Photosynthetic activity and water use efficiency of dune species: the influence of air temperature on functioning

L. GRATANI, L.VARONE, and M.F. CRESCENTE

Department of Plant Biology, Sapienza University of Rome, P.le A. Moro 5, 00185, Rome, Italy

Abstract

Differences in leaf traits among the dune species developing along the Latium coast were analysed. *Cakile maritima* Scop. subsp. *maritima*, *Elymus farctus* (Viv.) Runemark *ex* Melderis subsp. *farctus*, *Ammophila arenaria* (L.) Link subsp. *australis* (Mabille) Lainz, *Ononis variegata* L., *Pancratium maritimum* L., *Eryngium maritimum* L., and *Anthemis maritima* L. were considered. The considered species showed a similar net photosynthetic rate (P_N) and chlorophyll content (Chl) during the year, with a peak from the end of April to the middle of May [13.0±3.6 μmol (CO_2) m^{-2} s^{-1} and 0.63±0.21 mg g^{-1}, respectively, mean values of the considered species], favoured by air temperature in the range 13.3–17.5°C, and 6% of soil water availability. In June–July, the increase of air temperature (T_{max} = 28.4°C), associated with a lower water availability (42 mm, total rainfall of the period) and a 1% of soil water availability determined a significant decrease of P_N (59%, mean of the considered species) and Chl (38%), and an increase of the carotenoid (Car)/Chl ratio (59%). The significant correlation between P_N and stomatal conductance (g_s) ($p<0.05$) explained 67% of P_N variations. Moreover, the correlation between P_N and leaf temperature (T_l) underlined that the favourable T_l enabling 90–100% of the highest P_N for the considered species was within the range 23.4 to 26.6°C. P_N decreased below half of its maximum value when T_l was over 35.8 and 37.4°C for *E. farctus* subsp. *farctus* and *A. arenaria* subsp. *australis*, respectively and over 32.2°C for the other considered species (mean value). Leaf mass area (LMA) varied from 6.8 ± 0.7 mg cm^{-2} (*O. variegata*) to 30.6 ± 1.6 mg cm^{-2} (*A. arenaria*). PCA (principal component analysis) carried out using the considered morphological and physiological leaf traits underlined that the co-occurring species were characterised by different adaptive strategies: *E. farctus* and *A. arenaria* photosynthesized for a long period also when air temperature was over 35.8 and 37.4°C, respectively, because of their lower transpiration rates [*E*, 1.4 ± 0.1 mmol (H_2O) m^{-2} s^{-1}], which seemed to be controlled by the highest LMA. On the contrary, *A. maritima* and *C. maritima* subsp. *maritima* had a higher P_N (on an average 52% higher than the others) in the favourable period, allowed by the highest succulence index (SI, 85.7 ± 9 mg cm^{-2}) and the lower LMA. The results allowed us to hypothesize that *A. arenaria* and *E. farctus* might be at a competitive advantage relative to the other considered species with respect to the increase of air temperature, by their ability to photosynthesize at sufficient rates also during summer.

Additional key words: air temperature; carotenoid content; chlorophyll content; coastal dune plant species; gas exchange; leaf mass area.

Introduction

It is important for plant species growing in an environment where water is available for limited periods of the year to be able to make full use of favourable conditions for growth and reproduction (Gratani and Crescente 1997, Gratani *et al.* 2003, Niu *et al.* 2006, Perumal and Maun 2006). Coastal dune species suffer many environmental stresses caused by a low capillarity and water-holding capacity of the sandy soil (Ishikawa *et al.* 1990, Gratani *et al.* 2007, da Silva *et al.* 2008), associated with a low boundary layer resistance, a high substrate salinity (Donnelly and Pammenter 1983), and a low nitrogen availability (Kachi and Hirose 1983, Shumway 2000,

---

Received 7 May 2009, *accepted* 27 November 2009.

+Author for correspondence; fax: +39 06 49912358, e-mail: loretta.gratani@uniroma1.it

Abbreviations: Car – carotenoid content; C_E – relative carboxylation efficiency; Chl – chlorophyll content; C_i – substomatal CO_2 concentration; DM – dry mass; E – transpiration rate; FM – fresh mass; g_s – stomatal conductance; LA – leaf area; LMA – leaf mass per unit leaf area; PAR – photosynthetically active radiation; P_N – net photosynthetic rate; SI – succulence index; T_e – air temperature into the leaf chamber; T_l – leaf temperature; $T_{100\%}$ – leaf temperature enabling 100% of the highest photosynthetic rates, $T_{100–90\%}$ – leaf temperature enabling 100 to 90% of the highest photosynthetic rates; $T_{90–50\%}$ – leaf temperature enabling 90 to 50% of the highest photosynthetic rates; WUE – instantaneous water use efficiency.

Gilbert *et al.* 2008). Nevertheless, nutrient supply may be augmented after burial through the deposition of sand, providing a new source of nutrients (Willis 1965). Moreover, the sand raised by wind, associated with high irradiance and air temperatures (Perumal and Maun 2006, da Silva *et al.* 2008) causes erosion of the below-ground plant portion (Maun 1994, Yura and Ogura 2006). Only few species are capable of withstanding the stress imposed by the limited environmental resources and a recurrent disturbance in coastal dunes; these species have some individual traits that allow them to survive (Yura and Ogura 2006). Annual species form a significant element of the flora of sand dunes (Watkinson and Davy 1985).

The physiological ecology of coastal dune species, however, has not been studied extensively. Previous studies have suggested that adaptive features of coastal dune species include the tolerance of high air temperatures (Barbour *et al*. 1985, Perumal and Maun 2006), alterations of photosynthetic rates (Kent *et al.* 2005), adjustments of chlorophyll content (Disraeli 1984), specific leaf area (Martínez and Moreno-Casasola 1996), and leaf thickness (Kent *et al.* 2005). Data on transpiration rates are rarely reported (Gilbert and Ripley 2008). Coastal dune species have a high instantaneous water use efficiency (WUE, amount of CO_2 fixed per unit of water lost) as a result of high assimilation rates rather than low transpiration rates (Ripley and Pammenter 2004).

The ecological conditions of coasts are often stressful or even critical and their flora grows under environmental unfavourable conditions, due to both natural instability and anthropogenic load (Voronkova *et al.* 2008). As coastal dunes are found at almost all latitudes, the climate and vegetation developing on them are very diverse, covering ecological habitats which range from polar to tropical latitudes and from deserts to tropical rain forests. Thus, one of the most outstanding features in these ecosystems is their broad distribution and ecological diversity, in terms of geomorphology, environmental heterogeneity, and species variability (Martínez *et al.* 2004). Coastal dunes are widespread along the European coastline, though their distribution is uneven (Heslenfeld *et al.* 2004).

