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A sunny day at the beach: Ecophysiological assessment of the photosynthetic adaptability of coastal dune perennial herbs by chlorophyll fluorescence parameters

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Abstract

Light is critical in determining plant structure and functioning in dune ecosystems, which are characterised by high incident and reflected radiation. Light variations demand great plasticity of the photosynthetic apparatus. This study assessed the phenotypic plasticity of foredune species by analysing their light response and dark recovery curves measured under field conditions. We also addressed the question how coexisting species, structurally distinct, differed in their photochemical efficiency in response to short-term changes in light. Finally, we examined how the varying intensity of stressors operating along a dune gradient affected responses to light. The species differed in light use strategies but showed similar patterns of the dark recovery. Species differences in photochemistry varied seasonally, with species being winter specialists, summer specialist or generalists. Some aspects of their photochemistry varied significantly along the gradient. Unexpectedly, other traits did not vary as predicted. For example, changes in light efficiency of plants along the gradient were not consistent with assumed directional changes in the severity of stressors. The different light use strategies observed in coexisting species did not conform to the prediction that stressors constrain the range of possible functional designs in harsh environments. However, the species followed very similar patterns of post-illumination recovery, which suggests that evolutionary pressures might be acting to maintain similar recovery mechanisms. Our results indicated that dune gradients might be nondirectional, which determines unpredictable patterns of variation in leaf traits along the dune gradient. Seasonal differences in the relative performance may allow species to coexist where otherwise one species would exclude the other.

Additional key words: *Eryngium maritimum*; *Euphorbia paralias*; light curve; *Matthiola sinuata*; nonphotochemical quenching; *Pancratium maritimum*; photochemical quenching; quantum yield of photosystem II.

Introduction

Coastal, sand dunes are hostile environments in which plant establishment, survival, and growth are severely limited by the harshness of the abiotic conditions and highly recurrent natural and human disturbances (Hesp 1991, Maun 2009). Many environmental constraints, which plants must cope with in sand dune systems, include low availability of soil water and nutrients, high winds, sandblasting, burial by sand, high soil salinity, salt spray deposition, and high soil surface temperatures (Chapman 1976, Watkinson and Harper 1978, Payne and Maun 1984, Barbour *et al.* 1985, Maun 1994, 2009). Solar radiation also plays an essential role in dune systems, which are characterised by high intensity of incident solar radiation and of radiation reflected by sand surfaces (Barbour *et al.* 1985, Hesp 1991, Davy and Figueroa 1993). The lack of a dense overstory that attenuates radiation in many dune systems, especially in foredunes, may further enhance the effects of high irradiance on dune plants. Plant growth has been directly related to the plant ability to intercept solar radiation and convert it into dry

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Abbreviations: F_0 – minimal fluorescence of the dark-adapted leaf; F_0' – minimal fluorescence of the light-adapted leaf; F_m – maximal fluorescence of the dark-adapted leaf; F_m' – maximal fluorescence of the light-adapted leaf; F_v/F_m – maximum quantum yield of PSII; q_N – nonphotochemical quenching index; q_P – photochemical quenching index; Φ_{PSII} – effective quantum yield of PSII.

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matter (Monteith and Moss 1977, Woodward 1987). Apart from its unique role in photosynthesis, light also controls many developmental processes in plants, such as germination, leaf and stem expansion, chlorophyll (Chl) synthesis, flower induction, and phototropism (Fitter and Hay 2002). Consequently, light has been considered the main factor determining ecosystem structure and functioning (Whatley and Whatley 1980).

In nature, the intensity of light varies greatly both temporally and spatially. Light may vary seasonally, daily, or even within a few seconds as a result of shading by clouds. Large changes in irradiance may also be observed at a small spatial scale, because of differences in the position of a given plant stand within the canopy (Björkman and Demmig-Adams 1995, Battaglia *et al.* 2002) or because of different exposure due to microtopographical heterogeneity (Stoutjesdijk and Barkman 1992). Competition for light is also likely to increase along the dune gradients (Gilbert *et al.* 2007). The large variation in this essential resource demands great plasticity, at both large and small scales, and in the responsiveness of the photosynthetic apparatus (Björkman and Demmig-Adams 1995, Valladares *et al.* 2000). The correct dose of PAR provides plants with the energy needed for their photosynthetic function, which is fundamental to plant metabolism and crucial for the ecological success of plants. At low PPFD, light must be absorbed with maximum efficiency, otherwise it may fall below the compensation point, *i.e.* the point at which respiration costs are greater than photosynthetic income in plants. On the other hand, an excess of excitation energy may damage photosynthetic reaction centres if light energy absorption exceeds the capacity for light use in photosynthesis (photoinhibitory damage). Although light is of paramount importance for plant life, the responses of dune plants to varying light intensity have been poorly studied at the level of leaf physiology. In particular, very few physiological studies have been carried out under natural conditions, in which the responses of plants to light may be strongly influenced by multiple stress factors, such as water and nutrient deficiency, soil salinity, wind exposure, and extreme temperatures (Demmig-Adams and Adams 1992, Osmond 1994, Lichtenthaler and Burkart 1999, Naumann *et al.* 2009), all of which occur simultaneously with high PPDF in sand dunes. Dune environments are spatially very heterogeneous and some of the above-mentioned stressors may vary widely over relatively short distances (Salzman and Parker 1985, Houle 1997b, Gagné and Houle 2001). At larger spatial scales, the intensity of stressors may increase or decrease consistently over long shoreline-inland dune gradients (Kachi and Hirose 1979, Maruyama and Miura 1981, Miura and Maruyama 1983, Hesp 1991). Generally, the most hostile environmental conditions occur at the coastal end of such gradients because of the greater severity of abiotic factors (*e.g.* high airborne and soil salinity, low availability of nutrients, burial by sand, and sand blasting) (Ishikawa *et al.* 1995, Costa *et al.* 1996, Houle 1997a, Griffiths 2006, Lortie and Cushman 2007, Kim and Yu 2009).

