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PHYSIOLOGICAL PERFORMANCE OF A COASTAL MARSH PLANT *HYDROCOTYLE VULGARIS* IN NATURAL CONDITIONS IN RELATION TO MINERAL NUTRITION AND MYCORRHIZAL SYMBIOSIS

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Fluctuating soil salinity and competition for light are the main factors affecting plant distribution and performance in coastal salt marshes. The aim of the present study was to assess plant performance by means of non-destructive instrumental methods in a highly heterogeneous natural habitat. More specifically, environmental factors affecting growth and physiological performance of a clonal plant Hydrocotyle vulgaris *L. were investigated. Changes in soil salinity, soil mineral characteristics, leaf nutrient concentrations, morphological parameters, chlorophyll fluorescence, and mycorrhizal symbiosis were analysed in different experimental plots of naturally growing* H. vulgaris *plants. The dynamic nature of interaction between sea water flooding-affected changes in soil salinity and competition-dependent changes in light availability led to micro-environmental heterogeneity differentially affecting physiological performance and growth of* H. vulgaris *in natural conditions. Plant growth was mostly affected by intensity of photosynthetically active radiation in the respective plots. Increased growth rate in shaded conditions specifically pointed to shade tolerance strategy of* H. vulgaris*. High heterogeneity of mineral nutrients between the plots was established. However, considerable plasticity of metabolism in respect to highly variable soil concentration of mineral nutrients together with effective mineral adaptation mechanisms ensured optimal supply of material for growth. Photochemistry of photosynthesis was only marginally affected by differences in microenvironmental conditions as shown by respective changes in chlorophyll a fluorescence parameters. Mycorrhizal symbiosis was stimulated by moderately increasing soil salinity and suppressed by relatively high salinity. When the effect of soil salinity was omitted, intensity of mycorrhizal symbiosis was positively associated with intensity of photosynthetically active radiation. In general, a relatively high stable level of photosynthetic performance across a wide range of micro-environmental conditions indicates an adequate level of physiological adaptation of* H. vulgaris *to conditions of a coastal salt marsh. The present data clearly reflect complex interactions between environmental factors and plastic physiological responses of* H. vulgaris*.*

Key words: *chlorophyll, chlorophyll a fluorescence, growth, natural conditions, photosynthetic performance, salinity.*

INTRODUCTION

In natural environments, simultaneous effect of various environmental constraints affect plant performance. Fluctuating soil salinity together with soil edaphic conditions are among the main factors affecting plant distribution and performance in coastal salt marshes (Packham and Willis, 1997). In addition, competitive processes, i.e. competition for light, are of special importance for efficient photosynthetic productivity in salt marshes (Ungar, 1998). However, studies on the effect of increased soil salinity on naturally growing plant populations have been relatively rare. No

studies so far have described light–salinity interactions in a shade-tolerant species.

Coastal habitats are characterised by a relatively high heterogeneity of environmental conditions (Ievinsh, 2006). Plants adapt to heterogeneous conditions mostly due to the plastic morphological and physiological traits of possible adaptive character. Therefore, micro-environmental heterogeneity could have both negative and positive consequences for native plants. Firstly, individuals of species with a relatively low level of phenotypic plasticity could be eliminated from micro-environments with prevailing suboptimal levels of certain critical factors, e.g., low nutrient levels, high salinity, water shortage etc. Secondly, it can be effectively used by clonal plants to establish ramets in patches with abundant resources. Changes in clonal growth parameters of clonal plants due to changes in environmental conditions reflect effects on physiological integration related to behaviour in heterogeneous conditions. Thus, small-scale heterogeneity in soil factors has been shown to affect photosynthetic efficiency and habitat selection in clonal plants (Roiloa and Retierto, 2006).

Estimation of plant vitality and performance in natural conditions has been a problem by itself. In ecophysiological studies, different characteristics of plant vigour have been used, including fluctuating asymmetry of leaves (Fair and Breshears, 2005) or electrical admittance of plant tissues (Pukacki and Kamińska-Rożek, 2005). Chlorophyll *a* fluorescence measurements were introduced for analysis of plant performance in natural conditions. Chlorophyll fluorescence measurements allow assessing activity of photosynthetic apparatus at different levels of organisation (Maxwell and Johnson, 2000). The idea of using chlorophyll fluorescence as a tool to measure plant vitality is based on the fact that all suboptimal environmental factors affect photosynthesis either in a direct or indirect way (Teskey *et al*., 1995). Therefore, functional changes of photosynthetic apparatus can be used to evaluate physiological status and performance of plants before any structural stress-related changes occur. Recently, we successfully used chlorophyll *a* fluorescence measurements in natural conditions to reveal physiological status of *Eryngium maritimum*, an endangered coastal plant (Andersone *et al*., 2010)

Mycorrhizal symbiosis is a well-known type of biotic interaction in salt marshes. It is assumed to increase plant performance by stabilising nutrient uptake in heterogeneous environments (Hirrel and Gerdemann, 1980) or by increasing water use efficiency (Giri *et al*., 2003). However, other studies have indicated that a fungal component of the symbiosis could be less tolerant to suboptimal changes in environmental conditions in salt marshes (e.g., high salinity) in comparison to host plants, often leading to decreased intensity of mycorrhizal symbiosis (Juniper and Abbott, 2006).

Hydrocotyle represents a cosmopolitan genus of approximately 130 perennial clonal plant species widely distributed in moist habitats. Different *Hydrocotyle* species have been used to investigate different aspects of "clonality": clonal integration (*H. bonariensis*; Evans and Whitney, 1992; *H. peduncularis*; Peterson and Chesson, 2002), local adaptation and genetic differentiation (*H. bonariensis*; Knight and Miller, 2004), and effects of flooding and growing season length (*H. umbellata*; Dawe and Reekie, 2007; Lusk and Reekie, 2007). It was concluded that high morphological plasticity as a result of environmental changes is a characteristic feature of *Hydrocotyle* species. In the present study, *H. vulgaris* was used as a model species. In contrast to other regions where *H. vulgaris* grows exclusively in open habitats (Dong, 1995), in the Baltic region *H. vulgaris* has characteristics of a putative shade -tolerant species growing both under trees and in coastal grassland. In the coastal area of the Baltic Sea, *H. vulgaris* plants are present in habitats with seawater inundation-dependent relatively moderate fluctuations of soil salinity within a season (EC 0.57–3.32 $dS \cdot m^{-1}$) and a wide range of light conditions (from deep tree canopy shade to full sun; Ievinsh *et al.,* unpublished results). Therefore, it can be expected that both fluctuating salinity and light conditions affect growth and development of *H. vulgaris* in natural conditions.

