

Desmoschoenus spiralis displacement by *Ammophila arenaria*: the role of drought

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Abstract: The exotic sand-binder *Ammophila arenaria* (marram grass) has displaced the native sedge *Desmoschoenus spiralis* (pingao or pikao) from many of New Zealand's coastal dunes. This study explores the possible role of drought as a mechanism promoting marram invasion and pingao displacement. The response of the two sandbinders to conditions of increasing soil water deficit was compared in a four-week pot trial. Water potential, relative water content and stomatal conductance were measured every 3–4 days on randomly selected individuals from a control and two drought treatments. *Desmoschoenus* exhibited significant signs of water stress within eight days, while *Ammophila* did not show significant signs of stress until day 18. Only 5% of *Desmoschoenus* individuals recovered after four weeks without water, compared with 80% of *Ammophila*. Although pot trials have limited applicability, these results suggest that *Ammophila* is relatively tolerant of desiccation compared with *Desmoschoenus*. This may give *Ammophila* a competitive advantage over *Desmoschoenus* during drought events, potentially resulting in the displacement of the native sedge.

Keywords: *Ammophila arenaria*; blowout; *Desmoschoenus spiralis*; drought; displacement; foredune; marram grass; pingao

Introduction

Until the 1960s extensive transgressive dune systems were characteristic of New Zealand's exposed sandy coasts. The primary colonising species, *Desmoschoenus spiralis* (pingao or pikao), *Austrofestuca littoralis* (sand tussock) and *Spinifex sericeus*, occurred widely (Cockayne, 1911). Associations of these and other specialist dune species were interspersed with areas of wetland, coastal turf, shrubland and large areas of unvegetated sand. Older dunes occur inland of these active dune systems in most regions, evidence of earlier, late-Holocene, phases of dune expansion and subsequent vegetation and stability (Muckersie and Shepard, 1994).

The area of unvegetated and semi-vegetated coastal dunes has declined rapidly since the 1960s, from 129 000 ha in the 1950s to 39 000 ha in the late 1990s (Hilton *et al.*, 2000). Northland, Auckland and the Manawatu regions lost 76%, 68% and 81%, respectively (Hilton *et al.*, 2000), primarily as a result of afforestation by the New Zealand Forest Service and industry (McKelvey, 1999). *Ammophila arenaria* (marram grass) was introduced in the 1870s to stabilise dunes prior to planting and for erosion control. *Ammophila* subsequently became naturalised and

spread throughout New Zealand. It has displaced the indigenous colonisers listed above from many dune systems, but particularly along the west coasts of the North and South Island and southern South Island dune systems (Hilton, *in press*). For example, the Otago region contained 1775ha of coastal dunes in the 1950s and 1039ha in the late 1990s. Most of this dune area is now dominated by *Ammophila*: less than 2 ha of *Desmoschoenus* remains in Otago (Hilton *et al.*, 2000).

There are several possible mechanisms for the displacement of *Desmoschoenus* by *Ammophila*. *Ammophila* has an extensive rhizomatous root system that may give it a competitive advantage over *Desmoschoenus* in terms of accessing water and nutrients (Partridge, 1995). Sand burial is thought to be the principal method of native species displacement at Mason Bay, Stewart Island, at least in the foredune environment (Hilton *et al.*, *in press*). The tussock habit of *Ammophila* creates eddies in the lee of the plant, forming pyramidal shadow dunes (Hesp, 1981). *Desmoschoenus* is less tolerant of burial and darkness, compared with the native sedge (Sykes and Wilson, 1990a; 1990b) and plants located in the lee of the *Ammophila* tussocks may experience lethal rates of sand burial.

Tolerance of drought may also be a displacement mechanism. *Ammophila* is extremely tolerant of high

temperatures and moisture deficits compared to other coastal species, both in the field and in glasshouse conditions (Huiskes, 1979). The deep root system of the exotic grass and the ability of marram to roll its leaves to prevent water loss (Hesp, 1991) contribute to this competitive advantage. In contrast, the water relations of dune species in New Zealand and their tolerance to water deficit are relatively poorly documented. Anecdotal evidence does suggest *D. spiralis* may be susceptible to drought. At Tolaga Bay on the North Island's East Coast, garden populations of the sedge used for weaving by Maori survived for two years until a drought caused serious damage (Herbert and Oliphant, 1991).