Considering that light is one of the main determinants of plant performance in dune systems, we aimed to characterize some aspects of plant plasticity under natural field conditions, such as the ability to adjust their photosynthetic responses to varying light doses and to regulate the level of excitation energy. We considered plants species that are structurally very distinct but that coexist in a homogeneous foredune area. We first addressed the differences in the responses of these plants to short-term changes in light availability, in terms of photochemical efficiency and the relative importance of the different strategies used to dissipate excessive excitation energy. We expected that the differences in leaf anatomy and life forms of the species studied would significantly influence the responses to light. In addition, we examined how the varying intensity of multiple stress factors operating along a shoreline-inland dune gradient influenced light responses in *Pancratium maritimum*, a species that grows along the entire dune gradient. We expected that changes in the severity of stressors along the dune gradient would greatly influence light responses in *P. maritimum*. More specifically, assuming that the severity of the complex of abiotic factors is greater at the shoreline end of the dune gradient, we predicted a lower capacity for light-saturated photosynthesis and slower post-illumination recovery in *P. maritimum* plants at the shoreline end of the dune gradient as the result of excessive light energy. We also examined how plant responses, in terms of photochemical performance, were affected by winter and summer conditions. As far as we know, no previous studies have addressed these important issues under natural field conditions, in which plant responses to light may be strongly influenced by multiple interactions with other factors. Plant phenotypic plasticity in response to short-term variations in the light dose was examined by analysis of light response curves and recovery curves of chlorophyll (Chl) fluorescence parameters after illumination. Light curves allow exploration of species differences in the response to light over a wide range of PPFDs. On the basis of the principle of pulse amplitude modulation, Chl fluorescence parameters provide information about qualitative and quantitative changes in the efficiency of PSII photochemistry (Maxwell and Johnson 2000). PSII is recognised as the part of the photosynthetic apparatus that is most vulnerable to light-induced damage (Björkman and Demmig-Adams 1995). Therefore, damage to PSII is often the first manifestation of stress in a leaf. To analyse the ability of the plants to regulate the level of excitation energy, we determined the relative amount of light channelled through photochemical processes (photochemical efficiency) and through alternative means of nonphotochemical dissipation, such as emission of fluorescence, mainly from PSII Chl *a*, and nonradiative dissipation of energy into heat. In this research, with focus in coastal dune plant species, we addressed the main following questions: (*1*) Do coexisting species with contrasting leaf structures differ in their responses to short-term variations in light and post-illumination recovery?; (*2*) Does the relative photochemical efficiency of these species change seasonally?; (*3*) Does the efficiency of PSII and heat dissipation in *P. maritimum* vary consistently with the assumed directional changes in the severity of the stressors along a shoreline-inland dune gradient?

Materials and methods

Species and location: Four perennial, dune herbs with contrasting leaf morphology and life forms were selected for study. *Eryngium maritimum* L. (Umbelliferae) is a C_3 hemicryptophyte with blue-green, three-lobed, folded leaves. The leaves are also stiff, leathery, and spiny. *Pancratium maritimum* L. (Amaryllidaceae) is a C_3 cryptophyte with a bulbous stem from which a long glaucous neck grows, ending in long, thick, linear-shaped leaves of up to 50 cm in length. *Matthiola sinuata* (L.) R. Br. (Brassicaceae) is a hemicryptophyte with a basal rosette of narrow, highly pubescent, pale grey-green leaves. The plants grow up to 40 cm in height and the leaves up to 10 cm in length. *Euphorbia paralias* L. (Euphorbiaceae) is a glaucous herb with both fertile and sterile branches growing from a woody base and with closely overlapping leaves. The leaves, a mean size of 20 mm, are thick and ovate to elliptic; white latex emanates when the leaves are excised. This plant is a C_3 chamaephyte, although it can switch facultatively to C_4 or CAM metabolism under certain environmental conditions (Elhaak *et al.* 1997, Ciccarelli *et al.* 2009).

Two coastal, dune systems in Galicia (NW Spain) were selected according to the objectives of the study. For interspecific comparisons, a homogeneous flat area of about 220 m^2 was selected in the foredune of the Lariño coastal dune system (42º46'00" N, 9º06'58" W; Galicia, NW Spain), where all the above species were interspersed. To study how the varying environmental conditions, which occur along dune gradients, influenced the photochemical efficiency of *P. maritimum*, we selected a 800 m long, coast-inland gradient in the coastal dune system of Nerga (42º15'50" N, 8º51'10" W; Galicia, NW Spain), where *P. maritimum* grows from shoreline to inland locations.

Chl fluorescence measurements: Light and dark-adapted Chl fluorescence parameters were measured in the field with a portable pulse amplitude modulated fluorometer (*Mini-PAM*, *Heinz Walz GmbH*, Effeltrich, Germany) attached to an *Arabidopsis* leaf clip holder *2060-B* (*Heinz Walz GmbH*, Effeltrich, Germany). The incident PPFD on leaves was supplied by an external halogen lamp (*2050-HB*, *Heinz Walz GmbH*, Effeltrich, Germany) coupled to the fluorometer. Minimum (F_0) and maximum (F_m) fluorescence emissions were measured under dark adapted conditions (Maxwell and Johnson 2000, Roháček 2002). The steady state or basal fluorescence emission (F_t) and the maximum emission of fluorescence (F_m') were determined in light-adapted samples (Maxwell and Johnson 2000, Roháček 2002). F_m and F_m' were measured after a light saturating pulse [>4,000 μmol(photon) m^{-2} s^{-1}, 0.8 s pulse length] of actinic white light (Maxwell and Johnson 2000, Roháček 2002). These basic Chl fluorescence parameters were used to compute different indices, as follows. The effective quantum yield of PSII was determined as $\Phi_{PSII} = (F_m' - F_t)/F_m'$ (Maxwell and Johnson 2000). This index, which measures the fraction of the light absorbed by Chl (associated with PSII) that is used in photochemistry, has been inversely correlated with the dissipation of excess radiation energy as fluorescence and is directly correlated with radiation use efficiency (Genty *et al.* 1989, Maxwell and Johnson 2000, Roháček 2002). The maximum quantum yield of PSII (F_v/F_m) was calculated from the measured values of F_m and F_0, after a saturation pulse, as $(F_m - F_0)/F_m$. This ratio was determined in dark adapted samples with all reaction centres of PSII fully open (*i.e.* all primary acceptors oxidised). The F_v/F_m ratio estimates the efficiency with which the excitation energy is captured by open PSII reaction centres and represents the proportion of incident photon energy that is processed photochemically (Krause and Weis 1991, Mohammed *et al.* 1995). In healthy leaves of most species, the value of F_v/F_m is about 0.8 (Krause and Weis 1991, Maxwell and Johnson 2000). F_v/F_m values below 0.8 have been considered symptomatic of stress-dependent photoinhibition (Björkman and Demmig 1987, Long *et al.* 1994, Maxwell and Johnson 2000). The amount of Chl fluorescence quenched photochemically was assessed by the photochemical quenching index (q_P), calculated as $(F_m' - F_t)/(F_m' - F_0')$ (Maxwell and Johnson 2000, Roháček 2002). The q_P index estimates the proportion of PSII reaction centres that are open, and it therefore estimates the availability of these reaction centres to process photon energy photochemically (Krause and Weis 1991, Maxwell and Johnson 2000, Roháček 2002). Finally, the nonphotochemical quenching of Chl fluorescence was calculated by the q_N index, as $1 - [(F_m' - F_0')/(F_m - F_0)]$ (Roháček 2002). The q_N index indicates the level of nonphotochemical energy dissipation in the PSII light-harvesting antenna relative to the dark-adapted state (Maxwell and Johnson 2000). It is commonly assumed that the reduction of fluorescence by nonphotochemical processes is caused by the loss of photon energy *via* thermal dissipation (Björkman and Demmig-Adams 1995, Buschmann 1999, Roháček 2002). Nonphotochemical quenching is induced by changes in the pH gradient at the thylakoid membrane, by state transitions, and by photoinhibitory processes (Krause *et al.* 1982, Horton and Hague 1988, Bilger and Björkman 1990, Krause and Weis 1991, Pospíšil 1997, Roháček 2002).

