

Plasticity of a dune plant *Alyssum gmelinii* in response to sand burial in natural conditions

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Abstract

Sand burial is one of the environmental factors affecting plant distribution on coastal dunes. The aim of the present study was to investigate putative morphological and physiological adaptations to sand burial in *Alyssum gmelinii* plants growing in natural conditions on coastal dunes. Morphological characteristics, photochemistry of photosynthesis and mycorrhizal symbiosis of plants growing on both grey dunes and white dunes with or without recent impact of burial by sand were analyzed. Burial conditions strongly affected the morphology of *A. gmelinii* plants. Plants on fixed dunes with no burial had a shrub-like appearance with lignified main stems. After burial by sand, new branches formed from vegetative buds located at nodes of a buried shoot and intensively elongated above sand surface. At the beginning of the next vegetation season new branches were formed from buds just above the soil surface. In relatively stable sand-level conditions buried stems formed well-rooted ramet-like underground structures. Burial did not affect intensity of mycorrhizal colonization in roots of *A. gmelinii*. No significant differences in mycorrhizal colonization parameters in plants between white and grey dunes were found except for a different trend of intensity of mycorrhizal symbiosis in July and September. Leaf chlorophyll content, potential quantum efficiency of photosystem II and apparent electron transfer rate of photosystem II was not affected by dune type and burial. Non-photochemical quenching was significantly affected by plant location (white or grey dunes) as well as by sand burial of plants growing on white dunes. It is concluded that *A. gmelinii* plants exhibit both morphological (induced clonality) and biochemical adaptations (induced thermal energy dissipation) to maintain high performance after sand burial.

Key words: adaptation, adventitious rooting, *Alyssum gmelinii*, mycorrhiza, photosynthesis, plasticity, sand burial, soil.

Introduction

Sand burial is one of the environmental factors suggested to affect plant distribution on coastal foredunes (white dunes; Maun 1994; Dech, Maun 2005). Apart from the direct effect of sand burial on seed germination and seedling establishment leading to changes in reproduction success (Maun, Lapierre 1986), burial by sand of whole plants or their parts affects physiology and, as a consequence, morphology of buried plants. Burial-induced

response in natural conditions of plants native to foredunes more likely has an adaptive significance. Consequently, in conditions of regular sand accretion plants have developed several physiological and morphological features allowing to withstand burial events.

A level of tolerance to sand burial varies significantly among foredune plants (Kent et al. 2001). Species well adapted to conditions of shifting sand exhibit growth activation in conditions of sand burial (Lee, Ignaciuk 1985; Cheplik, Demetri 1999). As a certain level of sand accretion is necessary for optimal growth of these species (Maun 1998), they can be designated as an "obligate-buried species". For these plants, it is necessary to experience regular episodes of sand burial in order to maintain a high level of fitness or vigour (Eldred, Maun 1982).

Ability to maintain high intensity of photosynthesis during sand burial as well as a capacity to restore photosynthetic activity after the burial event are suggested to represent physiological adaptations to shifting sand conditions (Kent et al. 2005). The exact mechanism of photosynthetic maintenance in buried conditions is not known. Low light intensity reaching buried leaves as well as low rate of oxygen diffusion might be the main problems. For obligate-buried species activation of photosynthesis in unburied parts of partially buried plants can be proposed. One of the indications of this process could be an increase of leaf chlorophyll content (Zhang 1996). Few studies so far have investigated the effect of sand burial on photochemistry of photosynthesis in natural conditions (Perumal, Maun 2006).

Mycorrhizal symbiosis is thought to play a certain role in nutrition of coastal dune plants (Rozema et al. 1985). In particular, mycorrhizal structures in buried roots enhance mineral uptake leading to increase in leaf area and biomass (Perumal, Maun 1999). Due to the established differences in the level of mycorrhizal colonization between different plant species, the benefits from the symbiosis could be also variable. Yet, enhanced mycorrhizal symbiosis is among factors of adaptive character facilitating the growth of sand-buried foredune plants (Maun 1998).