The Mediterranean region has a complex and heterogeneous coastline; the larger dune fields occur in deltas and coastal plains, like in parts of Italy (Heslenfeld *et al.* 2004). Yet, despite their seeming abundance on the global scale, many coastal dune ecosystems have been severely degraded as a result of an excessive exploitation of natural resources, chaotic demographic expansion, and industrial growth (Martínez *et al.* 2004). Sand dune ecosystems protect many coastlines from erosion by mitigating the action of sea from daily wave action and storm events (Liu *et al.* 2005).

The forecasted increase of air temperature might determine changes of the length and intensity of drought periods. Drought periods may facilitate the accumulation of salt from sea water spray within the soil, which would otherwise be leached out by rainfall (Greaver and Sternberg 2007). When prolonged or more severe drought periods occur, the capacity of different species to avoid damaging effects determines their survival (Peñuelas and Filella 2001, Pesoli *et al.* 2003, Gratani *et al.* 2003, Greaver and Sternberg 2007). Thus, it is important to study the adaptive capacity of sand dune species and their tolerance threshold with respect to increasing stress factors.

The main objective of this study was to analyse differences in leaf traits among the species co-occurring in the dunes developing along the Latium coast (S–SW of Rome, Italy). Besides, we analysed the optimal temperature range for the photosynthetic activity. The intrinsic link between net photosynthesis and biomass production suggests that photosynthesis and its response to drought is likely to play a major role in determining the ability of these species to persist in the distribution area, despite increasing air temperature (Larcher 1994, Pereira 1994, Crescente *et al.* 2002, Gulías *et al.* 2002, Gratani *et al.* 2008).

Materials and methods

Study site and plants: The dune area along the Latium coast is characterised by mobile dunes spreading from the shore to the inland for ca 150 m. The dune vegetation is described in Gratani *et al.* (1983). *Cakile maritima* Scop. subsp. *maritima*, *Elymus farctus* (Viv.) Runemark *ex* Melderis subsp. *farctus*, *Ammophila arenaria* (L.) Link subsp. *australis* (Mabille) Lainz, *Ononis variegata* L., *Pancratium maritimum* L., *Eryngium maritimum* L., and *Anthemis maritima* L. were considered. The nomenclature was in accordance to Conti *et al.* (2005).

Field measurements were carried on twelve plants per species. For repeated non-destructive measurements the selected individuals were labelled with nylon tape and monitored in the period January–August 2007.

Climate and soil humidity: The climate of the area was of Mediterranean type; total annual rainfall was 707 mm, the mean minimum air temperature of the coldest months (January and February) was 3.9°C and the mean maximum air temperature of the warmest months (July and August) was 30.4°C (data of the Meteorological Station of Castelporziano, for the years 1985–2006).

Soil moisture content had the highest values (80%) in autumn–winter, and the lowest one (1%) in summer (Gratani and Crescente 1997). The soil was characterised by 99% of sand and a low percentage of slime and clay; pH ranged from 7.0 to 7.5 (Gratani and Capannesi 1984).

Leaf morphology: Leaf morphological analysis was carried out monthly during the leaf expansion process (20 leaves per species on each sampling occasion).

Measurements of leaf morphology included projected leaf area (LA), obtained by the *Image Analysis System* (*Delta-T Devices*, UK), fresh mass (FM) and dry mass (DM) of leaves oven-dried at 80°C to constant mass.

Leaf mass per unit leaf area (LMA) was calculated from leaf dry mass and one-sided leaf area (Wright *et al.* 2004).

Succulence index (SI) was calculated as the ratio of the difference between DM and FM to the leaf surface area (Read *et al.* 2005, Omae *et al.* 2007).

Leaf gas exchange: Field measurements were carried out *in situ* on the external exposed leaves of the selected plants under natural conditions, on cloud-free days to ensure that near-maximum daily photosynthetic rates were measured (Reich *et al.* 1995). During the measurements leaves were retained in their natural inclination.

Photosynthetically active radiation (PAR), net photosynthesis (P_N), stomatal conductance (g_s), transpiration rate (E), air temperature into the leaf chamber (T_e), leaf temperature (T_l) and substomatal CO_2 concentration (C_i) were monitored during the study period with an infrared gas analyser *ADC-LCA4* system (*ADC BioScientific Ltd.*, Hoddesdon, UK), equipped with a leaf chamber (type *PLC*).

The instantaneous water use efficiency (WUE) was calculated by the ratio between net photosynthetic rates and transpiration rates (Niu *et al.* 2006).

Relative carboxylation efficiency (C_E, mol CO_2 fixed mol^{-1} CO_2 present in the substomatal spaces) was calculated by the ratio between the net photosynthesis and substomatal CO_2 concentration (Flexas *et al.* 2001).

The measurements were carried out in the morning (9.30–12.30 h), on 5 leaves from the uppermost plant portion per species on each sampling occasion (22th to 24th each month). During measurements of CO_2 concentration, the air humidity and flow rate inside the leaf chamber were set at 370 ppm, 65% and 400 μmol s^{-1}, respectively. The means of the measured maximum values during the three sampling days are shown.

Leaf pigments content was measured monthly (22th to 24th each month). Immediately after collection, fully expanded leaves from the selected plants were kept cool in the dark for 3 h.

Chl and Car contents were determined in leaf samples (5 samples per species), after grinding the leaves in acetone. The homogenates were centrifuged in a *4237R* Refrigerated Centrifuge (*A.L.C.*, Italy). Absorbance of the supernatants was measured with a *Jasco* model *7800LCD* (Japan) spectrophotometer at the wavelengths of 645, 663 and 440 nm for Chl *a*, Chl *b* and Car, respectively. Chl and Car contents per unit FM were calculated according to MacLachlan and Zalik (1963) and Holm (1954), respectively.

Statistical analysis: Differences in physiological and morphological leaf traits were determined by the analysis of variance (*ANOVA*) and *Tukey* test for multiple comparisons.

The regression analysis was carried out to evaluate the correlation among the physiological traits. The relationship between net photosynthesis and leaf temperature (photosynthetic thermal window *sensu* Larcher 1994) was tested by the regression between these variables. Leaf temperatures enabling 100%, 100 to 90%, and 90 to 50% of the highest photosynthetic rates ($T_{100\%}$, $T_{100–90\%}$ and $T_{90–50\%}$, respectively) were calculated according to Larcher (1994).

The principal component analysis (PCA) was carried out in order to evaluate the colinearity among the considered leaf traits in the species considered. The analysis was performed on the basis of a matrix of the normalised data.

All statistical tests were performed using a statistical software package (*Statistica, Statsoft*, USA).

Results

Leaf morphology: The considered species reached the maximum LA and DM between April and May (Fig. 1). *E. maritimum* had the highest LA and DM (67.1±1.8 cm^2, 981±1.1 mg, respectively), and *O. variegata* the lowest ones (0.40±0.03 cm^2, 2.7±0.3 mg, respectively).

LMA varied from 6.8±0.7 mg cm^{-2} (*O. variegata*) to 30.6±1.6 mg cm^{-2} (*A. arenaria*) (Table 1).