Measurement protocol: In February and August 2008, Chl fluorescence parameters were measured in one fully expanded leaf on the top of each of five randomly selected plants of each species in the Lariño dune system. At the Nerga site, Chl fluorescence parameters were measured, in April and June 2008, in one fully expanded leaf on each of five randomly selected *P. maritimum* individuals, at each of four locations (0, 150, 500, and 800 m) along a shoreline-inland dune gradient. The data required to construct light response curves for each of the selected plants were recorded as follows. The plants were covered with a portable shading structure opaque to PAR. After 30 min of dark adaptation, parameters F_0 and F_m were measured. Following the initial dark measurements, the external halogen lamp was switched on and a sequence of F_0' and F_m' measurements were made at increasing levels of PPFD (50, 100, 200, 350, 600; 1,000; and 1,500 μmol(photon) m^{-2} s^{-1}). The light-adapted parameters, F_0' and F_m', were measured after a prior adaptation period of three minutes to the current PPFD. After recording the final F_0' and F_m' measurements at the highest light intensity, the halogen lamp was switched off and plant recovery under dark conditions was recorded, as follows. At the Lariño site, F_0 and F_m were measured after 20 min of dark adaptation. At the Nerga site, a recovery curve was constructed with F_0 and F_m data measured after 1, 5, and 20 min of dark adaptation. F_0 and F_m, which were measured after the initial 30 min of dark adaptation, and F_0' and F_m', which were measured after the 3-min adaptation to the highest light intensity [1,500 μmol (photon) m^{-2} s^{-1}], were used to determine the maximum and effective quantum yield of PSII and also the q_P and q_N quenching coefficients.

Statistical analysis: Prior to analyses, all variables were checked for the normality and homoscedasticity assumed for analysis of variance (*ANOVA*). No variable severely deviated from the underlying assumptions, which justified the use of *ANOVA* (Zar 1984). Differences in Chl fluorescence parameters were analysed by two-way *ANOVA*, with species and season as fixed factors in the interspecific analysis, and species and position in the gradient analysis. The following functions, both with a type III error structure, were used: the *aov* function of the *Stats* package (R Development Core Team 2009) and the *ANOVA* function of the *car* package (Fox 2009). Light response curves were fitted to a nonlinear mixed model (Peek *et al.* 2002, Ritchie 2008) by the method of random slopes. PPFD was included as a mixed factor dependent on plant species, considering both single and quadratic effects. Stepwise analysis fitting was carried out, with the *lme* function (package n*lme*; Pinheiro *et al.* 2009) and *ANOVA* function (package *stats*; R Development Core Team 2009), to calculate the random effect in mixed models by the maximum likelihood method, as described by Crawley (2007). Recovery curves constructed with data obtained along the dune gradient were fitted, with the *lme* function, to a nonlinear mixed model by the method of random slopes, including single and cubic effects of time. Recovery lines from interspecific comparisons were fitted, with the *lme* and *ANOVA* functions, to a linear mixed model.

Results

Light responses in coexisting species

Photochemical efficiencies: Species differences in F_v/F_m were significantly influenced by the factor of season (Table 1). In *M. sinuata*, the F_v/F_m values were significantly lower in summer than in winter (Fig. 1*A*). The opposite trend was found in *E. maritimum*, where the winter F_v/F_m values were the lowest recorded among all species. However, in *E. paralias* and *P. maritimum*, the F_v/F_m values did not differ significantly between the seasons. Under high light conditions [1,500 μmol(photon) m^{-2} s^{-1}], species differed significantly in the Φ_{PSII} (Table 1); the photochemical efficiencies were the lowest in *E. paralias* and *P. maritimum* and the highest in *M. sinuata* (Fig. 1*B*). Differences in the ability of species to dissipate the excess excitation energy by thermal processes, as expressed by the q_N index, depended significantly on the season (Table 1). Although there were no differences between the summer and winter values of q_N in *E. paralias*, the values were higher in the winter than in the summer in *P. maritimum* and, especially, in *E. maritimum* (Fig. 1*D*). Conversely, in *M. sinuata*, the amount of absorbed light energy that is dissipated as heat was higher in the summer than in the winter (Table 1; Fig. 1*D*). The analyses did not detect any significant effects on the q_P (Table 1; Fig. 1*C*).