Plants on coastal sand dunes are characterized by a high level of morphological and biochemical plasticity manifested as environmental heterogeneity-induced adaptations (Ievinsh 2006). New model species representing different adaptation strategies to conditions of coastal environment should be established. The aim of the present work was to study putative morphological and physiological adaptations to sand burial in *Alyssum gmelinii* plants growing in natural conditions on coastal dunes. Both plants from foredunes (white dunes) and semi-stable dunes (grey dunes) were analyzed.

Materials and methods

Study species

Alyssum gmelinii is a perennial coastal plant growing on both foredunes (white dunes) and semi-fixed grey dunes. Particular plants on white dunes are buried by sand early in the spring before the start of the vegetation season due to dune micro-topography dependent wind-driven local sand accretion. As *A. gmelinii* plants flower relatively early in the vegetation season, buried plants have no opportunity to flower in the same vegetation season.

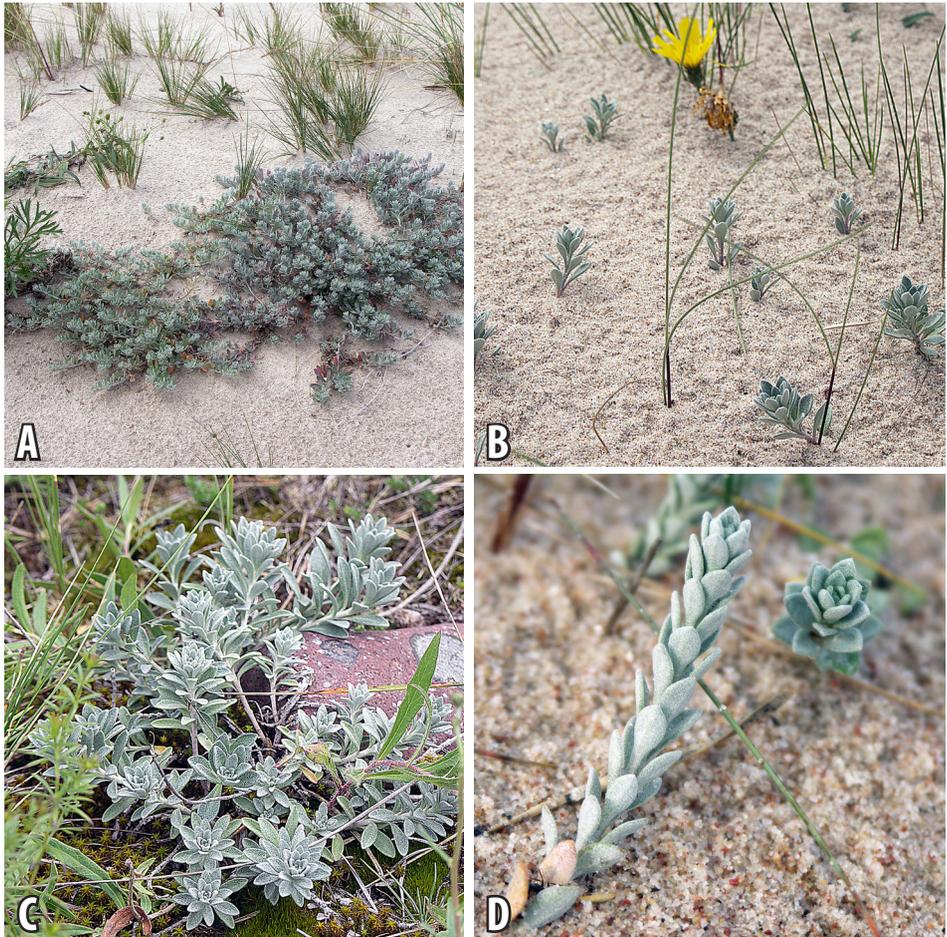


Fig. 1. Typical representatives of *Alyssum gmelinii* plants used in the study. A, unburied plants on white dunes; B, recently buried plants on white dunes; C, unburied plants on grey dunes; D, recently buried "autumn type" plants on white dunes.