C. maritima had the highest SI (96.4±0.9 mg cm^{-2}) and *E. farctus* the lowest one (28.3±0.4 mg cm^2) (Table 1).

Gas exchange: During the study period PAR and temperature in the leaf chamber varied from 1328±28 μmol(photon) m^{-2} s^{-1} and 18±1°C, respectively (February) to 1793±60 μmol(photon) m^{-2} s^{-1} and 32±2°C, respectively (July) (Fig. 2).

Table 1. Leaf mass area (LMA) and succulence index (SI) at the maximum leaf expansion of the considered species. Mean values (±SD) are shown. Mean values with the same letters are not significantly different (*ANOVA*, $n = 20$, $p>0.05$).

Species	LMA [mg cm^{-2}]	SI [mg cm^{-2}]
Ononis variegata	6.8±0.7 a	33.7±0.4 a
Anthemis maritima	8.2±0.5 b	49.9±0.6 b
Cakile maritima	8.4±0.4 b	96.4±0.9 c
Pancratium maritimum	11.9±1.2 c	79.2±0.2 d
Eryngium maritimum	14.6±0.4 d	81.5±0.3 e
Elymus farctus	21.9±1.2 e	28.3±0.4 f
Ammophila arenaria	30.6±1.6 f	44.6±0.5 g

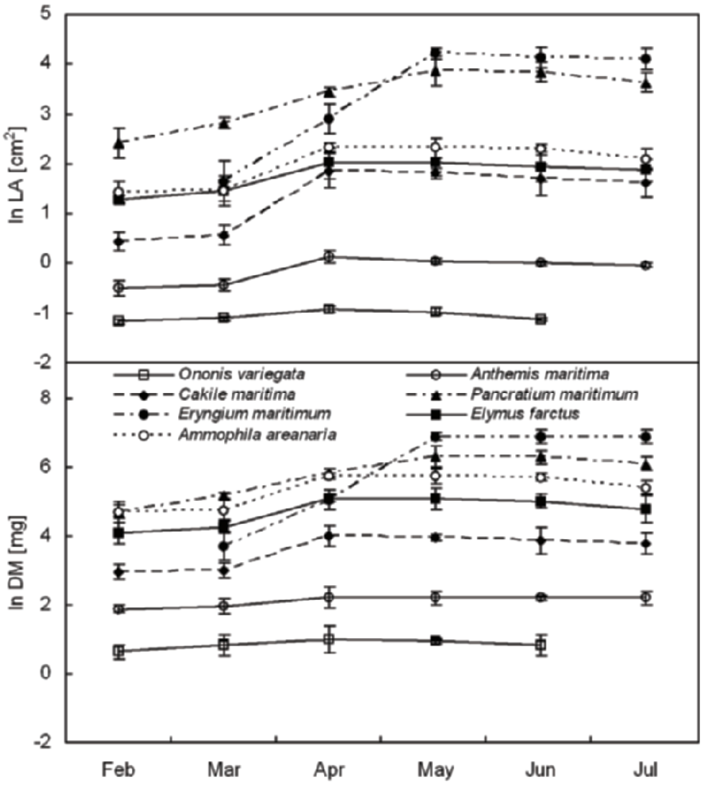

Fig. 1. Leaf area (LA) and leaf dry mass (DM) of the considered species during the study period. Mean values (±SD, n = 20) are shown. The shown values are the natural logarithm of the measured values.

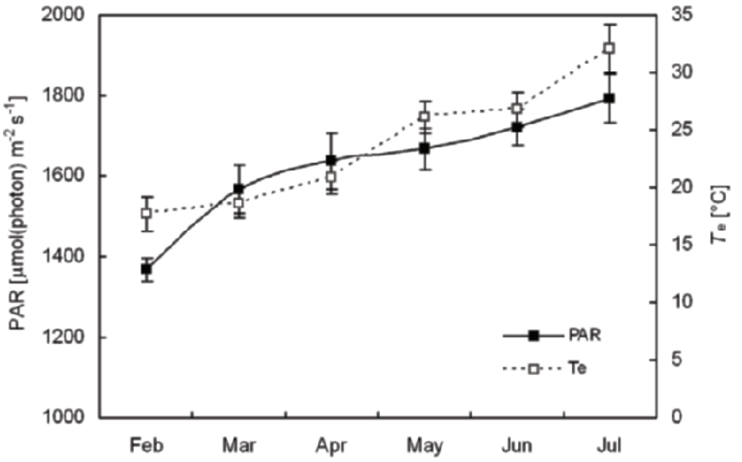

Fig. 2. Photosynthetically active radiation (PAR) and air temperature in the leaf chamber (T_e), during the study period. Mean values (±SD, n = 15) are shown.

The considered species showed a similar P_N trend during the year, with a peak from the end of April to the middle of May, when air temperature and soil water availability were favourable. *C. maritima* and *A. maritima* had the highest P_N [18.9±0.1 µmol(CO_2) m^{-2} s^{-1} and 15.6 ± 0.3 µmol(CO_2) m^{-2} s^{-1}, respectively], and *A. arenaria* and *O. variegata* the lowest ones [9.8 ± 1.1 µmol(CO_2) m^{-2} s^{-1} and 8.4 ± 0.8 µmol(CO_2) m^{-2} s^{-1}, respectively] (Fig. 3). P_N decreased by 48% (mean of the considered species) in summer (drought period); *E. maritimum* showed the lowest decrease (28%) and *P. maritimum* the highest one (60%).

g_s had the same P_N trend (Fig. 3) with the highest values [0.73 ± 0.40 mol(H_2O) m^{-2} s^{-1}, mean of the species considered] in April–May and a significant decrease (58%, mean of the considered species) in June–July.

C_E had the same P_N trend, with a significant (p<0.05) decrease (46%, mean of the considered species) in summer (Fig. 4). *C. maritima* had the highest C_E (0.043±0.024 mol mol^{-1}, mean of the study period) and *O. variegata* the lowest one (0.022±0.008 mol mol^{-1}, mean of the study period).

The highest E was recorded in April–May [3.1± 1.2 mmol(H_2O) m^{-2} s^{-1}, mean of the study period for all the considered species], decreasing 45% in summer (Fig. 5). *A. arenaria* had the significantly (p<0.05) lowest E [1.4 ± 0.3 mmol(H_2O) m^{-2} s^{-1}, mean annual value], and *A. maritima* the highest one [2.9 ± 0.6 mmol(H_2O) m^{-2} s^{-1}, mean of the study period].

