

The comparative seed ecology of marram grass (*Ammophila arenaria*) and pingao (*Desmoschoenus spiralis*)

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Introduction

Burrows (1994) wrote “seeds are beautiful and mysterious objects of great importance” and stated further that only “through careful observation and experiment can we get the seeds to reveal at least some of their secrets”. The uniqueness of New Zealand’s flora and the growing threats to those species by human activities makes an ecological understanding of seeds imperative to the conservation and restoration of our unique habitats.

Marram grass (*Ammophila arenaria*) from Europe has been used as a dune stabilising species in New Zealand for more than 100 years, and has become a primary threat nationwide to the conservation values associated with the indigenous coastal dune landscape. There is little known about the seed ecology of marram grass in New Zealand conditions, or of its native counterpart pingao (*Desmoschoenus spiralis*). Seed dispersal studies of *A. arenaria* and *D. spiralis* have not been undertaken previously, leaving a gap in the ecological understanding of the invader and emergent plant paradigm in the New Zealand coastal dune context.

Objectives of the research

The objectives of this research project (summarised in this article, and more fully documented by Pope, 2005) were to:

- Characterise and understand the differences and similarities in seed ecology between the two species, *A. arenaria* and *D. spiralis*.
- Determine the factors that affect their successful germination.
- Gain an understanding of their dispersal ecology.

Methodologies

Seed from both species was collected during the 2004 and 2005 summer periods for eight weeks from Toko Mouth in South Otago (Figure 1). The selection of the Toko Mouth site for seed collection was made principally because:

- The two species grow and compete adjacent to one another (Figure 2).
- Toko Mouth is the largest natural site of *D. spiralis* available for sampling on the Otago coastline.

The sampling area site was monitored for seasonal changes in sand movement, wind regime, temperature, and rainfall (Figure 3) throughout the study period.

Seeds of both species were germinated in a climate control unit as fresh seed, dried seed (dried at 22°C for 7 days), and stratified seed (stored at 4°C for 42–63 days), and samples were tested for viability using tetrazolium staining (Table 1).



Fig. 1 Location plan of Toko Mouth and weather stations.

Dispersal studies were also undertaken using measured wind speeds and seed distances in testing Phase I dispersal (initial dispersal from the parent plant) and Phase II dispersal (movement from or along a surface). The relative rollability of seeds of both species was tested using a rollability apparatus. This was the first time such an apparatus had been used in seed ecology to test the effects of morphological differences on dispersal behaviour.

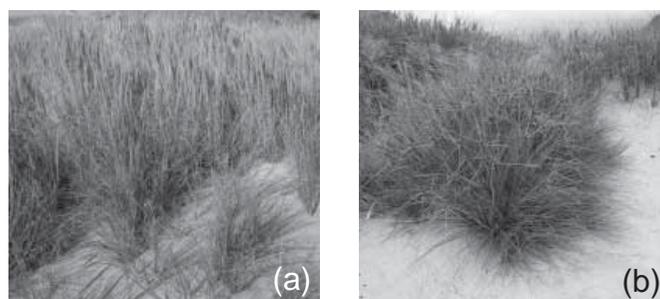


Fig. 2 *Ammophila arenaria* (a) and *Desmoschoenus spiralis* (b) growing at Toko Mouth, South Otago.

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Germination results

Table 1 The comparative results of *A. arenaria* and *D. spiralis* germinability between the two sample years and their associated treatments.

Species	Harvesting season	Fresh seed germination (%)	Dried seed germination (%)	Stratified germination (%)
<i>Ammophila arenaria</i>	Jan–March 2004	40.08%	7.37%	2.91%
<i>Ammophila arenaria</i>	Jan–March 2005	15.90%	7.75%	11.82%
<i>Desmoschoenus spiralis</i>	Jan–March 2004	1.56%	0.25%	0.23%
<i>Desmoschoenus spiralis</i>	Jan–March 2005	11.00%	2.5%	1.77%