Study area and sampling

Plant growing in different habitats at the same site were selected for the study. The site was located near Užava, NW Latvia (57°14' N; 21°25' E). Open sand dunes (foredunes, yellow dunes) were located 50 m from a coast line. The vegetation were periodically affected by wind-driven sand deposition leading to burial of *A. gmelinii* plants. Two types of plants were designated – unburied and recently buried based on observations of plant habit. Typical representative individuals of foredune plants used in the present study are shown in Fig. 1A, B. Fixed dunes (grey dunes) were located 100 m landward. The habitat was protected from wind-driven sand deposition by a group of pine trees (*Pinus sylvestris* L.). A typical representative from grey dunes is shown in Fig. 1C.

Analyses were performed once a month during the vegetation season from May until September. During each month five plants were sampled for leaf chlorophyll content

and chlorophyll *a* fluorescence analysis, and three plants were sampled for analysis of mycorrhizal symbiosis. For chlorophyll and chlorophyll *a* fluorescence analysis, three branches with leaves were picked from every plant. Branches were placed in sealed plastic bags and kept in darkness. Several plants from both habitats with putative different sand-burial history were excavated completely for analysis of morphology.

Measurement of chlorophyll content and chlorophyll a fluorescence

Leaf chlorophyll content was measured by a SPAD-502 chlorophyll meter (Konica-Minolta, Osaka, Japan). For chlorophyll measurement, 10 leaves from a branch were measured. For each leaf, five successive readings were made across the leaf surface. The mean of the analysis was calculated using the internal function of the chlorophyll meter.

Chlorophyll *a* fluorescence measurements were performed within 4 h after sampling. For the analysis, 10 leaves were randomly sampled from each branch.

Chlorophyll *a* fluorescence was measured by a pulse amplitude modulated portable fluorometer (PAM 2100, Walz, Germany) and leaf clip holder (2030-B, Walz, Germany) with integrated micro quantum-temperature sensor. A laptop computer equipped with an appropriate software (DA-2000, Walz, Germany) was used to drive the measurements. Leaves were dark adapted for 30 min. The minimal fluorescence level (F_0) was measured by low modulated light and the maximal fluorescence level (F_M) was determined by a saturating pulse on dark-adapted leaves. The ratio F_V/F_M was calculated, where F_V is the difference between the maximum fluorescence and the minimum fluorescence level F_0 . The steady-state fluorescence (F_S) was recorded after 6 min light adaptation and then the maximal fluorescence level in the light-adapted state (using a saturating pulse, F'_M) and the minimal fluorescence level (using far-red light, F'_0) was measured.

Maximum apparent electron transport rate (ETR) through photosystem II (PSII) was calculated on the basis of measured overall photochemical quantum yield ($\Delta F / F'_M$; where $\Delta F = F'_M - F_S$) and of photosynthetically active radiation (PAR) according to the equation: $ETR = \Delta F / F'_M \times PAR \times 0.5 \times 0.84$; assuming that transport of one electron requires absorption of two quanta (factor 0.5) and that 84 % of the incident quanta are absorbed by the leaf (factor 0.84).

Chlorophyll *a* fluorescence parameter F_V/F_M measured after a dark adaptation period reflects the potential quantum yield of PSII and thus is indicative of photoinhibition (Maxwell, Johnson 2000). The fluorescence induction curve with quenching analysis at 10 ms p^{-1} was recorded using a built-in standard procedure of DA-2000. Non-photochemical quenching (NPQ) was calculated according to the equation: $NPQ = (F_M - F'_M) / F'_M$. The NPQ emphasizes that part of non-photochemical quenching reflecting heat dissipation of excitation energy in the antenna system.

Root sampling and analysis of mycorrhizal colonization

For analysis of mycorrhizal symbiosis, three root samples were taken from a rhizosphere of a selected plant. Samples were placed in sealed plastic bags, transported to the laboratory and kept at 4 °C until fixation not longer than two months.