Light curves and post-illumination recovery: The statistical analysis of the light response curves showed significant contributions to the model by introducing the factor species (*P*=0.0014) and the species × season interaction (*P*=0.001). For all species and both seasons, the effecvive quantum yield of PSII decreased with increasing PPFDs (Fig. 2). In winter, at light intensities above 100 μmol(photon) m^{-2} s^{-1}, the photochemical efficiency (Φ_{PSII})

Table 1. Results of the two-way *ANOVA*, with species and season as fixed factors, for the comparison of the chlorophyll fluorescence parameters in the four species coexisting in the Lariño dune system. F_v/F_m – maximum and Φ_{PSII} – effective quantum yield of PSII; and q_P – photochemical and q_N – nonphotochemical quenching of chlorophyll fluorescence. Significant differences ($P \leq 0.05$) are marked *in bold*.

		F_v/F_m			Φ_{PSII}			q_P			q_N		
	df	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
Position	3	0.0133	1.71	0.185	0.093	3.75	**0.020**	0.241	2.72	0.061	0.044	0.93	0.439
Season	1	0.0004	0.18	0.674	0.0013	0.16	0.693	0.0011	0.04	0.845	0.007	0.46	0.501
Position × season	3	0.0314	4.14	**0.014**	0.034	1.38	0.267	0.194	2.19	0.109	0.155	3.27	**0.034**
Residuals	32	0.0801			0.264			0.947			0.504		

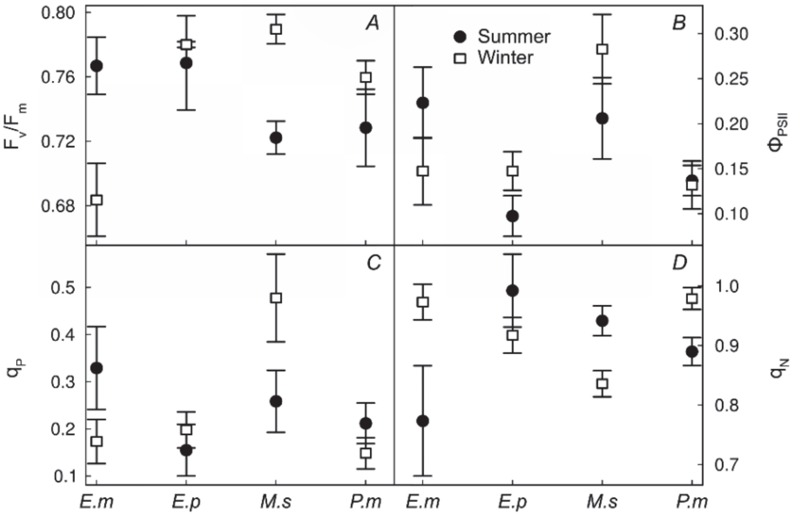

Fig. 1. Seasonal mean values (± SE, *n* = 5) of the chlorophyll fluorescence parameters: (*A*) maximum (F_v/F_m) and (*B*) effective (Φ_{PSII}) quantum yield of PSII; and photochemical (q_P) (*C*) and nonphotochemical (q_N) (*D*) quenching of chlorophyll fluorescence, for four species coexisting in the Lariño dune system. *E.m – Eryngium maritimum, E.p – Euphorbia paralias*, *M.s – Matthiola sinuata*, and *P.m – Pancratium maritimum*.

of *M. sinuata* was significantly higher than that of the other species, which did not differ from each other. However, in the summer, at light intensities between 50 and 1,500 μmol(photon) m^{-2} s^{-1}, the Φ_{PSII} of *E. paralias* was significantly lower than that of the other species, which did not differ from each other. Addition of the interactive component (species by season) to the model of the post-illumination recovery yielded a statistically significant effect (P=0.0067; Fig. 3). In the winter, the measurements made just after the light was switched off showed that the Φ_{PSII} was very similar in all species, with values below 0.2, except *M. sinuata*, in which the values were slightly lower than 0.3. After a 20 min period of dark recovery, the F_v/F_m increased to about 0.7, with *M. sinuata* again showing the highest values, slightly below 0.8, and *E. maritimum* showing the lowest values, slightly below 0.7. In the summer, at the beginning of the dark recovery period, the species differed slightly in Φ_{PSII}, with values of about 0.2 in *E. maritimum* and *M. sinuata*, and of about 0.1 in *P. maritimum* and *E. paralias*. At the end of the recovery period, the Φ_{PSII} of all species converged to very similar values, of about 0.7.

Light responses of *P. maritimum* along a dune gradient. Photochemical efficiencies: The F_v/F_m in *P. maritimum* did not vary significantly between the different positions along the dune gradient and was consistent and significantly higher in the summer than in the winter (Table 2; Fig. 4*A*). The Φ_{PSII} changed significantly with the position along the dune gradient (Table 2; Fig. 4*B*), decreasing from the coastal end to the 100 m position and increasing from there until the inland end of the gradient. Although neither season nor the interaction of season × position had significant effects (Table 2), the Φ_{PSII} of *P. maritimum* was clearly higher in the summer than in the winter at the inland end of the gradient (Fig. 4*B*). The q_P coefficient was not influenced by the position or the season (Table 2; Fig. 4*C*). However, changes in the q_N coefficient along the dune gradient differed significantly between the summer and the winter (Table 2; Fig. 4*D*). In the winter, q_N increased consistently from the coastal to the inland end of the gradient, and the opposite trend was observed in the summer. Thus, q_N was higher in the summer than in the winter at the shoreline but lower at the inland positions (Table 2; Fig. 4*D*).