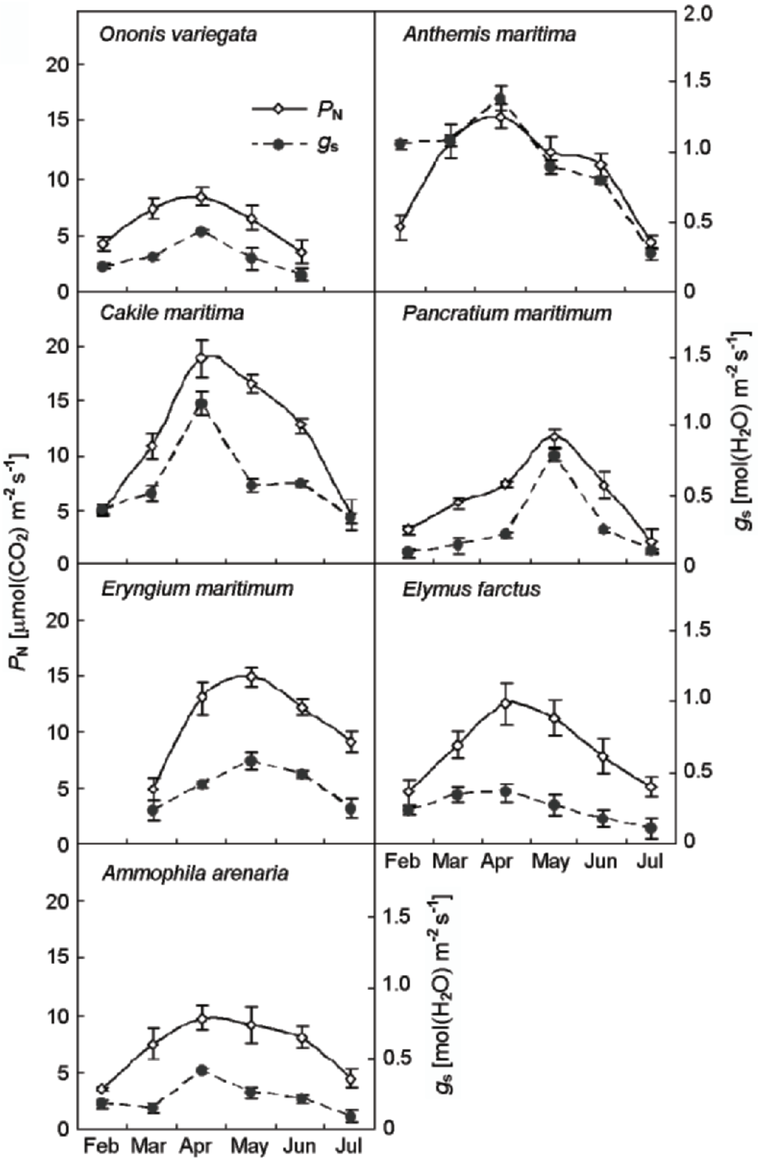

Fig. 3. Net photosynthetic rate (P_N) and stomatal conductance (g_s) of the considered species during the study period. Mean values (±SD, n = 15) are shown.

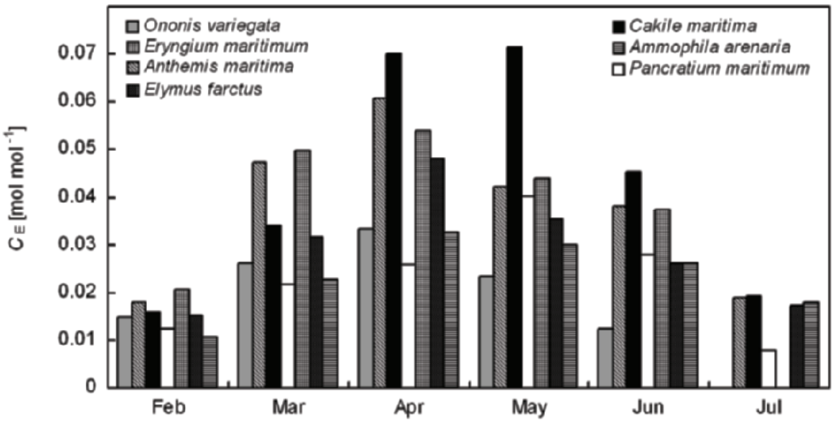

Fig. 4. Relative carboxylation efficiency (C_E) of the considered species during the study period. Mean values (±SD, n = 15) are shown.

During the study period, WUE was the highest [5.9 ± 1.2 µmol(CO$_2$) mmol^{-1}(H$_2$O)], (mean of the considered species) in April–May, decreasing 39% (mean value) in June–July (Fig. 5). *E. farctus* had the significantly ($p<0.05$) highest WUE [5.2 ± 1.3 µmol(CO$_2$) mmol^{-1}(H$_2$O), mean of the study period], followed by

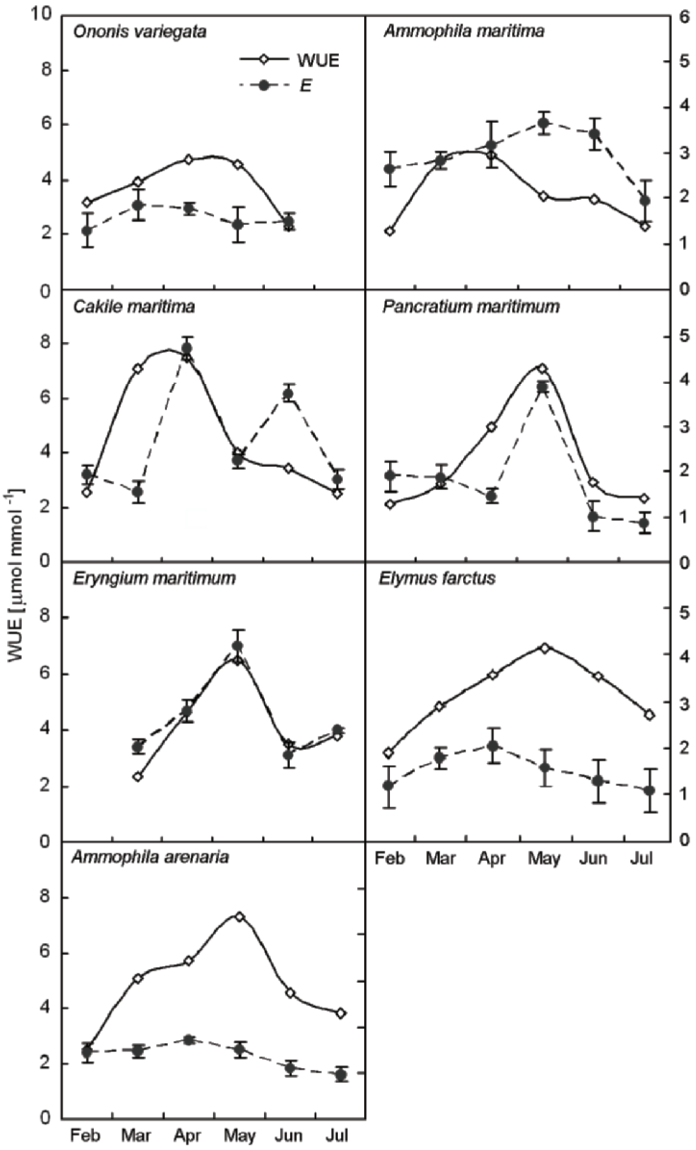

Fig. 5. Water use efficiency (WUE) and transpiration rate (E) of the considered species during the study period. Mean values (±SD, $n = 15$) are shown.