Understanding the response of species such as *Desmoschoenus* to drought conditions may therefore contribute significantly towards an understanding of how it has been displaced from New Zealand's dunes. In addition, differences in the tolerance of *Desmoschoenus* and *Ammophila* to drought conditions may have geomorphic implications in terms of the natural development of the coast. Sand-binders such as *Desmoschoenus* and *Spinifex* tend to form relatively low, discontinuous foredunes. Such foredunes may be susceptible to frequent blowout formation, where a saucer-, cup- or trough-shaped depression or hollow is created by wind erosion (Hesp, 1999). If *Ammophila* is considerably more tolerant of drought than *Desmoschoenus*, and this tolerance allows it to develop a greater cover, blowout development under *Ammophila* is likely to decrease. This has significant ecological implications, as the development of blowouts creates distinct habitats for coastal species in the deflation zone and depositional lobe, depending on the stage of blowouts or parabolic dune development.

Understanding how species such as *Desmoschoenus* respond to drought compared to the exotic sand-binder *Ammophila* is of importance for several reasons. The mechanisms by which *Desmoschoenus* has been displaced from coastal dunes need to be understood to provide information to enhance the success of revegetation programmes. The tolerance of sand-binders to environmental stress such as drought is also important in terms of understanding the driving mechanisms of blowout development and the natural development of the coast. This study seeks to determine the relative tolerance of the exotic grass, *Ammophila arenaria* and the native sedge, *Desmoschoenus spiralis*, to artificially imposed drought conditions in a four-week pot trial.

Methods

Preparation

During March 2002, approximately one hundred one-

year-old *Desmoschoenus* individuals grown from locally collected seed were sourced from a nursery in Dunedin. The same number of young *Ammophila* tussocks was collected from the strandline and toe of the foredune at Tomohawk and Aramoana beaches, Otago Peninsula. All plants were potted in size five planting bags in approximately 2.4 kg of a 2:1:1 mixture of horticultural sand, fine bark and peat. The growing medium also contained Osmocote® slow release fertiliser (8–9 months) with an NPK ratio of 16:3.5:10, and 1.2 Mg. The plants were stored in a glasshouse over winter and regularly watered until the growing season commenced. In mid September sixty of each species were selected on the basis of vigour and biomass similarity (within species) and transferred to a controlled temperature glasshouse for a two-week settling period. Plants were watered daily during these two weeks.

Treatments

Twenty *Desmoschoenus* and *Ammophila* plants were randomly selected as a control, twenty for treatment one and twenty for treatment two. The plants in the controls (DsC and AaC) were watered to saturation every day throughout the trial. Those in treatment one (DsW and AaW) were watered to saturation on days 12 and 24 and those in treatment two (DsD and AaD) were given no water throughout the four-week trial.

Leaf water potential, relative water content and stomatal conductivity to water were measured every 3–4 days during the trial at predawn and midday. Leaf material was cut from five randomly selected individuals of each species (from treatment and control populations) for the determination of leaf water potentials and relative water contents. Two neighbouring blades were cut from each plant selected. Blades were sealed in plastic bags between collection and measurement of water potential to minimise water loss.

Plant water potential for five of the blades was measured using a pressure chamber (PMS Instrument Company, Model 1000, Corvallis, Oregon, U.S.A.). The relative water content (RWC) of the remaining five blades from each treatment was estimated using the equation

$$\text{RWC} = 100((f-d)/(s-d))$$

where *f* is the fresh weight of each blade, *s* the saturated weight and *d* the dry weight. Fresh weight was recorded immediately after cutting, saturated weight after saturating the blades to a constant weight in a dark room and dry weight after drying the blades to constant weight in an oven at 108°C.

Measurement of stomatal conductance took place at midday on the same days as water potential and relative water content measurement. The stomatal

conductance of three blades from ten plants, randomly selected, from each treatment and species, were measured using a porometer (AP4 Porometer, Delta-T Devices, Cambridge, United Kingdom). Data from day 18 was excluded from the analysis for *Ammophila* as the equipment was not calibrated correctly.