Mycorrhizal colonization in root samples was analyzed as described previously (Druva-Lūsīte et al. 2008). Mycorrhizal colonization (abundance of hyphae, vesicles and arbuscules) was measured and both intensity of mycorrhizal colonization in the root system (M%) and frequency of mycorrhiza in the root system (F%) were calculated.

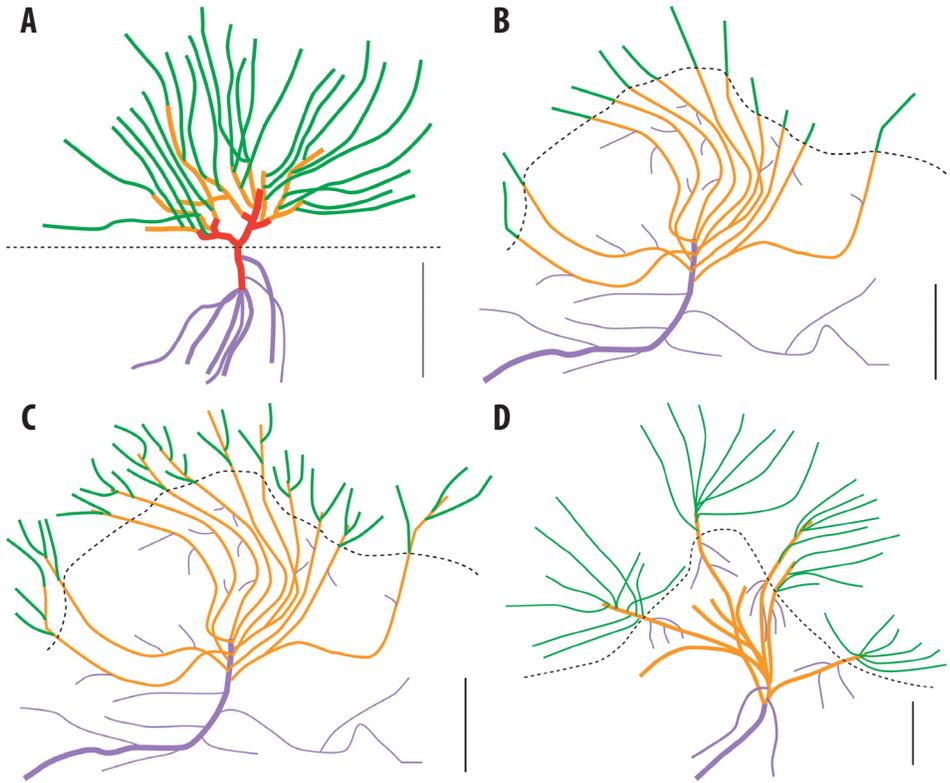


Fig. 2. Morphology of *Alyssum gmelinii* plants as affected by sand burial. A, unburied plants on grey dunes; B, recently buried plants on white dunes; C, plants buried in the past on white dunes. Dotted line indicates level of soil. Bar indicates 50 mm.

Measurement of soil parameters and mineral nutrients

Soil sampling and analysis was performed as described previously (Druva-Lūsīte et al. 2008). Briefly, soil samples were taken from the root zone near *A. gmelinii* plants (0 to 10 cm depth). For each sample five to eight subsamples were collected and thoroughly mixed to form one sample. Soil pH was measured in 1:2.5 soil to 1M KCl solutions. Soil electrical conductivity was determined in a 1:5 soil to deionized water volume ratio with a conductometer. Soil samples were air-dried and sieved and extracted with 1M HCl. The levels of Ca, Mg, Fe, Cu, Zn, and Mn were measured by an atomic absorption spectrophotometer with an acetylene-air flame. The amount of N, P, Mo and B were assayed by colorimetry, and concentration of S by turbidimetry. K and Na was measured by a flame photometer with an air-propane/butane flame. Chloride was determined by AgNO_3 titration.