The aim of the present study was to determine if plant performance could be assessed in a highly heterogeneous natural habitat by means of non-destructive instrumental methods as well as if performance indices can be used for explaining the effect of environmental factors on plant growth and photosynthetic productivity. More specifically, a hypothesis that local differences in soil salinity and light availability affect growth and performance of *H. vulgaris* plants in natural conditions was tested. Changes in soil salinity, soil mineral characteristics, leaf nutrient concentrations, and mycorrhizal symbiosis were analysed in different experimental plots of naturally growing *H. vulgaris* plants. To characterise performance of *H. vulgaris* plants, both morphological parameters and chlorophyll *a* fluorescence were measured.

MATERIALS AND METHODS

Growth and physiological performance of *Hydrocotyle vulgaris* L. were studied in natural conditions. Exact locations of eight experimental plots were chosen to represent the variability of the main environmental factors of interest: sea-affected fluctuating soil salinity and vegetation-affected different degree of shade (Table 1). Control plots (A and B) without any effect of sea-dependent changes in soil salinity were located on a coast of a freshwater lake Būšnieks near Ventspils, Latvia. Sea-affected plots were located about 90 km to the east in a coastal salt marsh near Mērsrags, Latvia. Differences in distance from the sea between the plots resulted in a different rate of flooding with seawater and, as a result, fluctuations in soil salinity. Plots C and E were flooded with sea water only within the winter period, in the first part of the season flooding occurred in plots F and G, while plots D and H were flooded at the end of the season. The plots varied also in respect to photosynthetically active radiation available for plants. Measurement of photosynthetically active radiation (PAR) in experimental plots was

Table 1. Characteristics of sampling plots with *Hydrocotyle vulgaris.* Photosynthetically active radiation (PAR) was measured on a clear day once a month from June to September with a quantum sensor attached to a chlorophyll fluorometer PAM-2100 (Walz, Germany). Light conditions are characterised at the plant level relative to PAR for full sunlight at 1.5 m height in an unshaded spot at the particular location

Plots	Distance from the sea (m)	Shading by vegetation	Flooding by sea water
A	–	Trees, 19 % PAR	None
B	–	Trees, 11 % PAR	None
C	18	Trees, 9 % PAR	Only in winter season
D	< 2	Short herbs, 59 % PAR	Significant
E	18	Trees, 30 % PAR	Only in winter season
F	< 2	Short herbs, 68 % PAR	Significant
G	> 10	Tall herbs, 42 % PAR	Moderate to significant
H	< 2	Short herbs, 72 % PAR	Significant

performed on a clear day once a month four times during the vegetation season from June to September with the quantum sensor attached to a chlorophyll fluorometer PAM-2100 (Walz, Germany). Light conditions for a particular plot were determined as the average value from five readings at plant height and expressed relative to photosynthetic photon flux density for full sunlight at 1.5 m height for unshaded spots in a particular location. Intensity of radiation varied from 9% in deep shade resulting from a location of the plot inside an *Alnus glutinosa* L. stand (plot C) to 72% resulting from short herbaceous vegetation (plot H).

Plant measurements and sampling for analysis were performed once a month between the 12^{th} and 17^{th} days of each month of the vegetation season from May to September.

Leaf chlorophyll content was measured non-destructively using a SPAD-502 chlorophyll meter (Konica-Minolta, Japan). A near-linear relationship exists between chemically analysed total chlorophyll content on fresh mass basis and SPAD values measured by a chlorophyll meter (Samsone *et al.,* 2007). For measurement, 30 leaves of average size were randomly sampled from every plot. For each leaf, five consecutive readings were made across the leaf surface and the mean was calculated using the internal function of the chlorophyll meter.

Non-destructive analysis of chlorophyll *a* fluorescence was performed by a pulse-amplitude modulated portable fluorometer PAM-2100 (Walz, Germany) using a leaf clip holder with an integrated micro quantum and temperature sensor 2030-B (Walz, Germany). A laptop computer with appropriate software DA-2000 (Walz, Germany) was used to drive the measurements. For analysis, five leaves of average size were randomly sampled from each plot. Leaves were dark adapted for 30 min using appropriate leaf clips. Fluorescence measurements were performed according to manufacturers' instructions as described elsewhere (Samsone *et al.,* 2009). Briefly, the ratio F_V/F_M, reflecting the potential quantum yield of photosystem II, was calculated from the minimal fluorescence level in the dark adapted state F_0 measured by low modulated light and the maximal fluorescence level in the dark adapted state F_M determined by a saturating pulse according to the equation $F_V/F_M = (F_M - F_0) / F_M$. The fluorescence induction curve with quenching analysis at 10 $ms \cdot p^{-1}$ was recorded using a built-in standard procedure of DA-2000. The steady-state fluorescence F_S was recorded after light adaptation of 6 min and then the maximal fluorescence level in the light adapted state (F'_M, saturating pulse) and the minimal fluorescence level (F'_0, far-red light pulse) was measured. Maximum apparent electron transport rate ETR in photosystem II was calculated from the overall photochemical quantum yield and photosynthetically active radiation. Non-photochemical quenching NPQ was calculated according to the equation $NPQ = (F_M - F'_M) / F'_M$.

Root samples with soil for analysis of mycorrhizal symbiosis were excavated at three randomly selected spots for every experimental plot. The collected samples were placed in sealed polyethylene bags and stored at 4 °C until analysis. Root samples were prepared according to a method of Hayman (1970) with some modifications as described previously (Druva-Lūsīte *et al*., 2008). Mycorrhizal colonisation (abundance of hyphae, vesicles and arbuscules) was measured and both intensity of mycorrizal colonisation (M%) and frequency of mycorrhiza in the root system (F%) were calculated with the computer program Mycocalc according to the method of Trouvelot *et al*. (1986) as described previously (Druva-Lūsīte *et al*., 2008).

Soil samples were taken from the root zone near *H. vulgaris* plants in a depth of 0 to 10 cm. For every experimental plot, at every time point, five to eight subsamples were randomly taken and thoroughly mixed to form one sample.

For analysis of leaf mineral constituents, 30 leaves of average size per plot were randomly sampled in three replicates for every time point. The leaves were used for measurement of morphological parameters and then transported to laboratory for chemical analysis of mineral nutrient concentrations.

Leaf tissues were dried in oven (60 °C), weighed and ground into a fine powder by means of a ball mill. The samples were dry-ashed in concentrated HNO_3 vapour and redissolved in HCl solution in deionised water (3:100, v/v). Soil samples were air-dried and sieved through a metal sieve (2-mm mesh size). Samples were extracted with 1M HCl (soil to extractant 1:5; v/v). Soil pH was measured in 1:2.5 soil to 1M KCl solution. Soil electrical conductivity was determined in a 1:5 soil to deionised water volume ratio with a conductometer.

Nutrient concentrations were analysed in leaf and soil samples by atomic absorption spectrophotometry (Ca, Mg, Fe, Cu, Zn, Mn), colorimetry (N, P, Mo, B), turbidimetry (S), flame photometry (K, Na) and $AgNO_3$ titration (Cl) as described previously (Karlsons *et al*., 2008).

