluble sugar contents of the roots were significantly higher (approximately 2-fold) than in shoots of noninfected and host plants. The roots

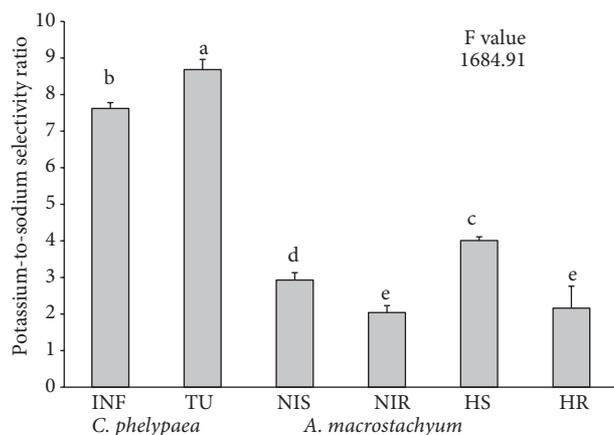


Figure 4. Potassium to sodium selectivity ratio ($S_{K/Na}$) in the different parts of the root parasite *Cistanche phelypaea*, its host, and the noninfected *Arthrocnemum macrostachyum* plants growing under natural conditions in the coastal salt marsh, Al-Dhakhira region, Qatar. Vertical line above each bar represents one standard deviation of the mean ($n = 6$). F represents the value of the variance ratio of one-way analysis. Degrees of freedom (df) = 24, while level of probability equals 0.000 in all analysed cases. Different letters above bars indicate that values in the different organs of the plants are significantly different. HR = host root, HS = host shoot, INF = inflorescence of the parasite, NIR = root of the noninfected plant, NIS = shoot of the noninfected plant, TU = tuberous body of the parasite.

of noninfected plants showed significantly higher soluble sugars content (1.5-fold) and lower total free amino acids contents (41.4%) compared to the host plants. The highest starch contents occurred in the tuberous part (11.12 g 100 g⁻¹ dry mass) (Table 4) and in the inflorescence of the parasite. The starch contents of the underground tuberous part of the parasite and roots of the host and noninfected plants were significantly higher (2.32 ± 0.15 to 11.12 ± 0.54 g 100 g⁻¹ dry mass; $df = 24$, $F = 634.46$, $P = 0.00$; Table 4) than the starch content of the above-ground organs (inflorescences and shoots).

4. Discussion

Soil studies in Qatar show that the inland and coastal saline habitats (known as sabkha in Arabic) occupy a total area of about 700 km², or 6.06% of the country's area (Batanouny, 1981). The unique terrestrial frontal mangrove belt of *Avicennia marina* in the study area at Al-Dhakhira is intermingled with the salt marsh frontier vegetation of *Arthrocnemum macrostachyum*, which had a total cover of 20.8% (Fahmy and Al-Thani, 2006). These conditions characterised the vegetation zone of *Arthrocnemum macrostachyum* as a low-salt marsh habitat that is frequently inundated with seawater. My field study revealed that the target parasite preferred to infect hosts located at the upper fringes of the vegetation zone, away

from the coast and not subjected to direct inundation. In such saline areas (Batanouny, 1981; Abulfatih et al., 2001; Fahmy and Al-Thani, 2006) the soil was finely textured, moist (soil moisture content $19.0 \pm 2.3\%$ oven-dried soil; Table 1), and nonflooded, and the water table was shallow. Therefore, it can be concluded that the root parasite not only infected a particular host, but also preferred individuals growing in moist, nonflooded soil away from the coast.

Despite the occurrence of 3 other halophytic species associating with *Arthrocnemum macrostachyum*, the root parasite *Cistanche phelypaea* was restricted to the study species. This host preference has been reported in previous studies (Babikir and Kürschner, 1992; Fahmy et al., 1996; Press and Phoenix, 2005; Fageer and Assubaie, 2006; Fahmy, 2008).

The host *Arthrocnemum macrostachyum* was sensitive to infection since its crown diameter and dry mass were significantly lower (crown diameter was 58.3% and dry mass was 64.4% of that of the noninfected plant, respectively) than those of the noninfected plant ($df = 10$, $t = 3.93$, $P = 0.01$). Previous studies reported that reductions in the dry mass in the hosts of halophytic and xerophytic species ranged from 60% to 72% due to infection by the angiosperm root parasites *Cynomorium coccineum* L. (Fahmy, 1993) and *Cistanche phelypaea* (Fahmy et al., 1996; Fageer and Assubaie, 2006). The area and dry weight of the leaves of the host tree *Alnus glutinosa* Gaertn., which were infected by the hemiparasite *Viscum album* L., were significantly lower than those of noninfected control trees (Daryaei and Moghadam, 2012).