A. arenaria [4.8 ± 1.6 µmol(CO_2) mmol^{-1}(H_2O)], *C. maritima* and *E. maritimum* [4.3 ± 0.2 µmol(CO_2) mmol^{-1}(H_2O), mean of the study period for the two species], and by *O. variegata*, *P. maritimum* and *A. maritima* [3.6 ± 0.2 µmol(CO_2) mmol^{-1}(H_2O), mean of the study period for the three species].

Pigment contents: The considered species had a similar total Chl trend during the year, with a peak in April–May (0.63 ± 0.16 mg g^{-1} is related to fresh mass, mean of the considered species) and a significant ($p<0.05$) decrease (38%, mean value) in summer (Fig. 6). *E. farctus* had the highest Chl (0.61 ± 0.15 mg g^{-1}, mean of the study period).

The considered species had the lowest Car/Chl contents ratio in April–May (0.22 ± 0.04, mean of the considered species) showing a significant ($p<0.05$) increase (59%, mean of the considered species) in June–July (Fig. 6).

Statistical analysis: There was a significant correlation between P_N and g_s ($p<0.01$), explaining 67% of P_N variations in the considered species (Fig. 7).

E was significantly ($p<0.01$) correlated with g_s ($r = 0.48$) (Fig. 7).

The polynomial correlation between P_N and T_l indicated that P_N dropped below half of its maximum value when T_l was 37.4°C and 35.8°C for *A. arenaria* and *E. farctus*, respectively, and 32.2°C (mean value) for the other species (Table 2).

PCA extracted two factors explaining 91% of the total variance (63% factor 1 and 28% factor 2) (Fig. 8). Factor 1 was positively correlated with P_N, g_s and C_E, and negatively with LMA and $T_{50\%}$. Factor 2 was positively correlated with WUE.

Along the factor 1, *A. arenaria* and *E. farcus* were characterised by the highest LMA and $T_{50\%}$ and by the lowest P_N, g_s and C_E. *E. maritimum*, *C. maritima* and *A. maritima* had an opposite trend, while *O. variegata* and *P. maritimum* were in the middle.

Along the factor 2, *A. arenaria*, *E. farctus* and *C. maritima* had a higher WUE than the other species.

Discussion

The results on the whole underline that the considered species developing on the sand dunes along the *Latium* coast are characterised by adaptive strategies resulting from a combination of morphological and physiological leaf traits.

The species considered show a similar P_N and Chl trend during the year, with a peak from the end of April to the middle of May, favoured by air temperatures within the range 13.3 to 17.5°C and a soil water availability of 6%. *C. maritima*, *E. maritimum*, and *A. maritima,* have the highest P_N and C_E, and *A. arenaria*, *E. farctus*, *O. variegata,* and *P. maritimum* the lowest ones.

In the period of June–July, the increase of air temperature (T_{max} = 28.4°C), associated with a low water availability (42 mm, total rainfall of the period) and a decreased soil moisture content (80% of the winter value) determines a significant decrease of P_N (48%, mean of the considered species) and Chl (38%), and an increase of the Car/Chl ratio (59%). The increased Car/Chl ratio during drought reduces the risk of overexcitation and photooxidative damage, according to Kyparissis *et al.* (2000) and Balaguer *et al.* (2002). In summer, as stomatal conductance decreased, a decline of C_E (46%) also takes place, according to the results of Flexas *et al.* (2001), and confirmed by the significant correlation between P_N and g_s explaining 67% of P_N variations. The considered species have a WUE [4.2 ± 0.6 μmol(CO_2) $mmol^{-1}$(H_2O), mean value] which is within the range for temperate and subtropical dune species (De Jong 1978, Pammenter 1985, Ripley and Pammenter 2004).

E is significantly correlated with g_s, confirming a higher adaptability of stomata to changes in water availability, according to Gratani and Ghia (2002a) and Niu *et al.* (2006). The efficient use of water by stomatal regulation is an important feature for plant species survival in coastal dunes.

The polynomial relationship between P_N and T_l represents the influence of temperature on these processes (Larcher 1994, Gratani *et al.* 2000). The correlation between the two variables underlines that the favourable T_l enabling 90–100% of the highest P_N in the considered species is within the range of 23.4 to 26.6°C. P_N drops

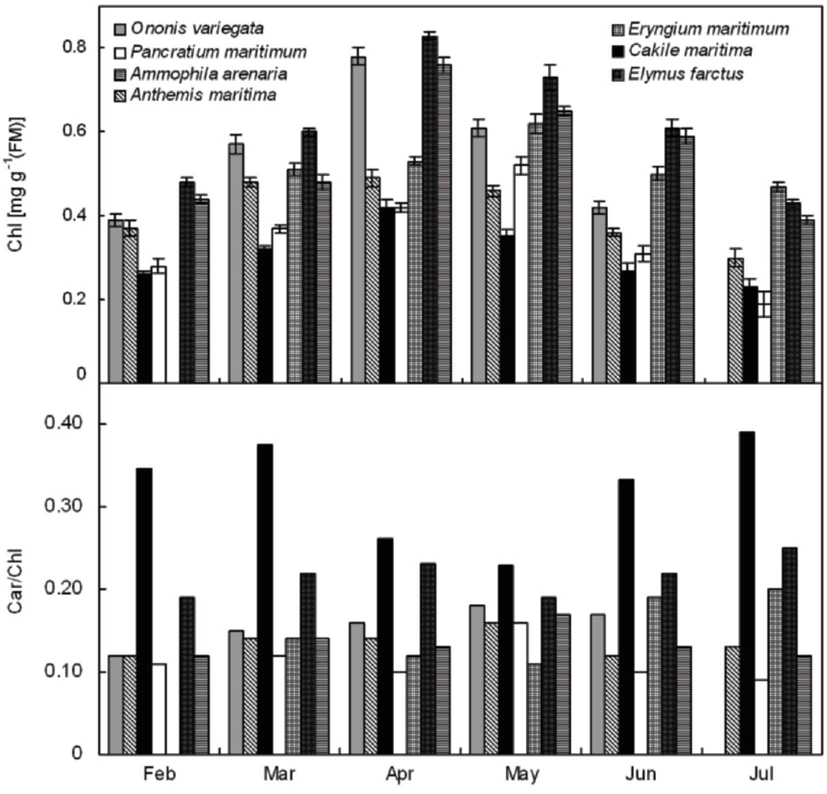

Fig. 6. Chlorophyll (Chl) content and carotenoid to chlorophyll ratio (Car/Chl) of the considered species during the study period. Mean values (±SD, n = 15) are shown.