At the completion of the four-week trial all plants were watered to saturation and returned to a daily regime of watering to saturation. The plants that had received the drought treatment were monitored for another 4 weeks for signs of recovery.

Analysis

Two-way Analysis of Variance (ANOVA) (Minitab 12) was used to identify differences in water potential and RWC between the treatments and species. This analysis was run for each measurement period. Where differences in treatments were identified, one-way ANOVA, using Tukey's pairwise comparisons, was used to determine which treatment(s) were significantly different from the control. Students *t*-tests were used to identify differences in stomatal conductance between the two species and one-way ANOVA for differences between treatments.

Results

Water potential

There were no significant differences between treatments for *Desmoschoenus* or *Ammophila* in either predawn or midday water potential at the commencement of the trial ($P > 0.01$). The midday water potential for both species was lower than their respective predawn water potentials at the commencement of the trial, although this difference was very small in *Ammophila*. *Desmoschoenus* responded to the drought treatments with a reduction in its water potential (Fig. 1a,b). This was first evident in the predawn measurements by day 5 ($P < 0.001$), and water potential was significantly lower in both drought treatments at predawn ($P < 0.001$) and midday ($P < 0.01$) by day 8. In contrast, water potential for the individuals in the two *Ammophila* drought treatments showed very little difference from the control for the first 18 days (Fig. 1c,d). The AaD treatment first showed a significant lowering in water potential on day 22 ($P < 0.01$).

The re-saturation of the DsW treatment on days 12 and 24 resulted in an increase in water potential on

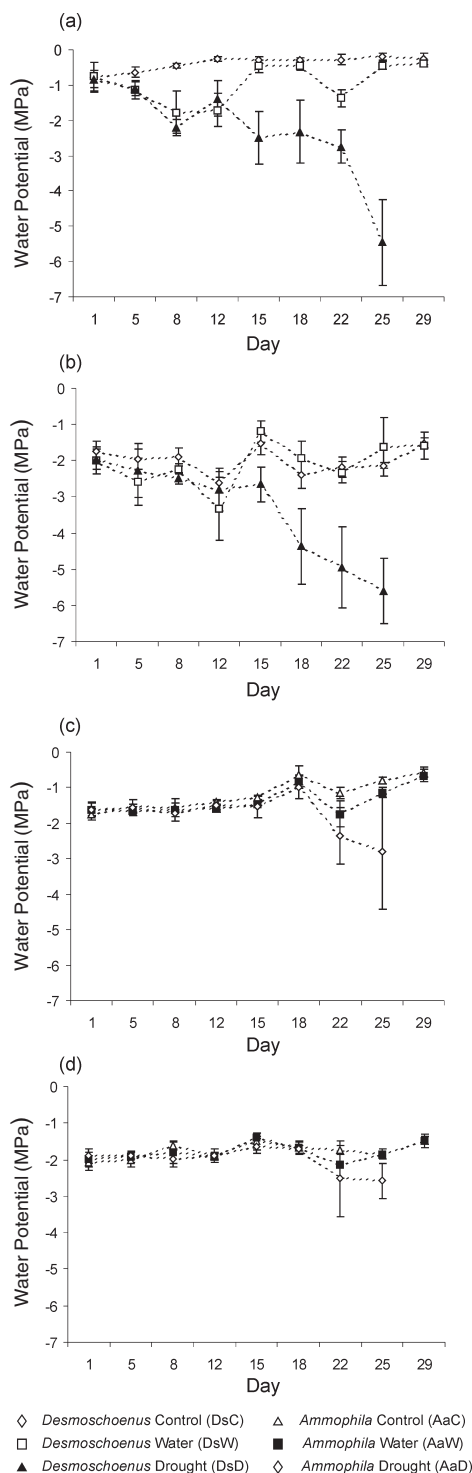


Figure 1. Leaf water potential of *Desmoschoenus* (a) predawn, (b) midday, and *Ammophila* (c) predawn and (d) midday, during a four-week drought trial.

days 15 and 25 (Fig. 1a,b). The re-saturation of the AaW treatment on the same days was not evident in the water potential on day 15, as the plants in the AaW treatment were not under water stress at this stage. However, the increase in water potential for AaW was evident on day 25 (Fig. 1c,d). The predawn and midday water potential of the plants in DsD dropped noticeably after day 15, reaching a maximum potential of -5.46 MPa. The plants were showing signs of severe desiccation by this stage so measurements were stopped for DsD on day 25. Although the plants in the AaD treatment were only just starting to show significantly decreased water potential, these measurements had to be ended at this stage too, due to the effect of frequent destructive sampling. Hence the final water potential readings for AaD were relatively small (-2.8 MPa) compared with DsD (-5.46 MPa).