Statistical analysis was performed by KaleidaGraph (version 4.0; Synergy Software). Significant differences between the parameters at all treatments were determined at $p \leq 0.05$. Both linear and non-liner regression was analysed. Different models instead of linear relationship were used to find the level of association between the parameters. All relationships were determined at $p \leq 0.05$.

RESULTS

Soil characteristics and mineral nutrition. Soil characteristics and soil mineral nutrient concentrations in experimental plots with *H. vulgaris* were analysed five times during the season. Average soil mineral concentrations are given in Table 2. Micro-environmental-dependent differences in mineral constituents between plots were observed, reflecting micro-environmental heterogeneity. There was no clear trend in differences of soil pH between experimental plots. Soil in the sea-affected experimental plots contained extremely high levels of organic material. High soil EC as well as high Na and Cl concentrations in sea-affected plots reflected the direct effect of flooding with seawater. In addition, these plots had significantly higher soil concentrations of K, Mg, Fe, S and B as compared to control plots. Some peculiarities in average seasonal concentrations of several minerals for individual plots were evident. Soil of control plot B had extremely high Zn concentration, and plot D had the highest soil Ca concentration. At the end of the vegetation season in September, soil Fe concentration showed an extreme increase in plots D and F, as well as significant increase in plot H (data not shown). This effect was most probably related to the location of these plots near the sea.

Changes in soil electrical conductivity and Na and Cl concentrations during the season reflected flooding by seawater (Fig. 1 A and B). Plots D, H, E, G and F had relatively high soil salinity early in the season, reflecting impact from

Table 2. Soil characteristics, Na, Cl and soil mineral nutrient concentrations ($mg \cdot l^{-1}$) in sampling plots with *Hydrocotyle vulgaris*. Data are means from 5 measurements throughout the vegetation season ± SE

Parameters	Plots							
	A	B	C	D	E	F	G	H
Soil EC ($dS\ m^{-1}$)	0.40 ± 0.05	0.99 ± 0.11	1.15 ± 0.16	6.92 ± 2.02	3.69 ± 0.82	5.24 ± 1.16	3.67 ± 0.60	3.88 ± 0.93
pH	6.67 ± 0.07	6.32 ± 0.17	5.91 ± 0.06	5.96 ± 0.04	6.22 ± 0.08	6.16 ± 0.12	6.11 ± 0.09	6.10 ± 0.10
Na	18 ± 2	35 ± 2	381 ± 66	1765 ± 508	967 ± 185	1184 ± 194	1145 ± 214	872 ± 163
Cl	9 ± 2	12 ± 3	464 ± 314	1538 ± 546	846 ± 236	1077 ± 172	857 ± 193	850 ± 191
N	21 ± 2	68 ± 8	31 ± 1	54 ± 14	39 ± 3	40 ± 3	40 ± 6	34 ± 4
P	85 ± 8	67 ± 8	134 ± 14	60 ± 4	143 ± 12	92 ± 13	129 ± 25	107 ± 6
K	24 ± 4	111 ± 10	81 ± 21	439 ± 162	220 ± 56	278 ± 25	241 ± 45	191 ± 51
Ca	755 ± 135	2664 ± 427	1200 ± 121	5485 ± 563	1495 ± 192	2270 ± 263	1670 ± 113	2413 ± 854
Mg	103 ± 13	263 ± 25	518 ± 81	1480 ± 252	975 ± 103	1153 ± 101	1018 ± 110	938 ± 155
S	9 ± 2	17 ± 3	18 ± 5	313 ± 61	53 ± 17	196 ± 60	127 ± 28	144 ± 52
Fe	334 ± 32	719 ± 130	448 ± 86	1151 ± 241	841 ± 263	1853 ± 310	503 ± 32	1022 ± 190
Mn	18 ± 2	97 ± 11	75 ± 16	15 ± 3	145 ± 30	33 ± 14	59 ± 14	26 ± 10
Zn	10 ± 2	37 ± 3	5 ± 1	10 ± 1	9 ± 2	10 ± 1	10 ± 1	8 ± 1
Cu	0.57 ± 0.13	3.01 ± 0.29	0.45 ± 0.12	2.41 ± 0.27	1.59 ± 0.38	2.68 ± 0.13	2.03 ± 0.16	2.09 ± 0.43
Mo	0.020 ± 0.006	0.028 ± 0.004	0.034 ± 0.004	0.030 ± 0.004	0.030 ± 0.003	0.028 ± 0.002	0.038 ± 0.007	0.034 ± 0.002
B	0.46 ± 0.22	1.20 ± 0.30	1.84 ± 0.29	4.86 ± 1.21	4.10 ± 1.02	3.82 ± 0.58	3.84 ± 0.88	3.80 ± 0.93

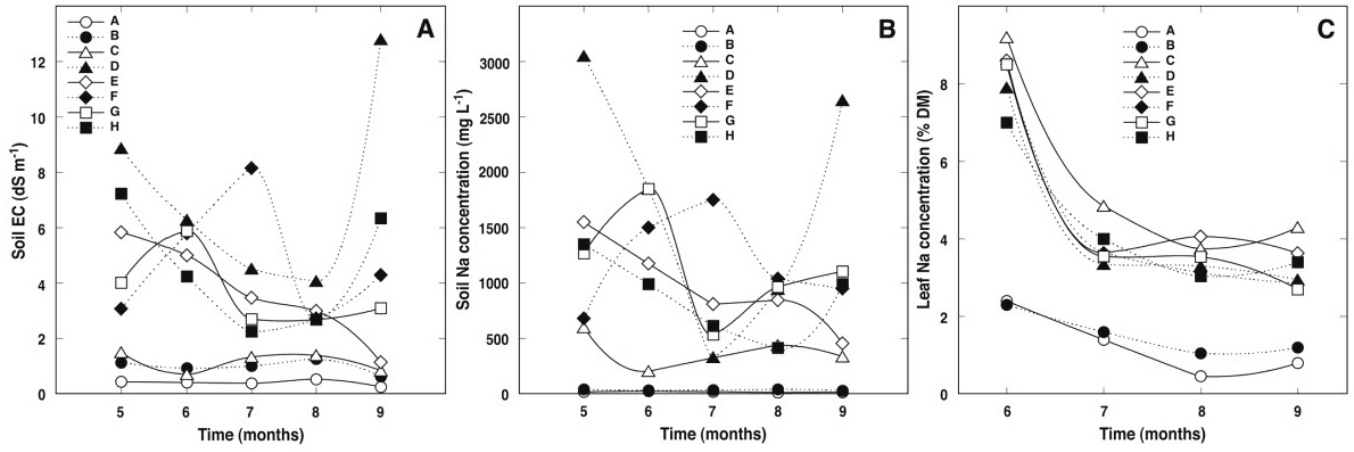


Fig. 1. Seasonal changes in soil electrical conductivity (A), soil Na (B) and leaf Na (C) concentrations of *Hydrocotyle vulgaris* at different experimental plots. Data are means from 3 measurements at every time point ± SE.

flooding during winter or early spring. Effect of sea flooding during the season was evident for plots G (June), F (June – July), D and H (September). There was a significant association between soil Na and Mg concentrations (r^2 = 0.91) for individual measurements at individual experimental plots during the season (data not shown). In spite of fluctuating soil Na and Cl concentration during the season for different experimental plots, leaf tissues of plants from sea-affected plots contained similar concentrations of both Na (Fig. 1 C) and Cl, indicating saturation of ion accumulation. Concentrations of both were higher in spring, reflecting higher capacity for NaCl accumulation in actively growing cells.