The tapping of water from the host by *Cistanche phelypaea* possibly decreased the hydraulic conductance to the host shoot. This conclusion is based on the work of Klaren and van Dijk (1976) and Ehleringer and Marshall (1995), who provided evidence that the occurrence of low water potential in the parasite creates problems, including reduced hydraulic conductivity in the parasite body and across the host-parasite interface. The result would be the observed low values of water content in the host organs, which coincided with increased solute concentration. The high concentration of solutes would cause the reduction of Ψ_s , Ψ_w , and consequently Ψ_p in the tissues of the host in comparison to the noninfected plants. Accordingly, a Ψ_w gradient of -0.51 MPa between the soil and host root and -2.19 MPa between the host root and tuberous part of the parasite appears to ensure water movement from the soil to the host root and, finally, to the parasite. Ehleringer and Marshall (1995) pointed out that water transfer across the haustorium can be unidirectional when the total Ψ_w of the parasite tissues is more negative.

The maintenance of positive values of Ψ_p (turgor pressure) in the cells of the tuberous part of the parasite,

Table 4. Carbon, nitrogen, ash, total free amino acids (estimated as glycine), total soluble sugars (estimated as glucose), and starch in the dry mass of the different parts of the root parasite *Cistanche phelypaea*, its host, and the noninfected *Arthrocnemum macrostachyum* plants growing in a coastal salt marsh, Al-Dhakhira region, Qatar. Results are means \pm standard deviation of 6 individual plants. Different letters within each column indicate significant differences between means at $P < 0.05$. HR = host root, HS = host shoot, INF = inflorescence of the parasite, NIR = root of the noninfected plant, NIS = shoot of the noninfected plant, TU = tuberous body of the parasite. For each parameter degrees of freedom (df) = 24, while level of probability equals 0.000 in all analysed cases.

Species	Organ	C			Ash	Total free amino acids (mg g ⁻¹)	Total soluble sugars (mg g ⁻¹)	Starch (%)
		C	N (%)					
<i>Cistanche phelypaea</i>	INF	42.44 \pm 0.43c	2.86 \pm 0.11a	9.72 \pm 0.54d	58.32 \pm 2.68a	267.40 \pm 14.72a	5.260 \pm 0.46b	
	TU	44.52 \pm 1.43b	1.38 \pm 0.08b	11.92 \pm 0.47c	12.90 \pm 1.30e	179.00 \pm 7.62b	11.12 \pm 0.54a	
<i>Arthrocnemum macrostachyum</i>	NIS	41.78 \pm 0.16c	1.37 \pm 0.08b	40.28 \pm 0.76a	18.82 \pm 1.14d	34.80 \pm 3.49e	1.46 \pm 0.06e	
	NIR	33.00 \pm 0.61d	1.06 \pm 0.06c	9.44 \pm 0.35d	13.80 \pm 1.26e	105.40 \pm 7.20c	3.76 \pm 0.17c	
	HS	45.62 \pm 0.37a	1.34 \pm 0.15b	35.20 \pm 0.49b	19.54 \pm 0.95c	28.80 \pm 2.28e	1.36 \pm 0.31e	
	HR	30.48 \pm 1.03e	1.02 \pm 0.11c	7.60 \pm 0.28e	33.32 \pm 1.89b	69.4 \pm 6.91d	2.32 \pm 0.15d	
	F-value of variance ratio by ANOVA test		312.00	214.76	4237.81	637.26	663.88	634.46

host, and noninfected plants allows for more turgid cells. This allows storage of water and solutes, particularly in the tuberous body of the parasite, which is rich with soft parenchymatous tissue (Fahmy, 2008). Studies have indicated that cells of the water storage tissue of plants have a low elasticity module (low ϵ), i.e. they can easily take up and release a lot of water (Nobel, 1991; Tyree, 2007). Moreover, it is apparent that the low values of Ψ_s in the tissues of the plants in the current study increase Ψ_p and maintain cell turgor.