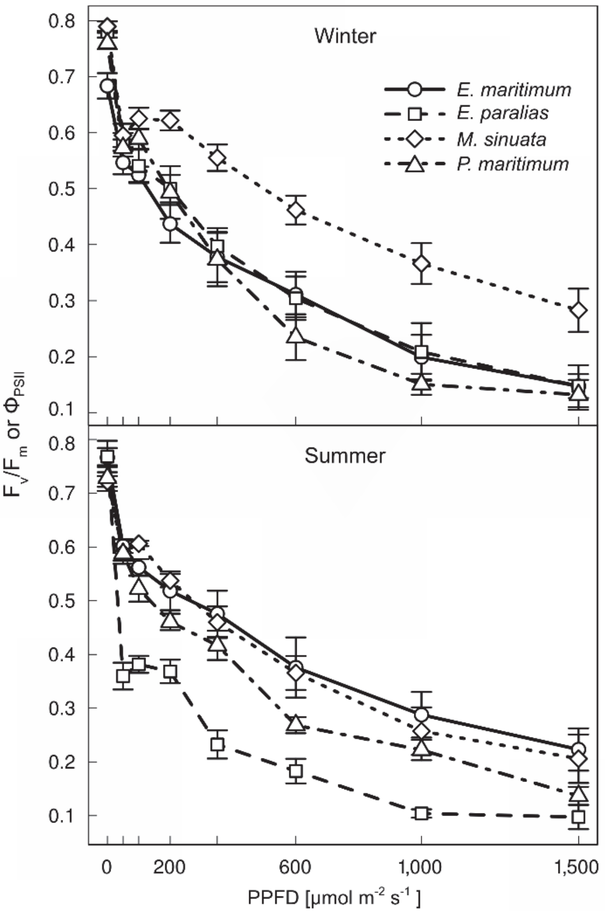

Fig. 2. Light-response curves for winter and summer, constructed with data measured *via* the quantum yield of PSII (F_v/F_m or Φ_{PSII}), as a function of the photosynthetic photon flux density (PPFD), for the species coexisting in the Lariño dune system (*Eryngium maritimum*, *Euphorbia paralias*, *Matthiola sinuata*, and *Pancratium maritimum*). Symbols represent mean values of quantum yield of PSII (± SE, *n* = 5) after 3-min illumination at the corresponding light intensity, except for the first point at 0 µmol(photon) m^{-2} s^{-1}, which was measured after 30 min of dark adaptation.

Light curves and post-illumination recovery: The statistical analyses revealed that the effect of season (*P*=0.0068) and the interactive effect of the position by season (*P*=0.0172) contributed significantly to the model of the responses of *P. maritimum* to light (Fig. 5). For all positions and both seasons, the Φ_{PSII} of *P. maritimum* plants decreased with increasing intensity of PPFDs. In the summer, differences in the light response curves emerged at radiation fluxes higher than 200 µmol(photon) m^{-2} s^{-1}; in *P. maritimum* plants growing in middle positions of the gradient, especially those at 100 m far from the shoreline, the quantum yields of PSII were lower than in plants growing at both extremes of the gradient. Differences in the light response curves in the winter were only apparent at light intensities equal to or above 50 µmol(photon) m^{-2} s^{-1} (Fig. 5). For the post-illumination recovery curves, the position (*P*=0.0021) was the only factor that significantly contributed to the model. Differences in the recovery curves (Fig. 6) were only perceptible in the winter after 5 min of dark adaptation: at this time, the F_v/F_m of *P. maritimum* plants growing at the shoreline was lower than that of plants growing at the other positions. However, by the end of the recovery period, the F_v/F_m of all *P. maritimum* plants, irrespective of their position along the gradients, was very similar.

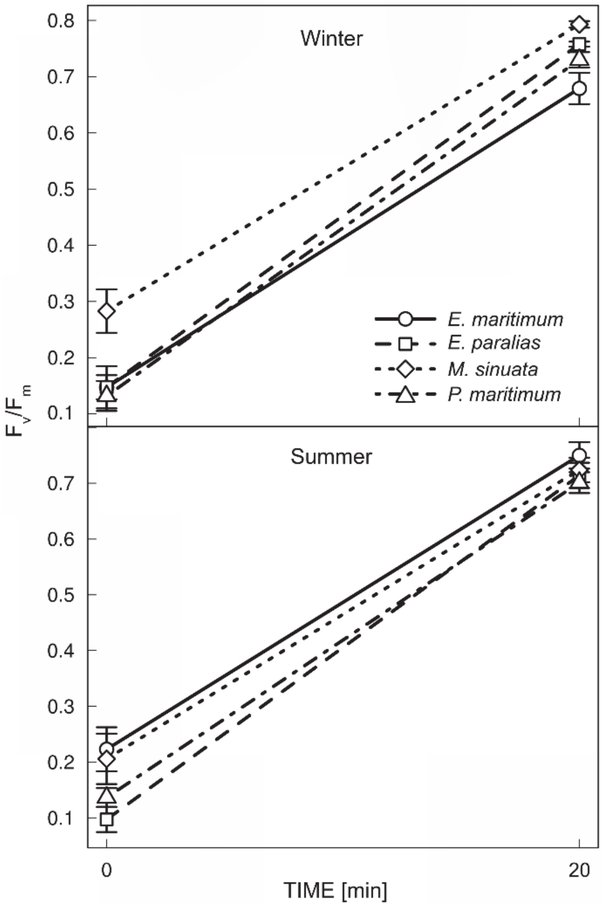

Fig. 3. Quantum yield of PSII (F_v/F_m), in winter and summer, as a function of dark recovery over time, for the species coexisting in the Lariño dune system (*Eryngium maritimum*, *Euphorbia paralias*, *Matthiola sinuata*, and *Pancratium maritimum*). Symbols represent mean values of quantum yield of PSII (± SE, *n* = 5) measured after 20 min of dark adaptation.

Table 2. Results of the two-way *ANOVA*, with species and position as fixed factors, for the comparison of the chlorophyll fluorescence parameters in *Pancratium maritimum* plants growing at four positions along the shoreline-inland gradient in the Nerga dune system. F_v/F_m – maximum and Φ_{PSII} – effective quantum yield of PSII; and q_P – photochemical and q_N – nonphotochemical quenching of chlorophyll fluorescence. Significant differences ($P \leq 0.05$) are marked *in bold*.