Average mineral nutrient concentrations for *H. vulgaris* leaves from individual experimental plots based on four measurements within the season are summarised in Table 2. In general, there was no significant relationship between average concentration of a particular mineral in a particular plot and respective average mineral concentration in leaves of *H. vulgaris* growing at the same plot. Tissue concentrations of particular minerals increased with increasing respective soil mineral concentration only for macronutrients Mg and S. However, the effect had an exponential character, indicating saturation at higher concentrations (r^2 = 0.91 and r^2 = 0.98, for Mg and S concentrations, respectively). In addition, Mg concentration in leaf tissues was significantly associated with tissue Na concentration (r^2 = 0.75). Significant fluctuations during the season were evident in the soil of sea-affected plots for other possibly flooding-dependent minerals (Mg, Fe; data not shown). Plants growing on plots C and H had extremely high concentration of Fe in leaf tissues, which was 7 and 14 times, respectively, higher than the average Fe concentration in leaves from other plots (Table 2). The concentration sharply increased in July, remained high during August and declined in September (data not shown).

Light conditions significantly affected the status of *H. vulgaris* leaf mineral nutrition. Leaf P concentration linearly increased with increase of relative PAR in experimental plots (r^2 = 0.85) while leaf N concentration linearly decreased with increase of relative PAR (r^2 = 0.88), generally leading to negative association between leaf N and P concentration (r^2 = 0.68). However, similar relationship was found between leaf P content and soil EC (r^2 = 0.82).

Growth and photosynthetic performance. Growth characteristics of *H. vulgaris* leaves were affected by micro-environmental conditions, as they significantly varied between the experimental plots. Regarding petiole height and mass, two groups of plots were clearly seen with no significant differences within the groups (Fig. 2). The first group, which had maximum petiole growth, includes control plots (A and B, 19 and 11% PAR, respectively) and plots C and E from the sea-affected site (9 and 30% PAR, respectively). In the second group, where petiole growth was significantly inhibited, plots with 42 to 72% PAR are included. This difference indicated that increase of illumination from 30 to 42% PAR reduced petiole growth. The same groups were evident for changes in leaf blade diameter (Fig. 3 A). While in general the same plots had also higher rates of increase of leaf blade fresh mass, the relationship was less evident due to significant differences within the groups (Fig. 3 B). For increase in leaf blade diameter, some growth inhibition was observed in plots C and E at the second part of the vegetation season.

However, plants in the plots with highest soil salinity within the season occurred in less shaded microhabitats. Consequently, inhibitory effect of salinity on leaf growth should not be excluded. A negative linear relationship both between different growth parameters and relative PAR and between leaf growth and soil EC was evident when the mean values within the season for respective plots were considered. Association between growth and relative PAR was more pronounced, with r^2 = 0.89 and r^2 = 0.92, for petiole height and leaf diameter, respectively, in comparison with r^2 = 0.76 and r^2 = 0.87, for the respective associations with soil EC.

There was a significant negative linear relationship between P concentration in the tissues and the leaf blade fresh mass (r^2 = 0.97) and leaf blade diameter (r^2 = 0.94) for average values during the season for individual experimental plots as well as monthly measurements for individual plots (r^2 = 0.77 and r^2 = 82, for fresh mass and diameter, respectively).

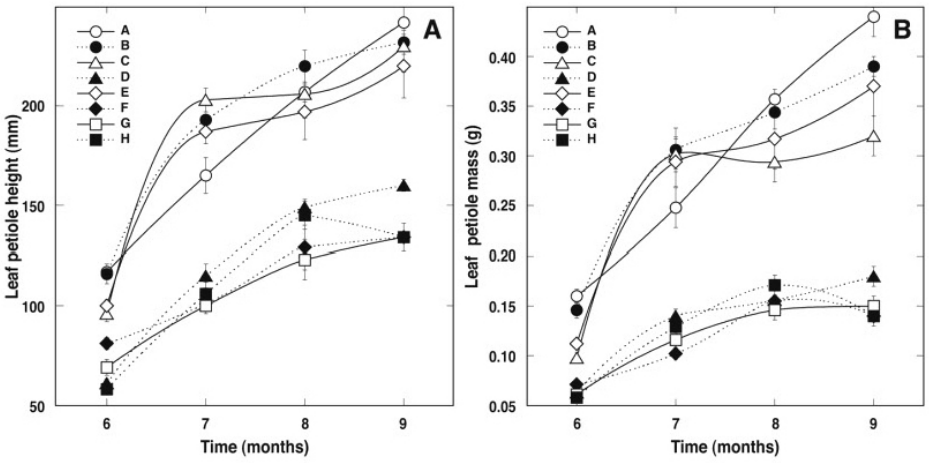


Fig. 2. Changes of leaf petiole height (A) and leaf petiole fresh mass (B) of *Hydrocotyle vulgaris* during the season at different experimental plots. Data are means from 30 measurements at every time point ± SE.

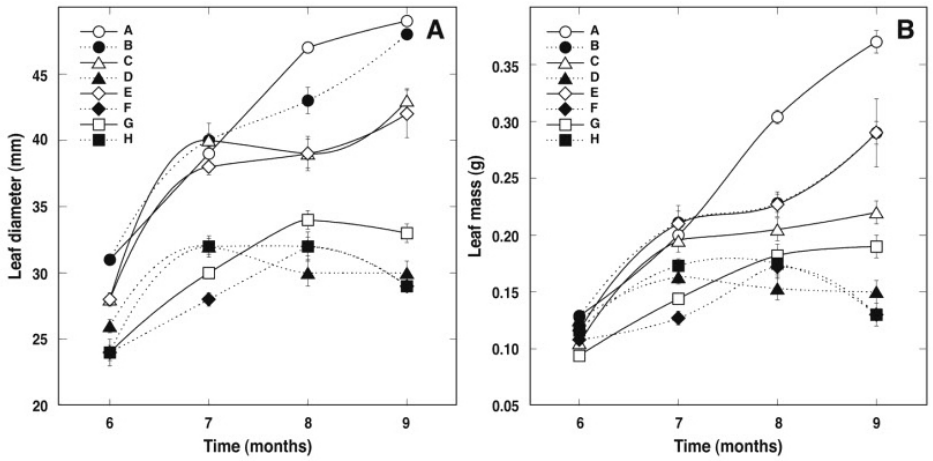


Fig. 3. Changes in leaf blade diameter (A) and leaf blade fresh mass (B) of *Hydrocotyle vulgaris* during the season at different experimental plots. Data are means from 30 measurements at every time point ± SE.