Results

Burial conditions strongly affected the morphology of *A. gmelinii* plants. Sequential changes of plant habit after the burial event are shown in Fig. 2. Plants on fixed dunes with

no burial in the life history had a shrub-like appearance with lignified main stems (Fig. 2A). Leafy branches were relatively long, with loosely deposited leaves. After burial by sand, new branches were formed from vegetative buds located at nodes of a buried shoot and exhibited intensive elongation above the sand surface (Fig. 2B). At the beginning of the next vegetation season new short branches were formed from buds just above the soil surface (Fig. 2C). Without further burial events in relatively stable sand-level conditions buried stems formed well-rooted ramet-like underground structures with relative independence from the mother plant (Fig. 2D). Burial stimulated abundant adventitious root formation on newly developed underground stems of *A. gmelinii* plants growing on semi-mobile white dunes (Fig. 3).

"Autumn type" plants of *A. gmelinii* appeared only in September, possibly as a result of long-term burial conditions. Morphologically, the "autumn type" plants were characterized by more pubescent leaves that were attached closer to the stem. Consequently, less photosynthetic leaf surface was exposed.

Putative burial events did not affect intensity of mycorrhizal colonization in roots of *A. gmelinii* (data not shown). Also, there were no significant differences in mycorrhizal colonization parameters in plants between white and grey dunes (Fig. 4) except for different trends of intensity of mycorrhizal symbiosis in July (higher in white dunes) and September (lower in white dunes; Fig. 4B). However, a characteristic increase of frequency of mycorrhizal symbiosis was evident during the vegetation season (Fig. 4A).

Leaf chlorophyll content did not exhibit significant changes during a vegetation season (Fig. 5). Also, significant differences in leaf chlorophyll content between white dune / grey dune and buried / unburied white dune plants were not found.

Potential quantum efficiency of PSII (F_v/F_M) in leaves of *A. gmelinii* was not affected by location of plants in white vs. grey dunes nor by burial events (Fig. 6A). However, in May and June a relatively low F_v/F_M indicated the possibility of photoinhibition of photosynthesis. Similarly, there were no differences in relative electron transport rate in PSII throughout a vegetation season (Fig. 6B). In contrast, non-photochemical quenching (NPQ) was significantly affected by plant location (white or grey dunes) as well as by sand



Fig. 3. Formation of adventitious roots on buried stems of recently buried *Alyssum gmelinii* plants on white dunes. A square indicates 5 mm.

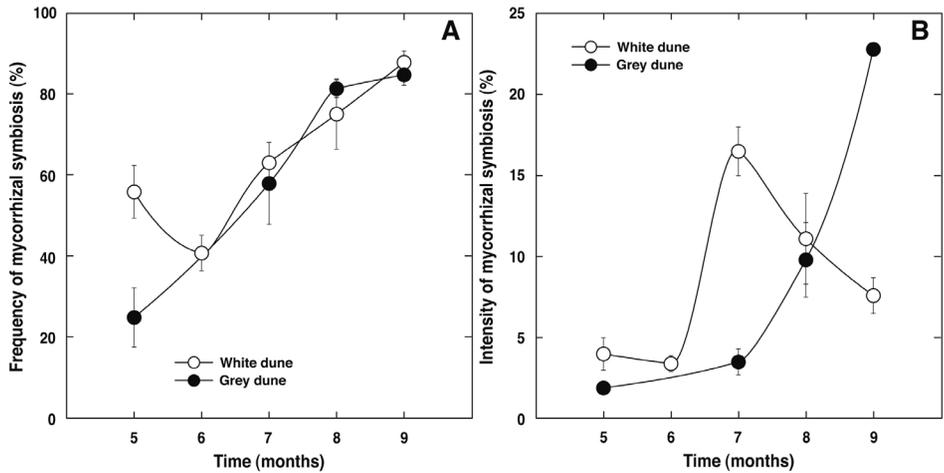


Fig. 4. Seasonal changes of frequency (A) and intensity (B) of mycorrhizal colonization in roots of *Alyssum gmelinii* in different dune types. Data are means \pm SE from three independent measurements for each dune type at every time point.