However, the drought conditions were having a physical impact on the *Ammophila* individuals in the drought treatment by day 25, with no new shoots evident, and considerable curling and discolouration of the blades compared with the control (AaC). Increased curling and discolouration of the blades was first observed around day 15 for *Ammophila*, while *Desmoschoenus* first showed signs of leaf discolouration between days 10–12.

Relative water content

At the commencement of the trials there was no significant difference between the relative water content (RWC) of the three treatments (DsC, DsW and DsD), at either predawn or midday ($P > 0.01$) (Fig. 2a,b). There were no significant differences between the three treatments for *Ammophila* at predawn or midday (Fig. 2c,d). Both species showed lower midday RWC compared with predawn, but this difference was more pronounced in *Desmoschoenus*. Both *Desmoschoenus* and *Ammophila* exhibited a decrease in relative water content (RWC) during the drought trial but, as with water potential, this change occurred sooner in *Desmoschoenus* (Fig. 2a,d). A significant lowering in RWC was evident in the predawn and midday measurements by day 12 for DsW and DsD ($P < 0.01$). There were no significant differences between the control and drought treatments for *Ammophila* until day 25 ($P < 0.001$). The re-saturation of treatments DsW and AaW on days 12 and 24 resulted in an increase in relative water content. The plants in the DsD treatment showed a steady decline in RWC after day 8, whereas the AaD individuals did not exhibit such a pattern until day 22. Predawn RWC for DsD had

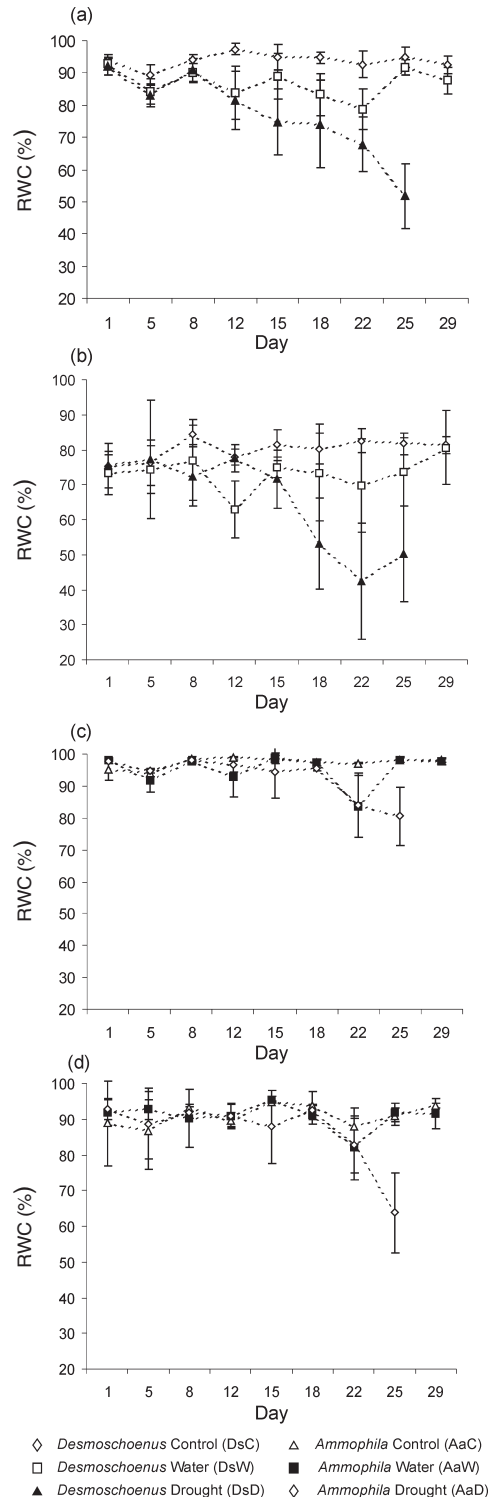


Figure 2. Relative water content (RWC) of *Desmoschoenus* (a) predawn, (b) midday and *Ammophila* (c) predawn and (d) midday, during a four-week drought trial.

decreased by 26% by day 22, and by day 25 had fallen another 18%. In comparison, the RWC for *Ammophila* only decreased by about 18% by day 25. Most of this water loss occurred in the final week, as the decrease in predawn RWC on day 18 for *Ammophila* was only about 2%.