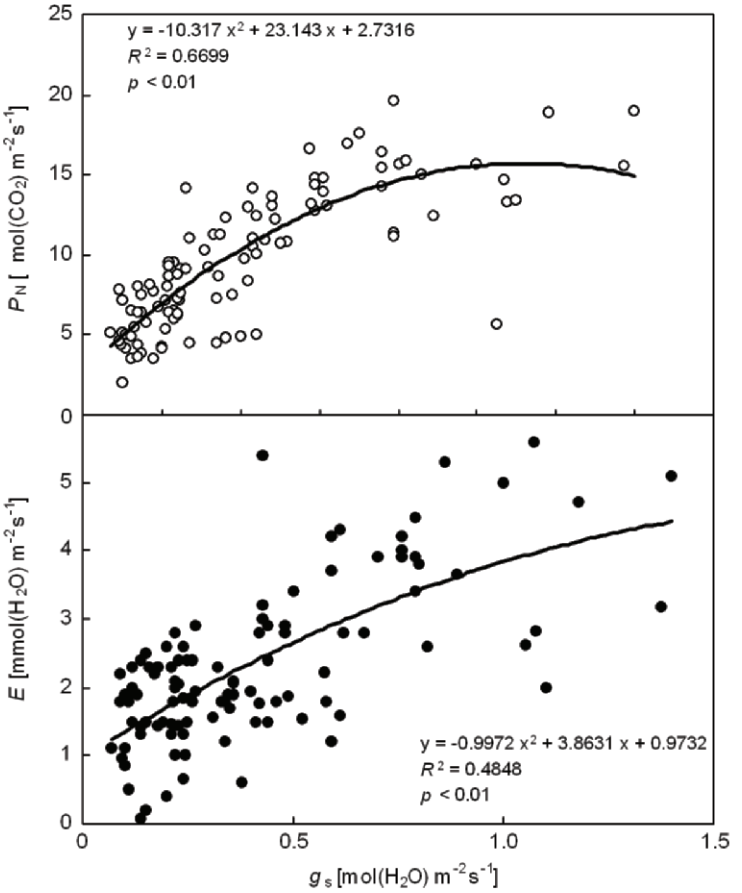

Fig. 7. Regression analysis between net photosynthetic rate (P_N) and stomatal conductance (g_s), and between transpiration rate (E) and g_s of the considered species. Equation of regression, determination's coefficient (r^2) and p-level are shown.

Table 2. Regression analysis between net photosynthetic rate (P_N) and leaf temperature (T_l) of the considered species, during the study period. $T_{100\%}$= leaf temperature enabling 100% of the highest photosynthetic rates; $T_{100–90\%}$= leaf temperature enabling 100–90% of the highest photosynthetic rates; $T_{90–50\%}$= leaf temperature enabling 90–50% of the highest photosynthetic rates. (n = 90).

Species	Relationship	$T_{100\%}$ [°C]	$T_{100–90\%}$ [°C]	$T_{90–50\%}$ [°C]
Ononis variegata	$P_N = –0.0542\, T_l^2 + 2.6684\, T_l – 25.966$	24.6	21.0–28.2	16.7–32.6
Anthemis maritima	$P_N = –0.1405\, T_l^2 + 7.0784\, T_l – 74.662$	25.2	21.9–28.4	18.0–32.4
Cakile maritima	$P_N = –0.1635\, T_l^2 + 8.3156\, T_l – 89.063$	25.4	22.2–28.6	18.3–32.6
Pancratium maritimum	$P_N = –0.1432\, T_l^2 + 7.6121\, T_l – 90.561$	26.6	23.9–29.3	20.5–32.7
Eryngium maritimum	$P_N = –0.2897\, T_l^2 + 14.813\, T_l – 173.27$	25.6	23.2–27.9	20.3–30.8
Elymus farctus	$P_N = –0.0625\, T_l^2 + 3.2852\, T_l – 31.95$	26.3	22.0–30.5	16.8–35.8
Ammophila arenaria	$P_N = –0.0202\, T_l^2 + 0.9462\, T_l – 3.2114$	23.4	17.2–29.7	9.5–37.4

below half of its maximum when T_l is over 35.8 and 37.4°C in *E. farctus* and *A. arenaria*, respectively, and 32.2°C in the other species considered (mean value).

At morphological level, LMA varies from 6.8 ± 0.7 mg cm^{-2} (*O. variegata*) to 30.6 ± 1.6 mg cm^{-2} (*A. arenaria*), and it is within the range of the Mediterranean evergreen species (Gratani and Bombelli 2001, Gratani and Varone 2006).

PCA carried out using all the considered traits underlines that the co-occurring species are characterised by different adaptive strategies: *A. arenaria,* and *E. farctus* can photosynthesize for a long period also when air temperature reaches higher values because of their lowest transpiration rates by the highest LMA. The high LMA is a recurrent plant trait in the Mediterranean climate region having a protective function for plants facing drought stress (Salleo and Nardini 2000). It can be used as a measure of investment per unit leaf area (Wright *et al.* 2004). Nevertheless, protective structures reduce photosynthetic rates as a result of diluting photosynthetic tissues with non-photosynthetic ones (Wright *et al.* 2004), and justifying the lower P_N in *A. arenaria,* and *E. farctus*. A higher internal competition for photons and CO_2 (Poorter *et al.* 1990), a higher internal resistance to CO_2 transfer (Lloyd *et al.* 1992), a low proportion of leaf nitrogen in the photosynthetic enzymes (Evans 1989,

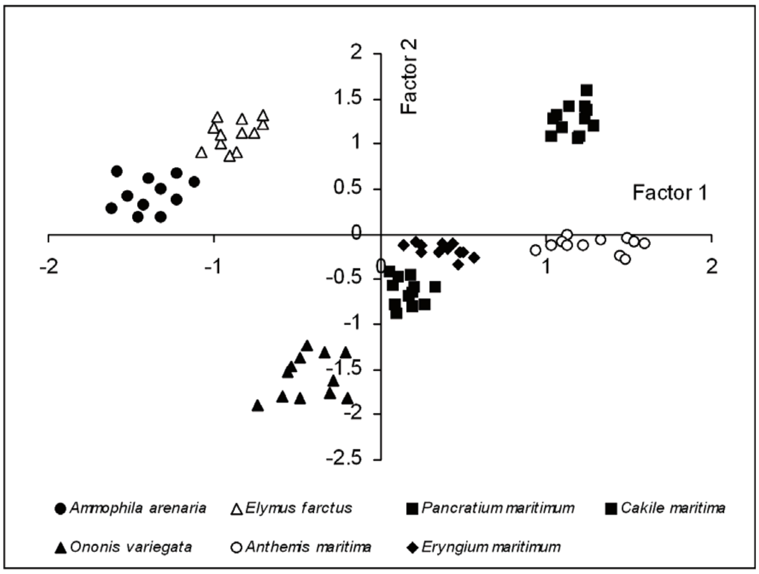

Fig. 8. Result of the Principal Component Analysis (PCA) for the considered species. Factor 1 was positively correlated to net photosynthetic rate (P_N), stomatal conductance (g_s) and relative carboxylation efficiency (C_E,) and negatively to leaf mass area (LMA) and leaf temperature enabling 50% of the highest photosynthetic rates ($T_{50\%}$). Factor 2 was positively correlated to water use efficiency (WUE).