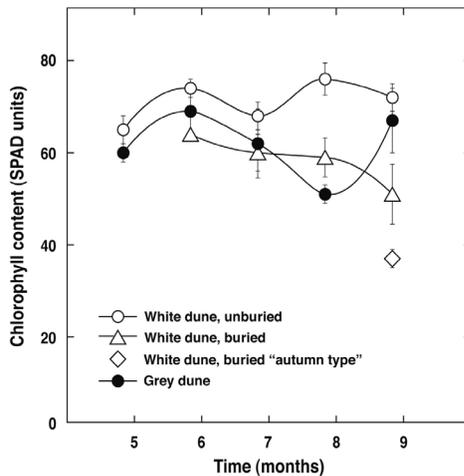


Fig. 5. Seasonal changes of leaf chlorophyll content of *Alyssum gmelinii* in different dune types and sand burial conditions. Data are means \pm SE from 20 independent individual leaf measurements for each dune type or sand burial condition at every time point.

burial of plants growing on white dunes (Fig. 7). Grey dune plants had a higher level of NPQ within a season in comparison to white dune plants. For white dune plants, sand burial resulted in increased NPQ in the first part of the vegetation season (June - July). The "autumn type" plants of *A. gmelinii* had no differences in photochemistry of PSII except higher NPQ (Fig. 7).

Soil macronutrient and micronutrient content was analyzed near *A. gmelinii* plants growing on both white and grey dunes to search for any putative differences in nutrient

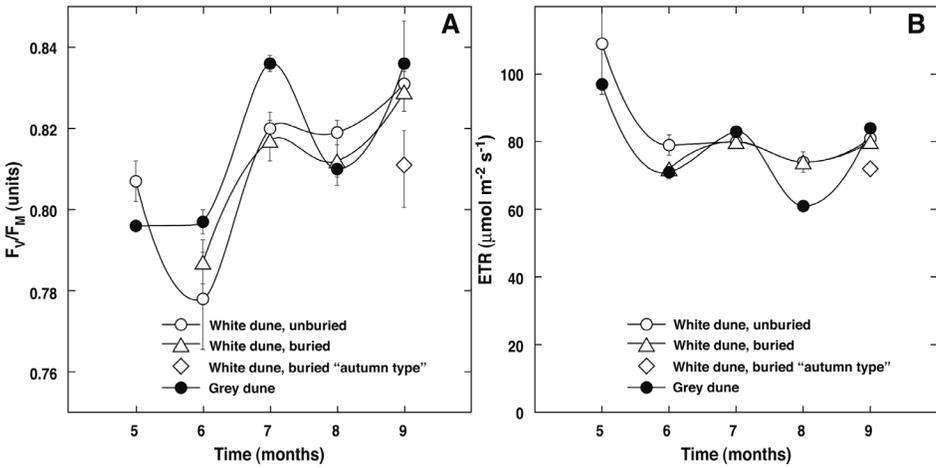


Fig. 6. Seasonal changes of maximum efficiency of PSII (F_v/F_m ; A) and relative electron transport rate in PSII (ETR; B) in leaves of *Alyssum gmelinii* in different dune types and sand burial conditions. Data are means \pm SE from 10 independent measurements for each dune type or sand burial condition at every time point.

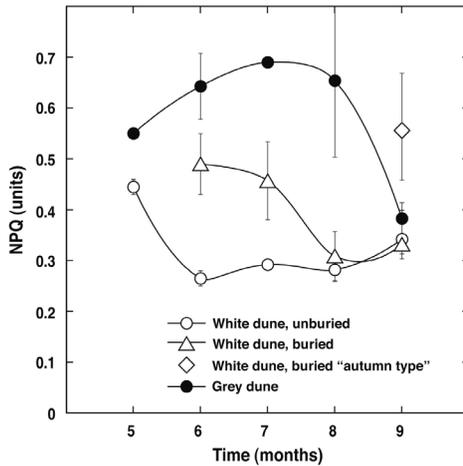


Fig. 7. Seasonal changes of non-photochemical quenching (NPQ) in leaves of *Alyssum gmelinii* in different dune types and sand burial conditions. Data are means \pm SE from 10 independent measurements for each dune type or sand burial condition at every time point.

availability. Both sites were characterized by extremely low N and K concentrations. Most of the nutrients showed similar concentrations between the two sites for most of the nutrients. As an exception, grey dune soil was characterized by significantly higher concentration of K and Zn, lower Ca as well as by more acidic pH (Table 1). Given the relatively low soil electrical conductivity as well as low overall Na, Cl, B and S concentrations at both sites, no direct effect of sea water was evident.