		F_v/F_m			Φ_{PSII}			q_P			q_N		
	df	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*	SS	*F*	*P*
Position	3	0.0024	0.56	0.641	0.037	3.50	**0.027**	0.080	0.50	0.687	0.009	2.03	0.130
Season	1	0.0124	8.59	**0.006**	0.004	1.26	0.270	0.130	2.44	0.128	0.005	3.41	0.074
Position × season	3	0.0015	0.35	0.784	0.018	1.70	0.187	0.315	1.96	0.140	0.026	5.67	**0.003**
Residuals	32	0.0452			0.112			1.715			0.048		

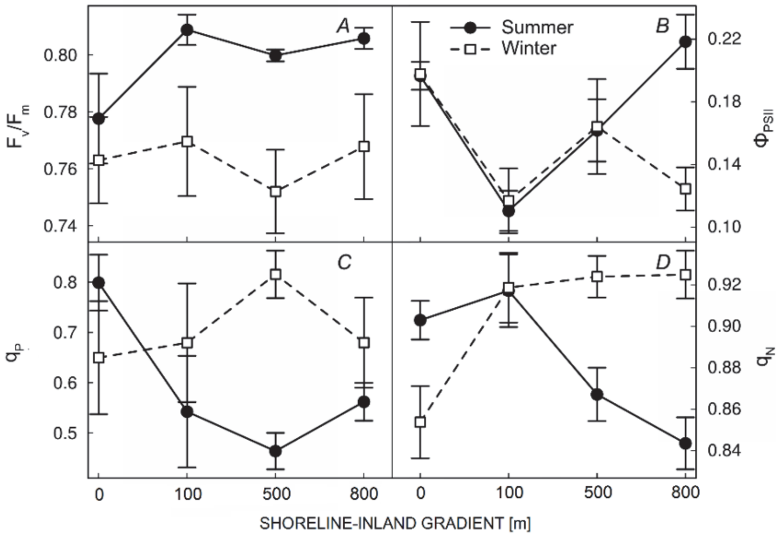

Fig. 4. Seasonal mean values (± SE, *n* = 5) for the chlorophyll fluorescence parameters: (*A*) maximum (F_v/F_m) and (*B*) effective (Φ_{PSII}) quantum yield of PSII; and photochemical (q_P) (*C*) and nonphotochemical (q_N) (*D*) quenching of chlorophyll fluorescence, for *Pancratium maritimum* plants growing at four positions (0, 100, 500, and 800 m) along a shoreline-inland gradient in the Nerga dune system.

Discussion

Light responses and post-illumination recovery in co-existing species: The four species studied, which coexist in a homogeneous area of the dune system, showed different light use strategies but quite similar patterns of post-illumination recovery. For most of the functional traits studied, species differences varied with the season. In *M. sinuata*, the seasonal values for the F_v/F_m differed markedly, although this parameter has been reported to be less seasonally variable than other fluorescence parameters (Adams III and Demmig-Adams 2004). In this species, the winter values of this parameter, which represents the maximum efficiency at which light absorbed by PSII pigments is converted to chemical energy (Butler 1978, Baker and Rosenqvist 2004), were the highest and the summer values were the lowest among all species. Considering that higher reductions in F_v/F_m below values remarkably consistent for nonstressed leaves, *i.e. ca.* 0.80, are symptomatic of stress-dependent photoinhibition (Björkman and Demmig 1987), the results of this study strongly suggested that *M. sinuata* is more susceptible than *E. maritimum* and *E. paralias* to photoinhibition induced by summer stress conditions, but it is more tolerant than all other species to winter conditions that could cause photoinhibition. The values of Φ_{PSII}, a measure of the proportion of light absorbed by Chl that is used in PSII photochemistry in light-acclimated plants (Genty *et al.* 1989), indicated that in the winter, the radiation use efficiency is the highest in *M. sinuata*. This result is consistent with the low q_N values measured in *M. sinuata* in the winter. The q_N values reflect the extent of activation of the PSII complexes that lead to the thermal dissipation of the excess excitation energy (Roháček *et al.* 2008), which occurs in light-acclimated plants when their capacity for photochemical energy conversion is limited (Genty *et al.* 1989, Grant *et al.* 2010). The dense pubescence of *M. sinuata* may provide protection against light stress (Ripley *et al.* 1999, Liakopoulos *et al.* 2006, Skelton *et al.* 2012) and may therefore explain why *M. sinuata* was capable of maintaining a high Φ_{PSII} in the winter. These results were consistent with the light response curves, which revealed that *M. sinuata* differs from the other species and is generally the most efficient in the use of light in the winter over the range of PPFDs of examined. Results from the post-illumination recovery

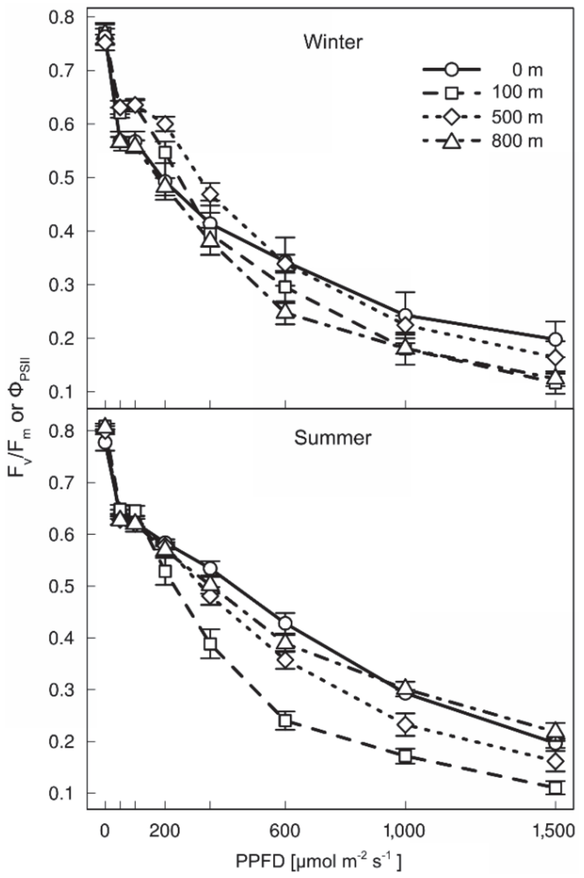

Fig. 5. Light-response curves in winter and summer measured *via* the quantum yield of PSII (F_v/F_m or Φ_{PSII}), as a function of the photosynthetic photon flux density (PPFD), for *Pancratium maritimum* plants growing at four positions (0, 100, 500, and 800 m) along a shoreline-inland gradient in the Nerga dune system. Symbols represent mean values of quantum yield of PSII (± SE, $n = 5$) after 3-min illumination at the corresponding light intensity, except for the first point at 0 µmol(photon) m^{-2} s^{-1}, which was measured after 30 min of dark adaptation.

suggest that species did not differ in their susceptibility to photoinhibition, because the F_v/F_m after 20 min of dark acclimation, increased in all species to the values representative of dark-adapted, healthy, nonstressed leaves. All species recovered at similar rates, as shown by their similar slopes in the recovery lines. Under natural conditions, dune plants may experience longer periods of exposure to higher PPFDs than those used in this study, and therefore we could not rule out the existence of species differences as regards susceptibility to photoinhibition.