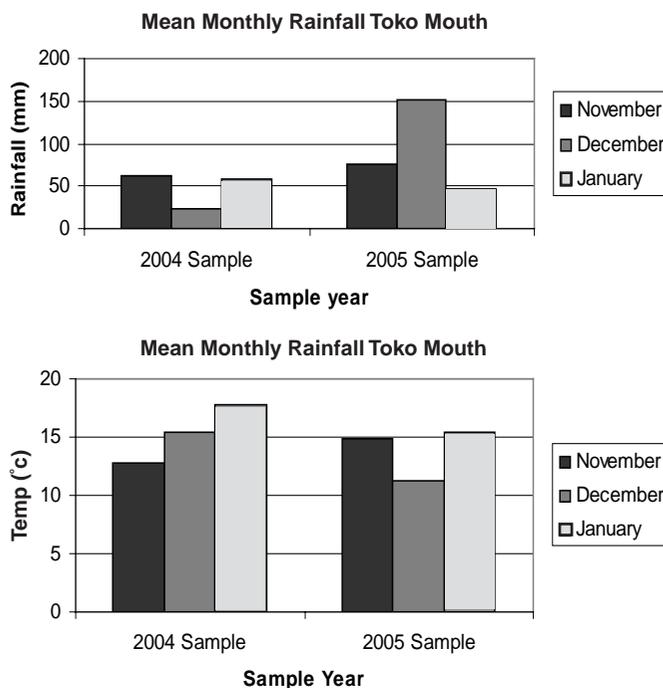


Fig. 3 Comparative differences in the weather patterns (mean monthly rainfall and mean monthly temperature) between the two sample periods.

Fresh seed

- *A. arenaria* produced the most germinable seeds when the early summer months of flowering were hot and dry.
- *D. spiralis* seed production was poor during this period, possibly due to pollination failure and/or a maternal response to drought stress, resulting in an observed accelerated dispersal of unripened seed.
- The hotter temperatures and low wind speeds may have caused pollen malformation and/or desiccation, disrupting pollen mass and dispersal in *D. spiralis*.
- *A. arenaria* seed showed lower germination success in 2005, possibly due to poor pollen dispersal and subsequent pollination failure during periods of heavy precipitation and low wind speed.
- *D. spiralis* seed germinability improved during 2005 possibly due to increased water content and lower temperatures.
- Flowering and pollen production times varied significantly between the two species. The variation in flowering and pollination times

combined with the contrasting weather patterns appear critical to pollination success and seed maturation in both species.

Dried seed

- In both species the heat and drying treatment was inappropriate and counter-productive to germination (compared to fresh seed germination) as a method for breaking physiological dormancy.
- The warmer weather in 2004 was associated with good germination success in fresh

A. arenaria seed, but the artificial drying treatment did not improve its germination (Table 1). This variability is likely to be the weak innate dormancy described by Huiskes (1977).

- The variability in germination may be directly related to the differences in seed weights and condition (Pope, 2005).

Stratified seed

- Stratified *A. arenaria* and *D. spiralis* seeds decreased in their germination success compared with fresh seeds in both years.
- Increases in the rate of germination in stratified seed were only comparable to the changes in the quality of the fresh seed that was harvested between the two sample periods.
- The lower number of viable fresh seeds produced in 2005 coincided with an increase in germination from stratified seeds, suggesting a higher level of expressed dormancy due to conditions that affected seed development.

The belief that *D. spiralis* seed requires stratification to break dormancy appears to be a result of enforced dormancy induced at the onset of autumn and winter. Stratification reduced viability in *D. spiralis* in the tetrazolium testing of seed stored at 4°C for 150–850 days (Pope, 2005). The onset of spring, changes to ground temperature and the accompanying changes to seasonal wind patterns, alters the movement of sand and assists in breaking seed banks open (or burying them further). These factors, accompanied with increases in ground temperature, appear to stimulate germination of seed that has been stored in dune areas, rather than the cold stratification itself.

Results – Phase I seed shadow patterns

Primary distribution patterns (seed shadows) refer to the post-dispersal distribution of seed from the maternal parent, and were measured from the point of dispersal to the initial landing area of the seed (Willson and Traveset, 2000).

- *A. arenaria* had more capacity to disperse a greater distance from the parental point source (78.22% dispersal shadow ≥ 1.0 metres).

- In *D. spiralis*, wind velocity did not markedly make a difference to the distances that the seed travelled (92.50% created a shadow ≤ 1.0 metre and 60.50% of the seed travelled ≤ 0.50 metres).
- Video footage of seed movement showed *A. arenaria* seed dragged its fine outer hairs along the surface. The aerodynamic shape of the seed and the combination of the hairs at the tip of the seed acted as an anchor and dragged the tip of the seed into the prevailing wind (Figure 4).

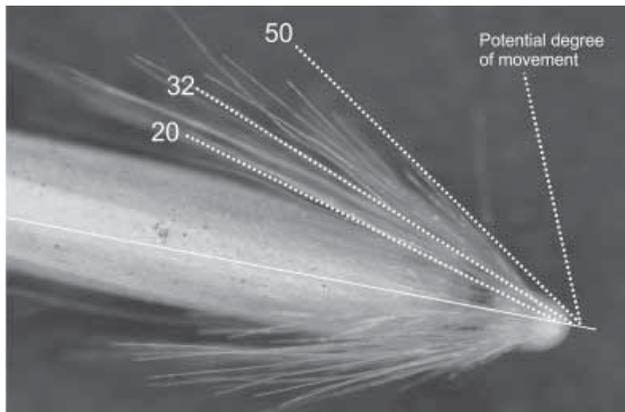


Fig. 4 *A. arenaria* seed and the angles of its outer hairs. The differences in the angles of the hairs affect the anchoring ability of the seed. Movement of the hairs while drying is rapid and spring-like.