Stomatal conductance

At the commencement of the trials there was no significant difference between the midday stomatal conductance of the three treatments for *Desmoschoenus* or *Ammophila* ($P > 0.01$). There was, however, a noticeable increase in stomatal conductance for both the controls over the course of the trial. Both species responded to the drought conditions by lowering stomatal conductance (Fig. 3a,b). For *Desmoschoenus*, the DsW treatment exhibited a significant drop in conductance after day 5; by day 8 both drought treatments were significantly lower than the control ($P < 0.001$). The drought treatments for *Ammophila* first showed a significant difference from the control on day 8, when the stomatal conductance for AaW treatment was significantly lower ($P < 0.01$). Increases in stomatal conductance were evident in treatments AaW and DsW as a result of re-saturation on days 12 and 24 (Fig. 3a,b).

The decrease in conductance for the DsD treatment occurred mostly within the first two weeks. By day 8 it had dropped just over 60% and on day 12 had decreased by 81%. On day 15 the conductance for DsD was $14.6 \text{ mmol m}^{-2} \text{ s}^{-1}$ and it changed very little for the remainder of the trial (Fig. 3a). The conductance for AaD reached its lowest level on day 15, 63% lower than at the commencement of the trial. However, from day 18 until the end of the trial the stomatal conductance actually increased for AaD, and by day 25 was 44% lower than at the start of the trial (Fig. 3b). The main difference between the two species was in the minimum conductance reached. The mean conductance for the drought treatments for *Ammophila* never dropped much below $100 \text{ mmol m}^{-2} \text{ s}^{-1}$. After only two weeks the mean conductance of the DsD treatment was less than $20 \text{ mmol m}^{-2} \text{ s}^{-1}$, from where it continued to decrease slowly.

Recovery

After the completion of the four-week trial all the plants in the DsD and AaD were watered to saturation and daily thereafter, and monitored for another four weeks for signs of recovery. After 8 days, one *Desmoschoenus* individual of the twenty in the treatment had recovered. Three weeks later, there were still no signs of recovery in the remaining *Desmoschoenus* plants. The *Ammophila* individuals were slow to recover, but at the end of the four-week recovery period, sixteen of the twenty plants had new shoots.

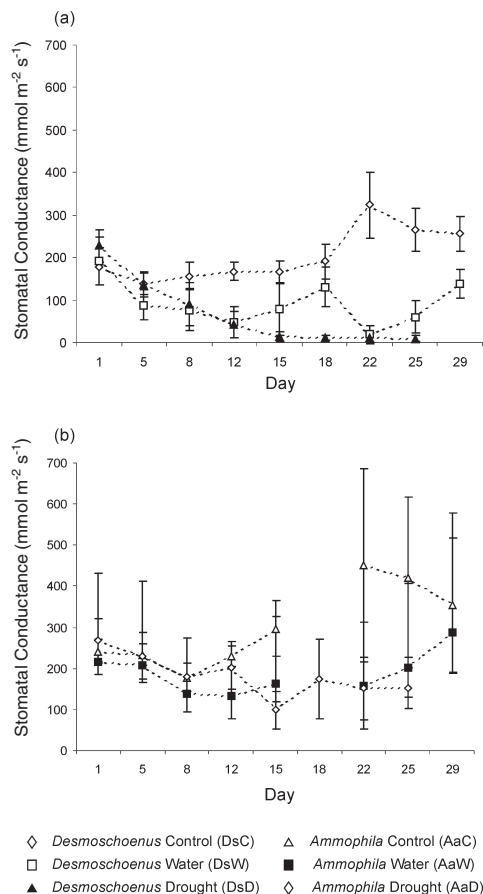


Figure 3. Stomatal conductance at midday for (a) *Desmoschoenus* and (b) *Ammophila* during a four week drought trial.