The strategy used by *E. maritimum* was quite different from that used by *M. sinuata*. Similarly as *M. sinuata*, the seasonal values of the F_v/F_m and q_N were very different in *E. maritimum*. However, unlike *M. sinuata*, *E. maritimum* seemed to use better (than all the other species) the amount light in the summer. In this period, *E. maritimum* exhibited the highest Φ_{PSII} of all species, and the second highest values of the F_v/F_m. It is also the only species in which Φ_{PSII} was higher in the summer than in the winter. These results are consistent with the summer q_N values in *E. maritimum*, which were the lowest among all the species, suggesting that in this species the nonphotochemical processes dissipating the excessive energy as heat were less active than in the other species, because of its greater Φ_{PSII}. The present findings are consistent with those of Andersone *et al*. (2011), who reported summer F_v/F_m values for *E. maritimum* in the range of 0.77–0.83. Light curves also confirmed that the relative photochemical performance of *E. maritimum* was higher in the summer, and that its efficiency was the highest over the whole range of PPFDs examined, especially at the highest light intensities, when the different species may differ in their light utilisation capacities. The particular leaf morphology of this species (thick, waxy cuticle, folded leaves) may contribute to minimising the intensity of incident sunlight and

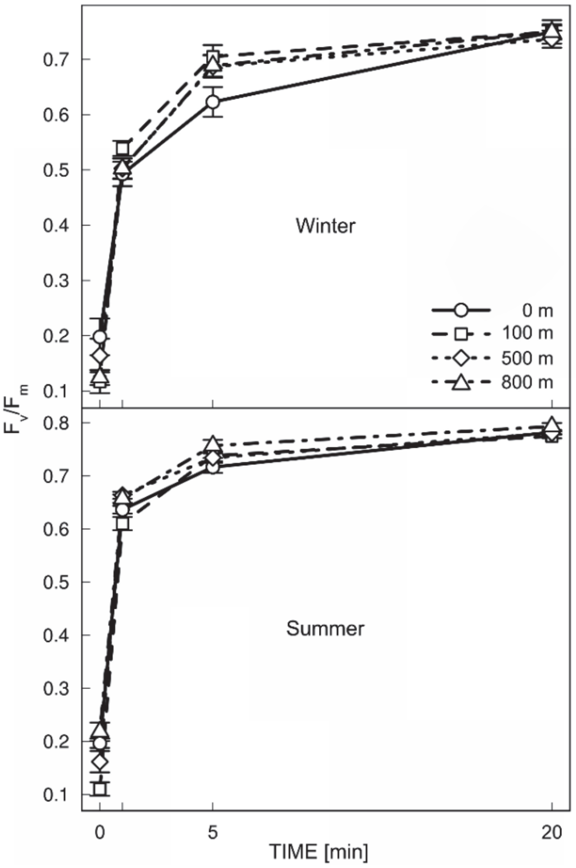

Fig. 6. Quantum yield of PSII (F_v/F_m), in winter and summer, as a function of dark recovery over time, for *Pancratium maritimum* plants growing at four positions (0, 100, 500 and 800 m) along a shoreline-inland gradient in the Nerga dune system. Symbols represent mean values of quantum yield of PSII (± SE, $n = 5$) measured after 1, 5, and 20 min of dark adaptation.

diminishing the amount of excess energy in summer (Pugnaire and Haase 1996, Pugnaire *et al.* 1996, Williams *et al.* 2003).

The strategy of *E. paralias* differs from those described for *M. sinuata* and *E. maritimum*, where the seasonal variations in various aspects of the PSII photochemistry differed. The photochemical performance of *E. paralias* was similar in the summer and winter. Closely related values of all four parameters (F_v/F_m, Φ_{PSII}, q_P, q_N) in both seasons indicated that this species is capable of maintaining a stable photochemistry, irrespective of the environmental conditions. However, light-acclimatised plants of this species showed low and quite low light use efficiency in the summer and in the winter, respectively, as it was expressed by the lowest Φ_{PSII}. The highest summer q_N values registered in this species suggested that heat dissipative processes are indeed very important for maintaining a stable photochemistry in *E. paralias* plants in environments where light energy absorption exceeds the capacity for light utilisation in photosynthesis. This interpretation conforms with the low PSII photochemical efficiencies recorded. The light response curves also confirmed that in this species the light use efficiency was very low over the PPFDs considered. This was particularly obvious in the light response curves recorded in the summer, when *E. paralias* showed the lowest PSII efficiency of all the species. Differences were apparent even at low light intensity.

We found that *P. maritimum* adopts a strategy somewhat similar to that described for *E. paralias*. Both species maintained similar seasonal values for the F_v/F_m and the Φ_{PSII}. However, the winter performance of *P. maritimum* in terms of F_v/F_m appeared to be slightly poorer than that of *E. paralias*. The highest winter q_N values recorded in *P. maritimum* denoted the high activity of nonphotochemical processes dissipating the excess of excitation energy as heat in this species, which was consistent with the low PSII efficiency in the light-acclimated plants. These results were consistent with the information provided by light curves; it showed the low winter efficiency of the PSII photochemistry in *P. maritimum* plants at light intensities higher than 350 μmol(photon) m^{-2} s^{-1}.

We acknowledge that these results may somewhat underestimate photochemical efficiencies in *P. maritimum*. In plants, such as *P. maritimum*, with thick leaves and multiple layers of overlapping cells, Chl fluorescence techniques may only characterize the chloroplasts of the upper, external, palisade parenchyma cell layers and it may thus underestimate the global efficiency of the whole leaf (Lichtenthaler and Burkart 1999).