Results – Phase II dispersal

Measurement of the dispersal distances along a surface shows that *A. arenaria* is capable of significant movement under high wind velocity after initial dispersal. However, aerodynamic capacity was reduced at high wind speeds. Figure 5 illustrates the seed dispersal model for *A. arenaria*.

- At higher wind speeds of ≥ 4.0 – 5.0 m/s *A. arenaria* seed moved in a rapid downward spiral motion to the ground and along the dune surface.
- At the lowest recorded wind speed of 0.66 m/s *A. arenaria* seeds travelled a maximum distance of 933.60 cm and a minimum of 248.60 cm.
- At the maximum wind speed recorded of 7.10 m/s *A. arenaria* seeds travel an initial 20 metres.

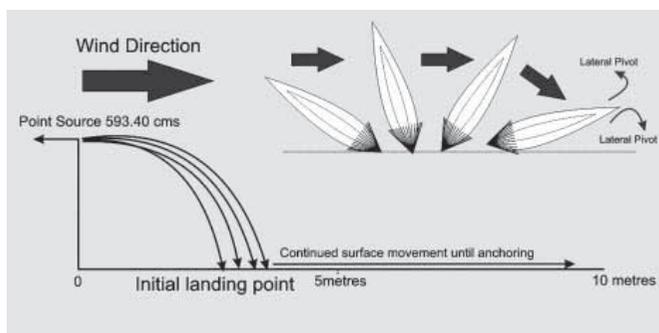


Fig. 5 *Ammophila arenaria* seed dispersal model.

In contrast, *D. spiralis* has none of the aero-dynamism of *A. arenaria* seed, with a smooth outer testa and no external outer hairs. The seed dispersal model for *D. spiralis* is illustrated in Figure 6.

- At high wind speeds (>3.0 m/s) *D. spiralis* relied more on the surface micro-topography to hold itself onto the surface.
- *D. spiralis* has the capacity to be blown 10 metres at wind speeds >5.0 m/s, but this was rare with most seeds moving ≤ 3.0 metres at high wind speeds.
- The shorter distances of the Phase I seed shadows means the opportunities for *D. spiralis* to disperse further from the shelter of the parent are rare. Exceptions would be during significant ground disturbance around the parent plants and extreme wind velocity.

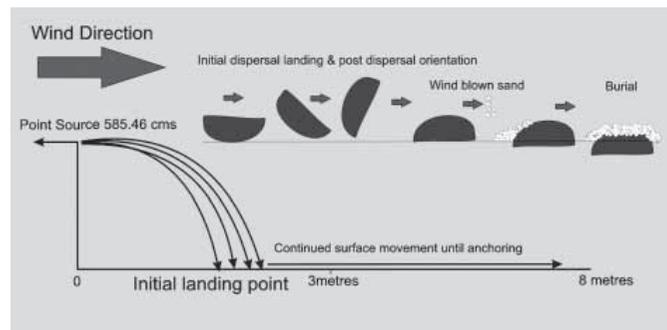


Fig. 6 *Desmoschoenus spiralis* seed dispersal model.

The relative rollability of seed

Relative rollability is normally associated with the measurement of the movement of sand grain particles. Rollability is related to the angle of the slope on which a grain rolls with a uniform motion, at a given velocity on a smooth uniform surface. The rotation of the rollability apparatus (Figure 7) pulls the seed upwards until the slope makes the seeds roll downwards. Thus the time it takes for the seeds to travel down the cylinder is the test of the seeds rollability. Weight, density and shape are important properties that influence the behaviour of particles during transport over a sand dune surface (Winkelmolen, 1971).