Table 1. General soil properties and concentrations of nutrients and Na and Cl (mg L⁻¹) at two sites (white dunes and grey dunes) with *Alyssum gmelinii*. Data are means from five measurements throughout the season \pm SE. *, significant differences between the sites ($P < 0.01$)

Parameter or nutrient	White dunes	Grey dunes
pH*	8.6 \pm 0.1	7.9 \pm 0.1
Electrical conductivity (dS m ⁻¹)	0.24 \pm 0.05	0.26 \pm 0.03
N	15.8 \pm 2.3	17.7 \pm 2.8
P	234 \pm 58	206 \pm 20
K*	16 \pm 2	27 \pm 5
Ca*	17363 \pm 2194	11267 \pm 2547
Mg	1097 \pm 135	817 \pm 134
S	11 \pm 1	10 \pm 1
Fe	296 \pm 27	250 \pm 20
Mn	44 \pm 3	40 \pm 1
Zn	4.4 \pm 0.4	5.3 \pm 0.2
Cu	0.500 \pm 0.005	0.400 \pm 0.130
Mo	0.030 \pm 0.006	0.020 \pm 0.006
B	0.1	0.1
Na	23 \pm 3	18 \pm 2
Cl	6 \pm 1	9 \pm 3

Discussion

Alyssum gmelinii is an interesting model species in sand burial studies as it occurs both on semi-open mobile white dunes with a relatively high frequency of sand burial as well as on fixed grey dunes. Consequently, *A. gmelinii* plants should possess adaptations for sand burial conditions.

Improved growth characters (vigour) of individual plants after sand burial is a characteristic feature of foredune perennials well-adapted to frequent sand accretion conditions (Maun 1998). Reemergence from the burial deposits represents a phase of mobilization of stored resources for growth in order to reach the surface and to establish a photosynthetic leaf area. After that, increased photosynthetic capacity would be advantageous to quickly replenish energetic and structural resources necessary for further growth and development. *A. gmelinii* plants showed characteristics typical for species well adapted to frequent burial events, e.g. elongation of buried stems, abundant formation of adventitious roots on buried stems as well as high intensity of photosystem II photochemistry.

"Obligate-buried" species from foredunes usually have low vigour when growing in conditions without sand burial (Eldred, Maun 1982). Surprisingly, *A. gmelinii* plants also grew well in conditions of grey dunes with no burial events. These plants showed the same maximal potential photochemical efficiency of photosynthesis (F_v/F_M) as plants on white dunes (Fig. 6A) indicating that no environmental changes-related photoinhibition of photosynthesis occurred in either site. However, a certain degree of possible photoinhibition was indicative for all plants earlier in the season (May - June).

No single mechanism of growth stimulation by sand burial has been established so far. More likely, burial itself acts as a signal for a buried plant to use stored resources for growth stimulation. In particular, both oxygen deficiency and absence of light should be considered as signals. When the surface has been reached by elongated plant parts, a positive light signal eventually leads to cessation of increased elongation with subsequent leaf formation and growth.

Morphological mechanisms for adaptation to sand burial are relatively completely described. Formation of adventitious buds and activation of dormant meristems on roots and rhizomes is a prerequisite for any form of growth stimulation in buried conditions when already buried plant parts are concerned. Formation of adventitious roots under the control of decreased internal concentration of oxygen and increased ethylene level (Visser et al. 1996) was noted also in the present study (Fig. 3). New roots are usually produced on higher parts of the buried stem providing increased access to oxygen, water and nutrients (Perumal et al. 2006).