Based on the low mobility of calcium in the phloem and the high mobility of potassium, Ziegler (1975) pointed out that the potassium-to-calcium ratio in a plant can be used to distinguish phloem-feeding and xylem-feeding parasites; a high ratio implies phloem-feeding. Apparently, the high ratio of potassium to calcium in the organs of the parasite indicates that it is phloem-feeding. The potassium-to-calcium ratio was 6 in the root parasite *Cynomorium coccineum*, infecting the 2 individual halophytic hosts *Arthrocnemum macrostachyum* (Chenopodiaceae) and *Limoniastrum monopetalum* (Gir.) Ktze. (family Plumbaginaceae) in a Mediterranean coastal salt marsh in Egypt (Fahmy, 1986). Holoparasites are also known as phloem feeders since they depend on their host phloem for resources (Hibberd and Jeschke, 2001; Bolin et al., 2010). Since nitrogen is a phloem mobile element (Hopkins and Hüner, 2004), the N:Ca value of >1 implies active feeding from the host phloem (Bowie and Ward, 2004; Yoder and Scholes, 2010). The results of the N:Ca value in *Cistanche phelypaea* ranged from 3.1 to 6.0 in the tuberous body and the inflorescence, respectively (compare the contents of N and Ca in Table 4 and Figure 3). Based on the high N:Ca value in the mistletoe (*Plicosepalus acacia*) parasitising *Acacia raddiana*, Bowie and Ward (2004) concluded that nutrient absorption was not coupled to water transport.

Comparing the ratios of potassium to sodium and potassium to sodium selectivity ($S_{K:Na}$) of the parasite and host indicated that the parasite displayed much higher discrimination against sodium than the host and noninfected plants. The values for $S_{K:Na}$ ratios for the parasite (7.6–8.6) are higher than those for the host and noninfected plants and the values reported for halophytes from Chenopodiaceae ($S_{K:Na} = 6$ at medium salinity; 101–201 mM NaCl) (Aronson, 1989). Studies have indicated that halophytes grown in nonsaline or medium-salinity culture solutions accumulate high concentrations of K (Yeo and Flowers, 1980). Therefore, it is concluded that the high $S_{K:Na}$ ratios for the parasite are directly related to tolerance. Studies have indicated that salt-tolerant plants keep high $S_{K:Na}$ values through the preferential uptake of K over Na, and that the capacity to maintain high K:Na discrimination is greater in halophytes (Gorham et al.,

1985; Koyro and Stelzer, 1988; Flowers and Colmer, 2008; Hameed et al., 2013). The differences in $S_{K:Na}$ values between *Cistanche phelypaea* and *Arthrocnemum macrostachyum* (the host and the noninfected plants) indicate variation in the mechanisms of salt tolerance between the 2 groups. The phloem-feeding nature of the parasite together with the possible selective nutrient element absorption of the haustorium may be advantages in fulfilling its demand for solutes, and this will maintain an osmotic potential that is lower than that of host roots.

In their study of the composition of cell sap in various halophytic plant families, Albert et al. (2000) found that members of the family Chenopodiaceae (to which *Arthrocnemum macrostachyum* belongs) accumulate high contents of Na and Cl in the cell sap. In typical halophytic succulents, the Cl:SO₄ ratio is displaced strongly in favour of chloride. The opposite of the above is observed in organs of the parasite *Cistanche phelypaea*, which showed much higher SO₄ content (about 5.11-fold) than *Arthrocnemum macrostachyum*. The properties of sulphate incorporation in organic structures (Marschner, 1995) may reflect their large proportion in the organs of the parasite. Based on the mobility of sulphur in both xylem and phloem (Pate, 1995) and the phloem-feeding nature of the parasite, it is possible that sulphur will enter the xylem stream if there is efficient transpiration by *Cistanche phelypaea*. Press et al. (1988) reported that transpiration of annual and herbaceous root parasites is a mechanism for maximising heterotrophic carbon gain.

The presence of carbon and nitrogen in *Cistanche phelypaea* in quantities matching those of the host (average C+N ranged from 39.3% to 45.6% oven-dried mass in the host and parasite, respectively) suggests 2 possibilities: the parasite completely depends on the withdrawal of organic forms of carbon and nitrogen from its host, and/or the parasite has carbon- and nitrogen-reducing enzyme systems similar to or different from those of the host. Since *Cistanche phelypaea* is an obligate holoparasite with no photosynthetic capacity, it gains all the reduced carbon from the host. The carbon gain by the holoparasite *Cistanche phelypaea* is similar to that of the unemerged young plant of the obligatory hemiparasite *Striga hermonthica* (Těšitel et al., 2010), which is achlorophyllous; hence, both are dependent on the host. For example, the mean proportion of heterotrophic carbon in the biomass of the unemerged young *Striga hermonthica* plant reached 100%. Orcutt and Nilsen (2000) pointed out that the transport of resources from the host does not occur by diffusion alone. A possible explanation is based on the quality of organic materials (carbohydrates, amino acids, and organic acids), which is different in parasites than in hosts. For example, Nandakumar et al. (1976) pointed out that holoparasites