Light responses and post-illumination recovery of *P. maritimum* along a dune gradient: As expected, we found that some functional traits related to light processing efficiency through PSII varied significantly in *P. maritimum* plants located along a shoreline-inland dune gradient. However, unexpectedly, other functional traits did not vary as predicted or did not vary at all. Community assembly studies suggest that in harsh environments, abiotic factors may function as environmental filters that constrain the range of plant physiological responses (Paruelo *et al.* 1998, Meinzer 2003, Bucci *et al.* 2004, Bermúdez and Retuerto 2013). On the basis of these results, we expected that the greater severity of stressors at the shoreline end of the dune gradient might constrain the capacity of light-saturated photosynthesis in plants and thus induce photoinhibitory PSII damage due to an increase in excitation energy. Nevertheless, the high F_v/F_m values measured along the whole dune gradient suggest that there was no irreversible damage to PSII in *P. maritimum* at any of the positions along the gradient. On the other hand, in light-acclimated plants, the Φ_{PSII} varied significantly along the dune gradient. Although we expected the lowest PSII values in plants growing at the shoreline, the lowest efficiencies were actually observed in *P. maritimum* plants growing 100 m from the shoreline. In a previous study, where we examined changes in physicochemical soil variables along a dune gradient, the lowest amounts of soil nitrogen and phosphorus and the highest soil salinity were recorded at a certain distance from the shoreline (unpublished). It is possible that airborne salt deposits (McLachlan and Brown 2006) might be larger immediately behind the foredune as a result of the wind turbulence caused by the dune ridge, and that this can affect adversely plant performance. These findings suggest that for some species, such as *P. maritimum*, stressful environmental conditions, which limit the plant capacity to process radiation energy efficiently, may not occur only at the shoreline end of the gradient. In this study, in both seasons, the highest values of q_N were recorded in *P. maritimum* plants located at 100 m from the shoreline, although in the winter, the q_N values were similar at three positions further inland. Since the nonphotochemical quenching is considered an indicator of the light stress severity, specifically, of the excessive absorbed light (Buschmann 1999), these findings suggest that at a distance of 100 m from the coast, stress factors may restrict the capacity of photosynthetic apparatus of *P. maritimum* plants to use the total amount of absorbed light energy for photochemistry. Under such conditions, nonphotochemical quenching is induced to dissipate the excess excitation energy by thermal processes, preventing overreduction of the electron transfer chain and, therefore, providing protection from light-induced damage (Buschmann 1999). Further results from this study reinforced the interpretation of severer environmental conditions at a certain distance from the shoreline. The light response curves constructed with data recorded in the summer revealed a more pronounced decline in PSII efficiency with increasing PPFD in *P. maritimum* plants growing at a distance of 100 m from the shoreline. However, dark-recovery curves constructed with data recorded in the winter revealed a slower recovery of the quantum yield of PSII (F_v/F_m) in *P. maritimum* plants growing at the shoreline. Nevertheless, at the end of the dark-recovery period, very similar F_v/F_m values were reached in all *P. maritimum* plants, irrespective of their position along the gradient. The values represented a high quantum yield of PSII, (F_v/F_m) indicating that the plants did not exhibit different susceptibility to irreversible light-induced damage of PSII reaction centres. An alternative, plausible explanation of the differences observed in PSII efficiencies of *P. maritimum* is that local adaptation processes may have originated in ecotype specially adapted to the local conditions of the shoreline, with improved efficiencies compensating the severer conditions at this extreme of the dune gradient. Previous studies support this interpretation. Crawford (1989) reported the occurrence of different ecotypes of *Plantago maritima* along the 80 m transect of cliff top vegetation, and Hodson *et al.* (1982) described a salt-tolerant coastal ecotype and a salt-susceptible inland ecotype of *Agrostis stolonifera*. Differences in photochemical efficiencies have also been explained by variations in interactions with mycorrhizal fungi (Ruiz-Sánchez *et al.* 2010), which are common in coastal dunes (Camprubi *et al.* 2011). At the coastal end of the dune gradient, the fungal colonisation could be inhibited by soil salinity (Mohammad*et al.* 2003, Cakan and Karatas 2006, Camprubi *et al.* 2010).

In conclusion, this study demonstrated that the coexisting species under study, growing in a homogeneous area of a harsh dune system, clearly diverged in various aspects of their photochemistry, indicating different strategies related to the light processing efficiency through photosystems. In relation to the different light use strategies, *M. sinuata* can be described as a winter specialist and *E. maritimum* as a summer specialist. *E. paralias* and *P. maritimum* could be considered to be more generalist species, since both were capable of maintaining similar photochemical efficiency during both seasons, although *E. paralias* displayed more efficient light use in the winter and *P. maritimum* in the summer. Although these differences conformed to our expectations based on the observed differences in leaf morphology and life forms of the species studied, they contrasted with the predictions often made in community assembly studies that in harsh environments, such as dune systems, stress factors may act as environmental filters that constrain the range of possible functional designs. The seasonal differences in the functional traits of the species showed that the relative performance of species in terms of photochemical efficiencies varied over time. When environmental conditions vary temporally and the relative performances of species also change, environmental variation may allow species to coexist where otherwise (*i.e.* under constant conditions) one species would exclude the other. Although many studies have reported that dune gradients are directional (*see* references above), with the intensity of stressors increasing or decreasing consistently along the dune gradients, this study indicated that changes along the dune gradient in the efficiency of PSII photochemistry and heat dissipation in *P. maritimum* were not consistent with the assumed, directional changes in the severity of the stressors. The study also demonstrated that some of these changes were seasonally dependent. From all this, we concluded that the combination of environmental factors that influence plant performance, which vary spatially and temporally, might determine unpredictable patterns of variation along the dune gradient in leaf traits related to the functioning of various aspects of PSII photochemistry. Finally, we found that, despite the large variation in leaf functional traits related to photochemical capacity and to the extent of dissipative mechanisms of excitation energy excess, the plants followed very similar patterns of post-illumination recovery, irrespective of the species, the season, the set of environmental conditions studied or whether different species were growing in a homogeneous area or a single species was growing along a dune gradient. This suggests that evolutionary pressures may be acting to maintain very similar recovery mechanisms.

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