Niinemets 1999), and an unequal distribution of nitrogen in the different enzymes involved in the CO_2 assimilation (Poorter and Evans 1998) have been proposed as key factors responsible for the low photosynthetic rates in high LMA leaves.

On the contrary, *A. maritima*, *C. maritima,* and *P. maritimum* have higher P_N in the favourable period, allowed by their highest SI and the lower LMA. Species with low LMA (*i.e.* high specific leaf area, SLA) tend to have a higher photosynthetic capacity per unit leaf mass, resulting from a larger light-capture area per leaf mass (Wright *et al.* 2004, Gratani and Ghia 2002b), and a shorter diffusion path from stomata to chloroplasts (Parkhurst 1994).

Not all species are able to withstand the same types or the same intensities of an environmental stress. Consequently, there is a great international concern about the possible extinction of certain species, particularly in such areas of the world as the Mediterranean Basin, where great temperature changes are expected to occur (Gulías *et al.* 2002). The results allow us to hypothesize about the response of the considered species to increasing air temperature. We hypothesised that the highest photosynthesis tolerance threshold to high air temperatures, as well as the highest leaf consistency (*i.e.* high leaf mass area, LMA) might be important leaf traits for plant survival in coastal dunes: *A. arenaria* and *E. farctus* might be at a competitive advantage, relative to the other species considered, by their ability to photosynthesize at sufficient rates also under high air temperatures, thus increasing their biomass (Larcher 1994, Gratani *et al.* 2000).

References

Balaguer, L., Pugnaire, F.I., Martínez-Ferri, E., Armas, C., Valladares, F., Manrique, E.: Ecophysiological significance of chlorophyll loss and reduced photochemical efficiency under extreme aridity in *Stipa tenacissima* L. – Plant Soil **240**: 343-352, 2002.

Barbour, M.G., DeJong, T.M, Pavlik, B.M.: Marine beach and dune plant communities. – In: Chabot, B.F., Mooney, H.A. (ed.): Physiological Ecology of North American Plant Communities. Pp. 296-322. Chapman and Hall, New York 1985.

Conti, F., Abbate, G., Alessandrini, A., Blasi C.: An Annotated Checklist of the Italian Vascular Flora. – Palombi Editori, Roma 2005.

Crescente, M.F., Gratani, L., Larcher, W.: Shoot growth efficiency and production of *Quercus ilex* L. in different climates. – Flora **197**: 2-9, 2002.

da Silva, G.M., Hesp, P., Peixoto, J., Dillenbur, S.R.: Foredune vegetation patterns and alongshore environmental gradients: Moçambique Beach, Santa Catarina Island, Brazil. – Earth Surf. Proc. Land. **33**: 1557-1573, 2008.

De Jong, T.M.: Comparative gas exchange of four California beach taxa. – Oecologia **34**: 343-351, 1978.

Disraeli, D.J.: The effect of sand deposits on the growth and morphology of *Ammophila breviligulata*. – J. Ecol. **72**: 145-154, 1984.

Donnelly, F.A., Pammenter, N.W.: Vegetation zonation on a Natal coastal sand-dune system in relation to salt spray and soil salinity. – South Afr. J. Bot. **2**: 46-51, 1983.

Evans, J.R.: Photosynthesis and nitrogen relationships in leaves of C_3 plants. – Oecologia **78**: 9-19, 1989.

Flexas, J., Gulías, J., Jonasson, S., Medrano, H., Mus, M.: Seasonal patterns and control of gas exchange in local populations of the Mediterranean evergreen shrub *Pistacia lentiscus* L. – Acta Oecol. **22**: 33-43, 2001.

Gilbert, M.E., Ripley, B.S.: Biomass reallocation and the mobilization of leaf resources support dune plant growth after sand burial. – Physiol. Plantarum **134**: 464-472, 2008.

Gilbert, M.E., Pammenter, N.W., Ripley, B.: The growth responses of coastal dune species are determined by nutrient limitation and sand burial. – Oecologia **156**: 169-178, 2008.

Gratani, L., Bombelli, A.: Differences in leaf traits among

Mediterranean broadleaved evergreen shrubs. – Ann. Bot. Fenn. **38**: 15-24, 2001.

Gratani, L., Capannesi, G.: [A critical approach to the problem of the vigour of *Ammophila littoralis* (Beauv.) Rothm.] – Collana dei Rapporti Tecnici dell'ENEA, ENEA-RT/PAS/84/18: 3-12, 1984. [In Ital.]

Gratani, L., Crescente, M.F.: Phenology and leaf adaptive strategies of Mediterranean maquis plants. – Ecol. Mediterr. **23**: 11-19, 1997.

Gratani, L., Crescente, M.F., Varone, L.: [Ecology and phenology of psammophilous species]. – Fitosociologia **44**: 11-16, 2007. [In Ital.]

Gratani, L., Crescente, M.F., Varone, L., Fabrini, G., Digiulio, E.: Growth pattern and photosynthetic activity of different Bamboo species growing in the Botanical Garden of Rome. – Flora **203**: 77-84, 2008.

Gratani, L., Ghia, E.: Changes in morphological and physiological traits during leaf expansion of *Arbutus unedo*. – Environ. Exp. Bot. **48**: 51-60, 2002a.

Gratani, L., Ghia, E.: Adaptive strategy at the leaf level of *Arbutus unedo* L. to cope with Mediterranean climate. – Flora **197**: 275-284, 2002b.

Gratani, L., Marinucci, C., Amadori, M., Bruno, F.: Relationship between phytosociological table and biomass estimation of psammophilous vegetation at Castelporziano (Rome, Italy). – Acta Oecol.-Oecol. Gener. **4**: 307-314, 1983.

Gratani, L., Meneghini, M., Pesoli, P., Crescente, M.F.: Structural and functional plasticity of *Quercus ilex* seedlings of different provenances in Italy. – Trees-Struct. Funct. **17**: 515-521, 2003.

Gratani, L., Pesoli, P., Crescente, M.F., Aichner, K., Larcher, W.: Photosynthesis as a temperature indicator in *Quercus ilex* L. – Global Planet. Change **24**: 153-163, 2000.

Gratani, L., Varone, L.: Long time variations in leaf mass and area of Mediterranean evergreen broad-leaf and narrow-leaf maquis species. – Photosynthetica **44**: 161-168, 2006.

Greaver, T.L., Sternberg, L.S.L .: Fluctuating deposition of ocean water drives plant function on coastal sand dunes. – Global Change Biol. **13**: 216-223, 2007.

Gulías, J., Flexas, J., Abadía, A., Medrano, H.: Photosynthetic responses to water deficit in six Mediterranean sclerophyll species: possible factor explaining the declining distribution of *Rhamnus ludovici-salvatorius*, an endemic Balearic species. – Tree Physiol. **22**: 687-697, 2002.