may depend upon their hosts to obtain their requirements of particular amino acids, which they cannot synthesise (such as isoleucine). Moreover, the stem parasites may depend on both nitrate and organic nitrogen from the host (Orcutt and Nilsen, 2000). When the stem parasitic plant was grown in medium containing only inorganic nitrogen (ammonium nitrate), it had reduced growth. Pennings and Simpson (2008) reported that when the host nitrogen was altered by fertilising plots, the percentage cover of parasite *Cuscuta salina* doubled. Certainly the low nitrate reductase activities reported for many parasitic species (McNally and Stewart, 1987) suggest that they obtain much of their nitrogen in an organic form. Therefore, the high C:N value in the parasite (14.8 in inflorescence and 32.3 in the tuberous part) shows that *Cistanche phelypaea* maximises carbon gain and, thereby, the demand for nitrogen. The high nitrogen content in the inflorescence of the parasite may be attributed to the presence of nitrogen-rich tissues, such as the reproductive structures.

The existence of statistically nonsignificant differences in nitrogen content between the host and noninfected *Arthrocnemum macrostachyum* in this study contradicts previous studies (Jeschke and Hilpert, 1997; Orcutt and Nilsen, 2000), in which there was an increase in nitrogen accumulation in host tissues due to infection. In their study of the holoparasite *Hydnora* (3 species) and 3 other hemiparasites, Bolin et al. (2010) found that the stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for holoparasites and $\delta^{15}\text{N}$ for hemiparasites) were significantly correlated with hosts. They explained that these relationships indicate complete dependence on the hosts for nitrogen.

The high soluble sugar and starch contents in *Cistanche phelypaea* are a common trend in parasitic angiosperms (Singh et al., 1968). The occurrence of high tissue concentrations of soluble sugars and potassium in the different parts of *Cistanche phelypaea* has been implicated in the generation of cell sap osmolarities of parasitic angiosperms (Ernst, 1986; Press et al., 1986; Fahmy, 1992) and the preservation of enzyme activity (Flowers and Colmer, 2008). It is suggested that the conversion of sugars to starch in the tuberous body of the parasite may lower their concentrations in the cells of the parasite and thus set up a concentration gradient for the transport of more sugars into the parasite via the haustorium. Studies have indicated that the stem parasite *Cuscuta reflexa* exerted a very strong sink and competed efficiently with the major host sinks by attracting 81% of the current photosynthate and 223% of nitrogen, more than was currently fixed (Press, 1995). Moreover, the presence of starch may imply the existence of a matric component (Wiebe, 1966) that produces surface forces that account for a minor portion of cell's water potential. Accordingly, the water retaining

forces of the parasite (especially the tuberous part with the highest starch content and nearest the host root) are expected to be higher due to the Ψ_w alone.

In conclusion, the root parasite *Cistanche phelypaea*, which infects the halophytic host *Arthrocnemum macrostachyum*, demonstrates a high degree of physiological adaptation. This host-parasite relationship can be outlined by the following points: 1) Host specificity and sensitivity to infection: despite the presence of other members of family Chenopodiaceae in the coastal salt marsh, the parasite was restricted to *Arthrocnemum macrostachyum*. The host suffers from infection since its dry mass was 66% lower than that of the noninfected plant. 2) Infection altered the water potential and its components: the host plants showed low values for osmotic potential (Ψ_s), water potential (Ψ_w), and pressure potential (Ψ_p) in comparison to noninfected plants. The existence of a Ψ_w gradient of -2.19 MPa between host root and parasite may ensure water transport to the parasite. 3) Particular nutrient elements composition: A- The parasite showed much higher discrepancy against sodium than its host. This feature is apparent from the high ratios of K:Na and the potassium-to-sodium selectivity ratio ($S_{K:Na}$). B- The high C:N value in the parasite shows that it maximises its carbon gain and, thereby, the demand for nitrogen. 4) The high starch content in the parasite possibly serves 2 functions: A- Starch in the parasite is unavailable to be diverted back to the host, and B- starch exerts a matric potential, which (in addition to the low Ψ_w) increases the water-retaining forces of the parasite.

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