No other soil or leaf mineral nutrient concentrations were significantly associated with leaf growth parameters.

While leaf chlorophyll content exhibited significant differences between the experimental plots, the highest leaf chlorophyll content throughout the season was evident for *H. vulgaris* plants growing in control plots (A, B; Fig. 4). Chlorophyll content significantly and sequentially decreased in plots C and E, showing putative response to decrease of shading level. Significant association for the exponential negative relationship between leaf chlorophyll content and relative PAR was evident (r^2 = 0.89). However, there was also a strong negative association of exponential character between the mean leaf chlorophyll content and average soil EC for individual plots (r^2 = 0.93).

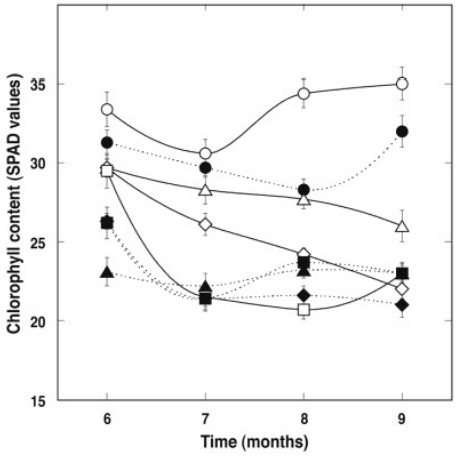


Fig. 4. Seasonal changes of leaf chlorophyll content of *Hydrocotyle vulgaris* during season at different experimental plots. Data are means from 10 measurements at every time point ± SE.

Average values of potential quantum yield of PS II (F_V/F_M) ranged from 0.80 in control plots (A, B) down to 0.78–0.79 in plots C, D, E, H and 0.76–0.77 in plots F and G (data not shown). The time course of F_V/F_M showed less pronounced changes during the season as well as less differences between the individual experimental plots than those of chlorophyll content (Fig. 5 A). While control plants from plots A and B did not have higher F_V/F_M in May they showed a constant increase of the parameter till August, reaching the highest levels in August and September. F_V/F_M values for plants in most of the plots besides A and B were well below 0.8, indicating some level of photoinhibition of photosynthesis. F_V/F_M was positively associated with chlorophyll content (r^2 = 0.72). When the data from the most sea-affected plots D and H were excluded, r^2 reached 0.87. However, there was only a weak positive linear relationship between F_V/F_M and soil EC (r^2 = 0.51) as well as between F_V/F_M and relative PAR (r^2 = 0.55). Also, there was a negative linear association between F_V/F_M and tissue concentration of P (r^2 = 0.50), Mg (r^2 = 0.57), S (r^2 = 0.51) and K (r^2 = 0.54).

Nonphotochemical quenching exhibited significant changes during the season (Fig. 5 B). Surprisingly, at the first half of the season, the highest level of NPQ was in plants growing in control plots A and B. These plants also had the lowest NPQ in September, when nonphotochemical quenching increased in leaves, indicating start of senescence. In general, NPQ was positively linearly associated with PAR (r^2 = 0.85), but only when the data from plot B were excluded from the analysis (data not shown). Only minor changes of ETR within the season were seen, except in September, when the electron transfer rate significantly decreased (Fig. 5 C). Paradoxically, the plants in control plot B constantly had the lowest ETR values within the season, except in September. Otherwise, only minor and mostly statistically no significant differences between the experimental plots in respect to ETR were evident.

In general, leaves with a larger blade diameter had higher F_V/F_M (r^2 = 0.70) for average values for individual plots within the season (data not shown). When the data from the most sea-affected plots D, F and H were excluded from the analysis, r^2 reached 0.92, indicating that salinity inhibited leaf growth without much effect on F_V/F_M. Indeed, the relationship between F_V/F_M and soil EC was negligible (r^2 = 0.51). A similar degree of association was found between F_V/F_M and PAR (r^2 = 0.55).

Mycorrhizal symbiosis. Parameters of mycorrhizal symbiosis varied both during the vegetation season as well as between experimental plots. Continuous increase of both intensity and frequency of mycorrhizal symbiosis in roots of

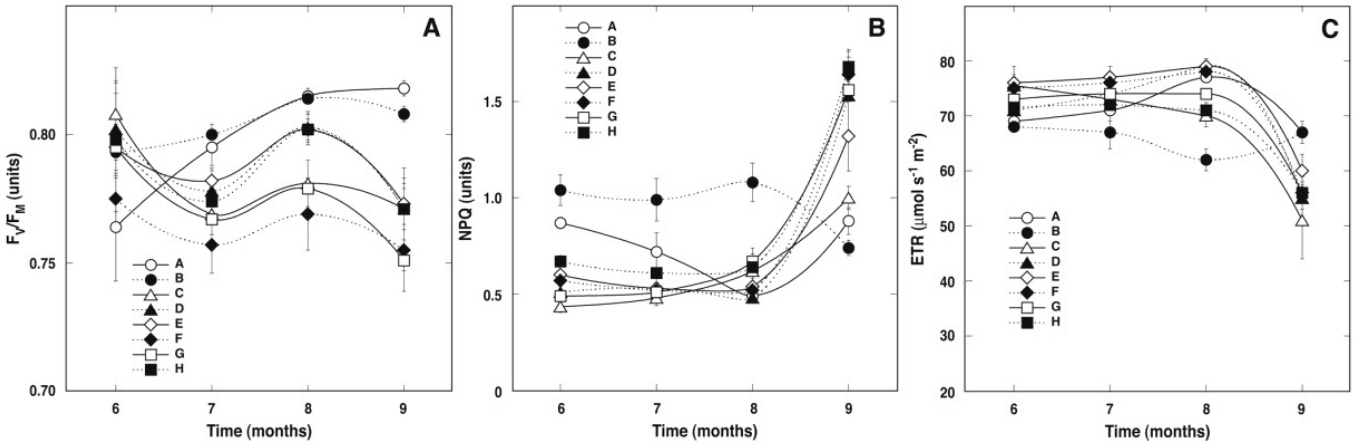


Fig. 5. Seasonal changes of potential quantum yield of photosystem II (A), non-photochemical quenching (B) and electron transfer rate of photosystem II (C) in leaves of *Hydrocotyle vulgaris* at different experimental plots. Data are means from 5 measurements at every time point ± SE.