In temperate regions, more than 95 % of sand movement on sea coasts occurs during the fall and winter months (Davidson-Arnott, Law 1990). Consequently, sand deposition in habitats with *A. gmelinii* results in burial of overwintering vegetative buds in a dormant state not on actively growing plants. Due to morphological changes after sand burial, leading to formation of relatively independent daughter plants, *A. gmelinii* represent facultatively clonal plants (clonality induced only after sand burial). On grey dunes, *A. gmelinii* grow as a shrub with lignified stems. A number of coastal plants exhibit clonal growth only after burial by sand. Formation of both adventitious roots and buds on submerged rhizomes of *Honckenya peploides* is a prerequisite for ubiquitous clonal growth during the following vegetation season (Gagne, Houle 2002).

However, biochemical mechanisms leading to adaptation to sand burial have not been extensively studied. An ability to recover high photosynthetic activity after emergence from burial is considered to be an important adaptation for survival of plants on mobile dunes (Kent et al. 2005). Maintenance of a high level of photochemical efficiency of PSII in leaves of *A. gmelinii* plants regrown after burial suggests that plants are effectively protected from adverse environmental effects on photosynthesis. Non-photochemical quenching (NPQ) was significantly increased in buried plants on white dunes in comparison to non-buried plants, indirectly suggesting that these plants exhibit better protection against formation of reactive oxygen species. However, grey dune plants exhibited even higher levels of non-photochemical quenching. The latter could be an indication of a certain protection mechanism of photosynthesis in stable substrate level conditions.

Sand burial induced increased non-photochemical quenching of PSII fluorescence (Fig. 7), indicating enhanced loss of absorbed light energy. However, PSII yield parameters did not change accordingly. Consequently, *A. gmelinii* plants after sand burial episode could be better protected against oxygen reactivation by excess absorbed energy by means of thermal energy dissipation through conversion of violoxanthin to antheraxanthin and zeaxanthin (Melis 1999). A similar phenomenon might exist in *A. gmelinii* plants growing on grey dunes. This protection mechanism can explain, at least to a certain extent, high general vigour of buried *A. gmelinii* plants, as there is no need to invest in antioxidative protection. As no photoinhibition of photosynthesis was evident later in the season (indicated by high F_v/F_m), non-buried white dune individuals of *A. gmelinii* might allocate resources towards protection against excessive light-dependent reactive oxygen species.

Increase of mycorrhizal colonization after sand burial is among the factors suggested to lead to enhanced plant vigour (Maun 1998). *Alyssum montanum* has been reported to be a nonmycorrhizal species with no mycorrhizal structures found in roots (Pawlowska et al. 1996). Other species of the genus also have been reported nonmycorrhizal, e.g. *Alyssum szovitsianum* was determined as obligate nonmycorrhizal therophyte on Mediterranean coastal dunes (Cakan, Karatas 2006). In our study, mycorrhizal symbiosis of *A. gmelinii* plants seemed to be not affected by sand burial. However, the results do not support the absence of an adaptive role of mycorrhizal symbiosis for plants growing in sand dunes. As it was argued that the major contribution of mycorrhizal symbiosis after sand burial is related to better exploitation of resources, even a moderate constitutive level of mycorrhizal symbiosis might stabilize general performance of *A. gmelinii* plants, especially after sand burial. Similarly, a coastal marsh plant, *Glaux maritima*, exhibit changes in mycorrhizal symbiosis due to fluctuation in soil salinity indicating an adaptive role of the symbiosis for halophytic species (Druva-Lūsīte et al. 2008).

Soil characteristics between white dune and grey dune sites did not differ significantly except higher K and Zn, lower Ca as well as more acidic pH in grey dune soil. It appears that these differences can not count for the observed differences in morphology and photochemistry of photosynthesis of *A. gmelinii* plants, as the levels of N and K were apparently limiting at both sites.

In conclusion, *A. gmelinii* plants show both morphological (induced clonality) and biochemical plasticity (induced thermal energy dissipation) to maintain high performance after sand burial allowing re-establishment of individuals on white coastal dunes.

Acknowledgements

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