Heslenfeld, P., Jungerius, P.D., Klijn, J.A.: European coastal dunes: ecological values, threats, opportunities and policy development. – In: Martínez, M.L., Psuty, N.P. (ed.): Coastal Dunes: Ecology and Conservation. Pp. 335-351. Springer-Verlag, Berlin 2004.

Holm G.: Chlorophyll mutations in barley. – Acta Agric. Scand. **4**: 457-471, 1954.

Ishikawa, S., Oikawa, T., Furukawa, A.: Photosynthetic characteristics and water use efficiency of three coastal dune plants. – Ecol. Res. **5**: 377-391, 1990.

Kachi, N., Hirose, T.: Limiting nutrients for plant growth in coastal sand dune soils. – J. Ecol. **71**: 937-944, 1983.

Kent, M., Owen, N.W., Dale, M.P.: Photosynthetic responses of plant communities to sand burial on the machair dune systems of the Outer Hebrides, Scotland. – Ann. Bot. **95**: 869-877, 2005.

Kyparissis, A., Drilias, P., Manetas, Y.: Seasonal fluctuations in photoprotective (xanthophyll cycle) and photoselective (chlorophylls) capacity in eight Mediterranean plant species belonging to two different growth forms. – Aust. J. Plant Physiol. **27**: 265-272, 2000.

Larcher, W.: Photosynthesis as a tool for indicating temperature stress events. – In: Schulze, E.D., Caldwell, M.M. (ed.): Ecophysiology of Photosynthesis. Pp. 261-277. Springer-Verlag, Berlin 1994.

Liu, P.L.F., Lynett, P., Fernando, H., Jaffe, B.E., Fritz, H., Higman, B., Morton, R., Goff, J., Synolakis, C.: Observations by the International Tsunami survey Team in Sri Lanka. – Science **308**: 1595-1595, 2005.

Lloyd, J., Syvertsen, J.P., Kriedemann, P.E., Farquhar, G.D.: Low conductances for CO_2 diffusion from stomata to the sites of carboxylation in leaves of woody species. – Plant Cell Environ. **15**: 873-899, 1992.

Maclachlan, S., Zalik, S.: Plastid structure, chlorophyll concentration, and free aminoacid composition of a chlorophyll mutant of barley. – Can. J. Bot. **41**: 1053-1062, 1963.

Martínez, M.L., Moreno-Casasola, P.: Effects of burial by sand on seedling growth and survival in six tropical sand dune species from the Gulf of Mexico. – J. Coast Res. **12**: 406-419, 1996.

Martínez, M.L., Maun, M.A., Psuty, N.P.: The fragility and conservation of the world's coastal dunes: geomorphological, ecological and socioeconomic perspectives. – In: Martínez, M.L., Psuty, N.P. (ed.): Coastal Dunes: Ecology and Conservation. Pp. 354-369. Springer-Verlag, Berlin 2004.

Maun, M.A.: Adaptations enhancing survival and establishment of seedlings on coastal dune systems. – Vegetatio **111**: 59-70, 1994.

Niinemets, U.: Components of leaf dry mass per area - thickness and density - alter leaf photosynthetic capacity in reverse directions in woody plants. – New Phytol. 144: 35-47, 1999.

Niu, S.L., Jiang, G.M., Wan, S.Q., Li, Y.G., Gao, L., Liu, M.: A sand-fixing pioneer C_3 species in sandland displays characteristics of C_4 metabolism. – Environ. Exp. Bot. **57**: 123-130, 2006.

Omae, H., Kumar, A., Kashiwaba, K., Shono, M. : Assessing drought tolerance of snap bean (*Phaseolus vulgaris*) from genotypic differences in leaf water relations, shoot growth and photosynthetic parameters. – Plant. Prod. Sci. **10**: 28-35, 2007.

Pammenter, N.W.: Photosynthesis and transpiration of the subtropical coastal sand dune pioneer *Scaevola plumieri* under controlled conditions. – South Afr. J. Bot. **51**: 421-424, 1985.

Parkhurst, D.F.: Diffusion of CO_2 and other gases inside leaves. – New Phytol. **126**: 449-479, 1994.

Peñuelas, J., Filella, L.: Response to a warming world. – Science, **294**: 793-795, 2001.

Pereira, J.S.: Gas exchange and growth. – In: Schulze, E.D., Caldwell, M.M. (ed.): Ecophysiology of Photosynthesis. Pp. 147-175. Springer-Verlag, Berlin 1994.

Perumal, V.J., Maun, M.A.: Ecophysiological response of dune species to experimental burial under field and controlled conditions. – Plant Ecol. **184**: 89-104, 2006.

Pesoli, P., Gratani, L., Larcher, W.: Responses of *Quercus ilex* from different provenances to experimentally imposed water stress. – Biol. Plantarum **46**: 577-581, 2003.

Poorter, H., Evans, J.R.: Photosynthetic nitrogen use efficiency of species that differ inherently in specific leaf area. – Oecologia **116**: 26-37, 1998.

Poorter, H., Remkes, C., Lambers, H.: Carbon and nitrogen economy of 24 wild species differing in relative growth rate. – Oecologia **94**: 621-627, 1990.

Read, J., Sanson, G.D., Lamont, B.B.: Leaf mechanical properties in sclerophyll woodland and shrubland on contrasting soils. – Plant Soil **276**: 95-113, 2005.

Reich, P.B., Kloeppel, B.D., Ellsworth, D.S., Walters, M.B.: Different photosynthesis-nitrogen relations in deciduous hardwood and evergreen coniferous tree species. – Oecologia **104**: 24-30, 1995.

Ripley, B.S, Pammenter, N.W.: Do low standing biomass and leaf area index of sub-tropical coastal dunes ensure that plants have an adequate supply of water? – Oecologia **139**: 535-544, 2004.

Salleo, S., Nardini, A.: Sclerophylly: evolutionary advantage or mere epiphenomenon? – Plant Biosyst. **134**: 261-277, 2000.

Shumway, S.W.: Facilitative effects of a sand dune shrub on species growing beneath the shrub canopy. – Oecologia **124**: 138-148, 2000.

Voronkova, N.M., Burkovskaya, E.V., Bezdeleva, T.A., Burundukova, O.L.: Morphological and biological features of plants related to their adaptation to coastal habitats. – Russ. J. Ecol. **39**: 1-7, 2008.

Watkinson, A.R., Davy, A.J.: Population biology of salt-marsh and sand dune annuals. – Vegetatio **62**: 487-497, 1985.

Willis, A.J.: The influence of mineral nutrients on the growth of *Ammophila arenaria*. – J. Ecol. **53**: 735-745, 1965.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulías, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R.: The worldwide leaf economics spectrum. – Nature **428**: 821-827, 2004.

Yura, H., Ogura, A.: Sandblasting as a possible factor controlling the distribution of plants on a coastal dune system. – Plant Ecol. **185**: 199-208, 2006.