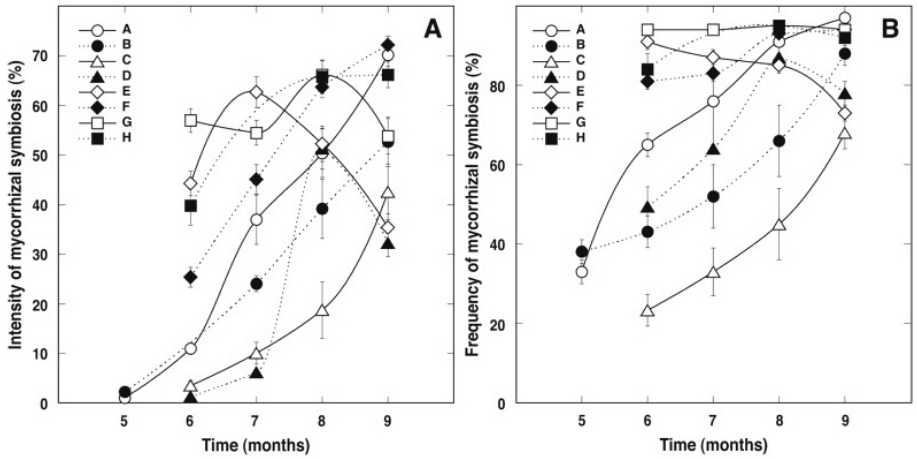


Fig. 6. Seasonal changes of intensity of mycorrhizal symbiosis (A) and frequency of mycorrhizal sysmbiosis (B) in roots of *Hydrocotyle vulgaris* at different experimental plots. Data are means from 3 measurements at every time point ± SE.

H. vulgaris throughout the season was evident for control plots A and B (Fig. 6). For plants in several other plots (C, F, H), intensity of symbiosis also increased throughout the season, while for the rest of plots (D, E, G), the initially high or increasing level of intensity started to decline in the middle or at the end of the season. In part, the decrease in mycorrhizal symbiosis coincided with the increase of soil EC and Na concentration for the respective plots (Fig. 1 A and B). When possible association between mycorrhizal symbiosis and soil salinity was analysed in more detail, it appeared that the mean values of mycorrhizal intensity increased in parallel with increase in soil EC up to 4 dS m^{-1} followed by a decrease with further rise of salinity. The relationship had clearly polynomial character (r^2 = 0.88).

In general, *H. vulgaris* plants growing on plots with higher relative PAR had higher intensity of mycorrhizal symbiosis (r^2 = 0.65). When the plots with low soil EC and those with high EC were analysed separately in respect to relationship of mycorrhizal symbiosis with relative PAR, both groups showed extremely strong positive linear association (r^2 = 0.99) indicating that the effect of soil salinity on mycorrhiza described above did mask the primary positive effect of light intensity on mycorrhizal symbiosis.

Only weak relation were found between the intensity of mycorrhizal symbiosis in *H. vulgaris* roots and P concentration in soil (r^2 = 0.39) or leaf tissues (r^2 = 0.38) suggesting that differential effect of abiotic factors on mycorrhizal fungi strongly affected physiological relationship between the mycobiont and the host plant.

Plants with a relatively high degree of mycorrhizal symbiosis had lower F_V/F_M, but this association was only moderate (r^2 = 0.56). ETR increased with increased intensity of mycorrhizal symbiosis up to 40% followed by a decrease at higher intensity (polynomial regression with r^2 = 0.76), which might be related to indirect relationship between mycorrhizal symbiosis and soil salinity as ETR itself showed only negligible relationship with soil EC (linear regression with r^2 = 0.38).

DISCUSSION

Environmental interactions. One of the most important problems in respect to the present study is how to separate the effects of salinity from those of light. As a rule there was a strong positive linear association between soil salinity and light availability between the experimental plots (r^2 = 0.82) because high salinity resulted in inhibition of growth of herbaceous plants in the plots near the sea. In contrast, plots not affected or less affected by sea flooding were located under tree canopies. This association was also caused

by the fact that in the control site with no direct sea impact no *H. vulgaris* plants were found in relatively well illuminated microhabitats like within herbaceous vegetation with no shade caused by trees. Thus, both environmental factors simultaneously affected performance of *H. vulgaris* plants: high salinity was accompanied by relatively high PAR while less soil salinity was concomitant with a low PAR. To distinguish between the effects of the two factors, a higher degree of association was assumed to reflect relatively higher impact of the particular factor on the parameter of interest.

However, it seems that different aspects of *H. vulgaris* physiology were differentially affected by soil salinity and light. While leaf growth was clearly stimulated in conditions of both decreased salinity and shade, the respective level of association was higher for soil EC (r^2 = 0.89 and r^2 = 0.92 for petiole height and leaf diameter, respectively) than for relative PAR (r^2 = 0.76 and r^2 = 0.87, respectively). Most importantly, *H. vulgaris* appeared to react to conditions of shade similarly to the majority of shade-tolerant plants. Also, leaf chlorophyll content was strongly negatively affected both by soil EC (r^2 = 0.93) and relative PAR (r^2 = 0.89). On the other hand, soil salinity masked a positive interaction between intensity of mycorrhizal symbiosis and relative PAR.

Increase in soil salinity clearly was the result of flooding with seawater. However, the effect of flooding itself, which is an important environmental constraint in wetlands, was not analysed in the present investigation. As flooding is inevitably associated with concomitant reduction in soil oxygen level, some physiological effects in frequently flooded plots near the sea could be related to oxygen shortage in the soil.

Physiological effects of salinity in *H. vulgaris* were not due to ion concentration in tissues of respective plants, because plants in all sea-affected plots had similar concentration of Na and of Cl. According to previous experiments in controlled conditions, *H. vulgaris* plants accumulate only limited concentration of Na and Cl in leaf tissues (Karlsons *et al*., 2008). This was clearly the case also in the present study, indicating that NaCl accumulation is saturable. Consequently, any effect of soil salinity on growth is primarily a result of osmotic effects at the root level.

Mineral nutrition and mycorrhiza. In general, it is widely accepted that leaf mineral nutrient concentrations are crucial determinants of plant vitality in a particular habitat (Aerts and Chapin, 2000). However, no simple relationship between soil concentration and tissue concentration of a particular mineral nutrient was found in the present study, with the exception of Mg and S. Similarly, there was no significant relationship between the concentration of a particular mineral nutrient and plant performance indices. Consequently, there was no clear mineral limitation for *H. vulgaris* in the analysed plots. *H. vulgaris* plants seemed to be well adapted to a relatively wide range of soil mineral conditions characteristic for coastal habitats. Some possible adaptive mechanisms could be analysed in more detail.

The fact that larger leaves of *H. vulgaris* had lower P concentration indicates that growth rate did not affect the rate of P uptake. It appears that no down-regulation of P uptake occurred in plots with high light and high soil salinity leading to higher concentration of P in relatively smaller leaves. More rapid growth in low salinity / low light conditions dilutes the P pool leading to decrease in tissue concentration. The same phenomenon can explain the generally poor sensitivity of wild plant tissue nutrient concentrations to soil nutrient availability (Chapin, 1980).