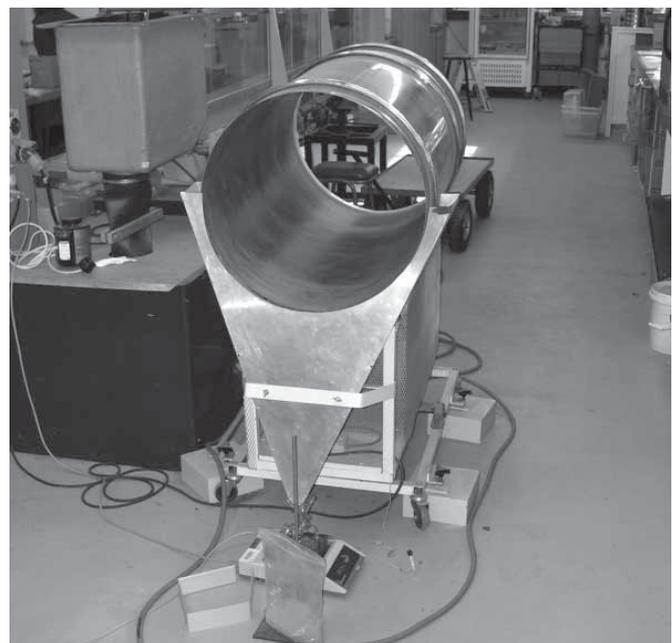


Fig. 7 The relative rollability apparatus, held at the Geography Department, University of Canterbury.

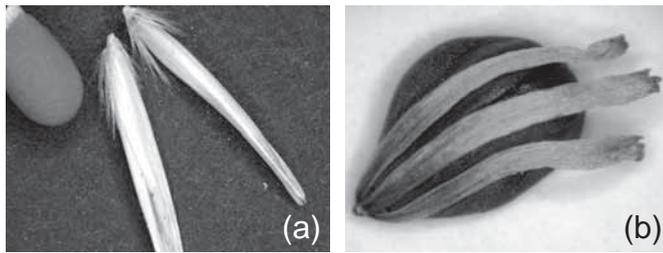


Fig. 8 a–b Comparison of seed shape in *Ammophila arenaria* (a), and *Desmoschoenus spiralis* (b).

The relative rollability of *A. arenaria* and *D. spiralis* seed revealed noticeably different settling times between the two species. The heavier *A. arenaria* seed rotated on the smooth cylinder surface and took a greater time to reach the end of the revolving cylinder than *D. spiralis*.

This is contrary to the assertion that heavier particles would move faster across the revolving cylinder. However, particle shape is a determining factor in relative rollability (Winkelmolen, 1971). This means that the morphological differences between the two seed species is a critical factor in their movement, and the outer hairs of the *A. arenaria* seed increased the time the seed took to travel along the cylinder. Relative rollability helps to confirm that the morphological difference between the species (Figure 8 a–b) alters the way the seeds will move and anchor on a sand surface during dispersal.

Conclusions and ecological consequences

The varied seasonal climate affected both species ability to flower, set seeds, and disperse viable seeds. The reproductive effort of *A. arenaria* in setting viable seeds during dry conditions can be negated by the conditions seeds are dispersed into, where desiccation and burial by dry moving sand is highly likely. In *D. spiralis*, the drier conditions and rapid dispersal of infertile seeds places the plant at risk of not being able to create viable seed banks or disperse seeds for further colonisation.

The investigation into dormancy and the treatment of seeds revealed that stratification may not be a factor in breaking dormancy of *D. spiralis*. The cold storage of seeds in a buried seed bed is a natural phenomenon, rather than a requirement for germination. The advent of disturbance and warmth is probably the critical factor in achieving germination. This has repercussions for plant propagation and those who are actively growing plants for restorative efforts.

Despite the effects of climate, *A. arenaria* still outperformed *D. spiralis* in its ability to produce viable seeds and disperse them successfully to new colonising areas. When coupled with the strong vegetative growth, *A. arenaria* exhibits an invasive advantage of over *D. spiralis*. However, colonisation by seed is risky, involving maximum reproductive effort during seasonal periods that are often the most difficult for seed to find suitable colonising space. The morphological differences between the two species shown in the rollability testing revealed two distinct

methods for reaching and colonising new sites. *D. spiralis* exhibited much lower fecundity in these trials and appears to have a hazardous mechanism for the production of new seedlings after dispersal potentially through autumnal burial into seed banks. Both species exhibited dependence on favourable seasonal climate to successfully produce viable seed for dispersal.

Acknowledgements

My sincere thanks to the Royal New Zealand Institute of Horticulture for awarding me the Peter Skellerup Scholarship in 2004. The award made this research project possible.

I also wish to acknowledge the support and assistance of the staff and students of the University of Canterbury and University of Otago, particularly my supervisors, Dr Janice Lord and Dr Mike Hilton. Thank you to the many people from the Coastal Dune Vegetation Network (CDVN) and the Pingao Recovery Working Group.

Thanks to Trevor Partridge, Murray Dawson and Andrew Maloy for the invaluable editing and review of this article.

Finally, to my wife Lyn for her efforts in counting seeds, organising our home, and her patient support and love.

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This article is based upon Paul Pope's MSc research project. Support for this project was provided by a RNZIH Peter Skellerup Scholarship in 2004. Paul has recently established an environmental consultancy business in Dunedin.