Discussion

Ammophila individuals in the drought treatments exhibited greater resistance to desiccation than *Desmoschoenus*, with only 5% of *Desmoschoenus* individuals recovering from four weeks without water compared with 80% of *Ammophila* individuals. *Ammophila* plants were also apparently able to maintain 'normal' growth function for longer than *Desmoschoenus*, as the stomatal conductance of *Ammophila* was considerably higher than *Desmoschoenus* throughout the trial. *Desmoschoenus* showed signs of water stress, reflected in significant changes in water potential and stomatal conductance after eight days. *Ammophila* individuals in the drought

treatments maintained levels of water potential and RWC similar to the controls for up to three weeks.

The response of *Ammophila* to soil water deficit in this study is similar to that of the coastal grass *Digitaria adscendens*, where the midday leaf water potential showed no significant decrease throughout a twenty-day drought pot trial (Park, 1990). However, other grasses exhibit signs of water stress more similar to that illustrated by the sedge *Desmoschoenus. Eleusine indica* exhibits a significant decrease in water potential after eleven days in a pot trial (Park, 1990), and the dune grass *Uniola paniculata* (sea oats) showed a significant drop in water potential between day six and nine, with the predawn water potential dropping to nearly -3.5 MPa by day nine (Hester and Mendelsohn, 1989). Thus, while coastal sand-binders are all relatively tolerant of soil water deficit, it would appear that *Ammophila* is particularly so.

The process of leaf rolling may contribute to the ability of *Ammophila* to maintain growth during periods of water stress. Leaf rolling may allow opening of a relatively high number of stomata for photosynthesis without excessive water loss (Hesp, 1991). Photosynthetic rates have shown to be near zero for the coastal grasses *Heteropogon contortus* and *Pennisetum setaceum* once stomatal conductance was below 50 mmol m⁻² s⁻¹ and water potentials were -3.0 and -2.5 MPa respectively (Williams and Black, 1994). A further advantage of having some stomata remain open during dry periods is to reduce heat (as opposed to moisture) stress, as high leaf temperatures may be reached rapidly when transpiration rates are low, even in temperate climates (Bannister, 1976). In a pot trial drought situation it is likely that *Ammophila* has an advantage over *Desmoschoenus* by being able to roll its leaves and keep a relatively high number of stomata open without excessive water loss.

The results of this study should be treated with care, as results from pot trials have limited applicability in field situations. Sand-binding species on dunes often have extensive root systems that allow access to water from deep in the dune profile. Other factors such as competition within and between species and the desiccating influence of sand abrasion and wind are also neglected in our pot trial. Similarly, temperature stress is likely to be greater on sand dunes in summer than in the glasshouse in this study, where shade covers automatically extend once the temperature reaches 25°C. On sand dunes, the reflection of solar radiation off the sand can result in temperatures close to 50°C near the surface, even if the air temperature is only in the high twenties (Hesp, 1991).

However, the results from this study illustrate that *Desmoschoenus* shows signs of water stress sooner than *Ammophila*, and is less likely to recover from desiccation. It could also be argued that in a 'real'

situation, *Ammophila* would have further advantages in terms of resisting desiccation. *Ammophila* forms a dense cover that would shade the sand surface and lower rates of evaporation from the substrate. In contrast, the relatively sparse cover formed by *Desmoschoenus* would have much less of a moderating effect on the temperatures around the plant. Further, *Ammophila* tends to have a deeper root system than *Desmoschoenus*, which spreads more laterally than vertically. This may be of benefit to *Ammophila* during periods of soil water deficit.

Therefore, it seems possible that periods of severe drought could create significant water stress on *Desmoschoenus*, and provide a mechanism whereby *Ammophila* could displace the native sedge from foredunes. It is also important to point out that there are regional differences in *Desmoschoenus* morphology, which raises the question of whether plants from different regions also have different physiological responses to environmental stress such as drought. If so, plants from southern regions may be more susceptible to drought, because they are exposed to these conditions relatively infrequently. Further experimental work needs to be undertaken to explore this possibility.

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