Flooding results in a decrease of soil redox potential leading to reduction of the respective ions to Mn^{2+} and Fe^{2+}, thus enhancing availability of Fe and Mn ions (Rozema *et al*., 1985). Most probably, formation of Fe^{2+} in flooded soil of plots D and H due to the activity of anaerobic bacteria enhanced availability of iron for plants. As iron uptake is not under metabolic control, this led to a seven- and 14-fold increase in leaf iron concentration in July in the plots with the highest soil salinity level in May due to intense flooding with sea water (Fig. 1 A). Similarly, Mn accumulation to a extremely high level in leaves was seen in plants from plot F, and there was a relatively high level of accumulation also in plants from plot H. It is known that high concentration of NaCl significantly decreases (more than three-fold) accumulation of Mn in shoot tissues (Singer and Havill, 1985), which can explain the relatively low level of Mn in plants from plot D where there was a high level of Na in soil. While high tissue Fe^{2+} is known to inhibit chlorophyll synthesis, no clear iron toxicity effects on physiological status of *H. vulgaris* plants from plots D and H were evident. It can be suggested, therefore, that *H. vulgaris* plants are highly tolerant both to Fe and Mn toxicity, as described for other salt marsh species (Rozema *et al*., 1985).

In controlled laboratory experiments with *H. vulgaris* and another salt marsh plant species, *Aster tripolium*, significant effect of increased substrate salinity on concentration of macro- and micronutrients in plant tissues was found (Karlsons *et al*., 2008). For *H. vulgaris*, a moderate substrate NaCl level (25 and 50 mM) significantly increased leaf concentration of P and Mn, resulting in a decreased K and Ca concentration. Does salinity affect mineral nutrition of *H. vulgaris* in natural conditions in the present study? Indeed, plants in sea-affected plots had significantly higher P and Mn concentrations, and P concentration was positively associated with soil EC. However, leaf K concentration was higher in salinity-affected plots, and Ca concentration seemed not to be affected by salinity. As discussed above, increase in leaf Fe and Mn concentrations could not be attributed to the direct effect of salinity, but rather to an effect of flooding on soil mineral availability.

In nutrient poor soils, mycorrhizal symbiosis is usually among the main adaptive factors leading to enhanced performance of host plants. For the majority of habitats, usually a negative correlation between soil phosphorus concen-

Table 3. Na, Cl, and mineral nutrient concentrations in leaf blade tissues of *Hydrocotyle vulgaris* at different sampling plots. Data are means from 4 measurements throughout the vegetation season ± SE. DM, dry mass

Parameters	Plots							
	A	B	C	D	E	F	G	H
Na (% DM)	1.3 ± 0.4	1.5 ± 0.3	5.5 ± 1.2	4.4 ± 1.2	5.0 ± 1.2	4.5 ± 1.3	4.6 ± 1.3	4.4 ± 0.9
Cl (% DM)	1.8 ± 0.2	2.7 ± 0.5	7.4 ± 0.2	4.3 ± 0.4	4.3 ± 0.6	3.4 ± 0.3	3.4 ± 0.1	4.3 ± 0.1
Macronutrients (% DM)								
N	1.8 ± 0.2	1.8 ± 0.2	2.0 ± 0.2	1.4 ± 0.2	1.4 ± 0.3	1.4 ± 0.3	1.5 ± 0.1	1.3 ± 0.2
P	0.19 ± 0.05	0.31 ± 0.09	0.34 ± 0.09	0.52 ± 0.06	0.30 ± 0.10	0.47 ± 0.08	0.40 ± 0.09	0.53 ± 0.06
K	1.57 ± 0.28	1.86 ± 0.46	2.98 ± 0.81	1.94 ± 0.58	2.82 ± 1.29	2.35 ± 0.64	2.64 ± 0.81	2.68 ± 0.47
Ca	1.58 ± 0.26	2.37 ± 0.63	4.61 ± 0.58	4.70 ± 0.76	1.65 ± 0.20	2.34 ± 0.37	2.06 ± 0.19	2.37 ± 0.63
Mg	0.44 ± 0.08	0.45 ± 0.11	0.96 ± 0.21	1.21 ± 0.30	0.97 ± 0.10	0.94 ± 0.20	0.98 ± 0.17	1.15 ± 0.26
S	0.16 ± 0.01	0.15 ± 0.03	0.16 ± 0.03	0.51 ± 0.15	0.28 ± 0.01	0.39 ± 0.04	0.39 ± 0.06	0.41 ± 0.08
Micronutrients ($mg \cdot kg^{-1}$ DM)								
Fe	128 ± 28	128 ± 23	258 ± 66	1286 ± 455	128 ± 123	119 ± 36	280 ± 58	2435 ± 894
Mn	103 ± 12	116 ± 13	119 ± 16	113 ± 22	126 ± 27	223 ± 38	151 ± 6	164 ± 14
Zn	195 ± 19	348 ± 51	89 ± 17	132 ± 29	109 ± 12	139 ± 22	125 ± 12	116 ± 11
Cu	13.8 ± 2.8	9.0 ± 1.7	8.4 ± 1.2	11.3 ± 1.9	9.6 ± 2.8	106 ± 2.6	10.6 ± 2.9	9.5 ± 2.0
Mo	0.99 ± 0.30	2.68 ± 1.17	1.95 ± 0.61	1.38 ± 0.19	1.03 ± 0.28	1.57 ± 0.19	1.76 ± 0.67	1.28 ± 0.29
B	13 ± 1	15 ± 3	21 ± 1	15 ± 2	26 ± 4	24 ± 3	21 ± 3	22 ± 3

tration and intensity of mycorrhizal symbiosis is found (Javot *et al*., 2007). In the present study with *H. vulgaris* plants in natural conditions, no functional relationship was found between the intensity of mycorrhizal symbiosis and soil or leaf P concentration. In addition, no direct positive relationship was found between mycorrhizal symbiosis and photosynthetic performance indices. Most probably, in conditions of highly heterogeneous habitats, e.g., salt marsh, abiotic environmental factors differentially affect mycorrhizal fungi and the respective host plants. It has been shown that in salt marshes both soil salinity and soil flooding may have negative impact on mycorrhizal symbiosis, while the host plants are not significantly affected by these conditions (Juniper and Abbott, 2006; Ipsilantis and Sylvia, 2007). In the present study, relatively low soil salinity stimulated development of mycorrhizal symbiosis, while higher salinity levels (above 4 dS m^{-1}) decreased it. When the salinity factor was excluded by separate analysis of strongly sea-affected plots, intensity of mycorrhizal symbiosis showed a high degree of positive relationship with light availability. Evidence from experiments in partially controlled conditions indicated that in deep shade plants had a relatively low level of mycorrhizal colonisation, in comparison to plants growing in full sunlight (Gamage *et al*., 2004). The authors concluded that plants in high light have more intense photosynthesis and, as a result, more carbohydrate is available for fungal growth. However, in the present study, *H. vulgaris* showed typical characteristics of shade tolerant plants, as photochemistry of photosynthesis did not significantly change with light conditions.

Growth and plant performance. A level of F_V/F_M below 0.83 might indicate photoinhibition of photosynthesis (Maxwell and Johnson, 2000). In controlled conditions, F_V/F_M of *H. vulgaris* in non-saline soil was around 0.80, while growth at 100 mM NaCl resulted in decrease of F_V/F_M to 0.77–0.78 depending on light conditions (Ievinsh *et al*., unpublished data). In the present study, average F_V/F_M values (0.80 for control plots and 0.76–0.79 for sea-affected plots) corresponded to these data and indicated only slight photoinhibition of photosynthesis as a result of increased soil salinity. Similarly, other parameters of photochemistry of photosystem II were not significantly affected by soil salinity, pointing to a high buffering capacity of photosynthetic apparatus of *H. vulgaris* against environmental heterogeneity.

However, leaf growth and concentration of chlorophyll in leaf tissues of *H. vulgaris* were more negatively affected by increased soil salinity than was photochemistry of photosystem II. Therefore, one may ask what was the cause for significantly decreased growth rate in spite of only small reduction in photochemistry? Firstly, stomatal effects of salinity-dependent photosynthesis inhibition at the level of CO_2 fixation could result in decreased overall photosynthetic performance without an effect on photochemistry (Redondo-Gómez *et al*., 2006). Secondly, increase of NPQ with increased PAR in *H. vulgaris* indicated that more efficient use of captured light energy occurred at low light intensity. Consequently, these plants were well adapted to low light conditions. The present data, together with the results from experiments in controlled conditions, indicate that *H. vulgaris* individuals from significantly shaded microhabitats were better protected against deleterious effects of soil salinity on plant performance in comparison to plants growing in full sunlight. At low light intensity (45 $\mu mol \cdot m^{-2} \cdot s^{-1}$), 25 mM NaCl even stimulated leaf growth of *H. vulgaris* while it was inhibited by the same NaCl concentration at high light intensity (600–800 $\mu mol \cdot m^{-2} \cdot s^{-1}$) (Ievinsh *et al*., unpublished data).

Growth and photosynthetic performance were also shown to be associated by the relationship between leaf size and F_V/F_M. However, this relationship was not true if the most saline plots near the sea were included, indicating that leaf growth inhibition and photoinhibition are not casually related. Shortage of oxygen in soil of permanently flooded or waterlogged plots also could be related to growth inhibition (Blokhina *et al*., 2003). Therefore, any difference in tolerance between growth and performance could be an indication of poor adaptation to waterlogging versus relatively good adaptation to osmotic stress.

CONCLUSIONS

The present data clearly reflect complex interactions between environmental factors and plastic responses of *H. vulgaris* to environment quality, as have been described for other perennial plants (Moriuchi and Winn, 2005). The dynamic nature of interaction between sea water flooding-affected changes in soil salinity and competition-dependent changes in light availability leads to microenvironmental heterogeneity, which differentially affects performance and growth of *H. vulgaris* in natural conditions. High plasticity of metabolism in respect to highly variable soil concentration of mineral nutrients, together with effective mineral adaptation mechanisms, ensure optimal supply of material for growth. Increased growth rate in shaded conditions specifically indicates a shade tolerance strategy of *H. vulgaris* plants. In general, a relatively high stable level of photosynthetic performance across a wide range of microenvironmental conditions indicates an adequate level of physiological adaptation of *H. vulgaris* to conditions of a coastal salt marsh.

In the light of the present data, plant performance can be assessed in a highly heterogeneous natural habitat (e.g., coastal salt marsh) by means of non-destructive instrumental methods — chlorophyll content and chlorophyll *a* fluorescence analysis. This approach is especially important in ecophysiological studies of endangered plant species in natural conditions, as performance indices can be used for explaining the effect of environmental factors on plant growth and photosynthetic productivity without disturbance effects on plant populations.

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PIEKRASTES MITRĀJU AUGA *HYDROCOTYLE VULGARIS* VEIKTSPĒJA DABISKOS APSTĀKĻOS SAISTĪBĀ AR MINERĀLO BAROŠANOS UN MIKORIZU SIMBIOZI

Mainīgs augsnes sāļums un konkurence par gaismu ir galvenie faktori, kas ietekmē augu izplatību piekrastes sāļajos mitrājos. Pētījuma mērķis bija analizēt augu veiktspēju ļoti heterogēna biotopa apstākļos, izmantojot nedestruktīvas instrumentālās metodes. Konkrētāk, pētīja vides faktorus, kas ietekmē klonālā auga *Hydrocotyle vulgaris* L. augšanu un fizioloģisko veiktspēju. Dažādos parauglaukumos analizēja augsnes sāļuma izmaiņas, augsnes minerālvielu saturu, dabiski augošu *H. vulgaris* augu lapu minerālvielu koncentrācijas, hlorofila fluorescenci un mikorizu simbiozi. Dinamiska rakstura mijiedarbība dabiskos apstākļos starp augsnes sāļumu, ko izraisīja applūšana ar jūras ūdeni, un no konkurences atkarīgām gaismas pieejamības izmaiņām radīja mikrovides heterogenitāti, kas dažādi ietekmēja *H. vulgaris* fizioloģisko veiktspēju un augšanu. Augu augšanu galvenokārt ietekmēja fotosintētiski aktīvās radiācijas intensitāte attiecīgajos parauglaukumos. Palielināts augšanas ātrums ēnas apstākļos norādīja uz *H. vulgaris* ēnas izturības stratēģiju. Starp parauglaukumiem pastāvēja augsta minerālvielu sastāva heterogenitāte. Tomēr, optimālu augšanai nepieciešamo izejvielu apgādi nodrošināja metabolisma plastiskums attiecībā uz augsti variablu minerālvielu augsnes koncentrāciju kopā ar efektīvu minerālās barošanās adaptāciju. Atšķirības mikorvides apstākļos tikai minimāli ietekmēja fotosintēzes fotoķīmiju, kā parādīja atbilstošas hlorofila *a* fluorescences parametru izmaiņas. Mērens augsnes sāļuma pieaugums veicināja mikorizu simbiozi, bet to samazināja salīdzinoši augsts sāļums. Ja sāļuma ietekmi neņēma vērā, mikorizu simbiozes intensitāte korelēja ar fotosintētiski aktīvās radiācijas intensitāti. Kopumā, salīdzinoši nemainīga fotosintēzes veiktspēja uz plašas mikrovides apstākļu variācijas fona parāda *H. vulgaris* pietiekamas fizioloģiskās adaptācijas līmeņa esamību piekrastes sāļā mitrāja apstākļos. Parādītie rezultāti skaidri atspoguļo mijiedarbību sarežģītību starp vides faktoriem un *H. vulgar*is fizioloģisko atbildes reakciju plastiskumu.