ASPECTS OF THE ECOLOGY OF

DESMOSCHOENUS SPIRALIS (A. Rich.) Hook. f.

A thesis

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Shannel P. Courtney

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ka tipu whakarunga, ka tipu whakararo,
te pingao hei here i te kirikiri

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ABSTRACT

The taxonomy and a general description of *Desmoschoenus spiralis* (pingao) is given.

The distribution of *Desmoschoenus* in New Zealand is mapped and discussed. Although pingao is still widespread throughout New Zealand, only remnant populations now exist in most of their former localities, and their numbers are still declining due to various human activities.

The germination of the seeds of pingao and the dispersal mechanisms of the fruits of pingao are investigated. Of the germination treatments none were successful above 10%. Pericarp scarification was most successful in promoting germination. Seeds were capable of germination after 50 days floatation in seawater. Transport of fruit by sea is put forward as a means of long distance dispersal while wind is responsible for short distance dispersal.

Fieldwork on aspects of the ecology of pingao was undertaken at Kaitorete Spit Scientific Reserve, Canterbury, New Zealand. Descriptions of the physical and climatic features of the Spit, its dune system, and the study area are made.

Seedling studies include monitoring leaf production and mortality of new seedlings, and of older seedlings with respect to browsing.

Selected measurements and counts of plants of pingao of the foredune zone and the reardune-grassland zones were made. These include tuft dispersion, percentage cover, habit type, vegetative and inflorescence measurements and counts, density counts and biomass estimates. Plants of each zone were also monitored for leaf production, leaf dieback, rhizome growth, and new tuft and inflorescence development. Differences between the foredune and reardune-grassland zones were found for most of these results.

By monitoring selected environmental factors of the foredune and reardune-grassland zones, it was found that sand was slowly accumulating around plants of the foredune but not around plants of the other zones. Water is more limiting to reardune-grassland plants than to foredune plants. Plants of the grassland zone on which sand was deposited for a year developed characteristics similar to plants of the foredune zone.

It is concluded that pingao requires a regular influx of sand to sustain vigour and survival by keeping the rooting zone far enough below the sand surface so that new roots are able to grow into moist sand. If sand influx ceases, as pingao plants grow, their rhizome changes its orientation from vertical to horizontal and spreads along the sand surface. New roots grow into the top few centimetres of sand which, due to its very low water content, is limiting to the growth of pingao.

CHAPTER I

INTRODUCTION

Desmoschoenus spiralis, pingao, or golden sand sedge, is the only representative of the genus *Desmoschoenus* and is endemic to New Zealand.

It is found only along the coast, being one of three major sand-binders and dune-builders in New Zealand. The other two are the indigenous *Spinifex hirsutus* found mainly in the North Island, and the introduced *Ammophila arenaria* (marram), a rhizomatous grass which has become the most common plant on sand dunes throughout New Zealand.

Desmoschoenus was once the most ubiquitous plant of New Zealand's dune systems. Today, although large populations still exist in some places, numbers have greatly declined due to the modification or destruction of its habitat. Unfortunately many of the factors which have been responsible for this decline still operate. It is for this reason that *Desmoschoenus* has been included in the Red Data Book of New Zealand (Nature Conservation Council, 1981) and other publications (Given 1981) as a vulnerable species, i.e. a species which is believed likely to become endangered in the near future if the factors responsible for its decline continue to operate.

In determining the status of pingao, the gathering of information regarding its distribution and estimated numbers is necessary. As far as is known, no distribution maps have yet been constructed for pingao, as compilations of localities of pingao in New Zealand are still incomplete. It is hoped that this thesis will add to the knowledge of pingao's distribution, and provide the information necessary to enable a monitor of future changes in distribution.

Despite its endemism to New Zealand, its importance as a sand-binder and its marked decline since European settlement, research on aspects of the biology of *Desmoschoenus spiralis* has been but cursory. This lack of autecological study holds for many of New Zealand's indigenous plants.

Cockayne (1906,1911) was probably the first to describe in any detail aspects of the ecology of pingao in his treatise on dune reclamation and sand stabilization. He noted the suitability of pingao's growth form and structure to the sand dune environment, as well as describing its associations with other dune plants. He elaborated on such information in his later works (Cockayne 1921).

Pegg (1913) studied aspects of pingao's growth form and anatomy and related her results to the xerophytic nature of sand dune plants. As far as is known, no further anatomical work has been attempted.

Esler (1969; 1970 Pro.N.Z.Ecol.Soc., 17: 41-46; 1978) in his investigations of the Manawatu sand country vegetation compares pingao's dune-building ability with the other two builders and relates the differences back to their growth forms. He found that dunes formed by pingao were low and slightly convex in profile, had a smooth topography and a slope of 8-14 degrees. This dune form he attributes to the open tufting of pingao. He also discusses the affects of various environmental factors such as sand movement and water availability on the establishment and survival of pingao, although such discussion is based on evidence gained only by observation rather than by being supplemented with experimentation. His suggestion, that *Desmoschoenus* is more vigorous where it receives regular additions of sand to keep its rhizomes submerged, is tested in this thesis.

Peace (1975) and Holland (1981) have done the most recent research on pingao, Peace with respect to phenology, response to environment, dune zonation and dune succession, and Holland by comparing the sand-binding and dune-building abilities of pingao and marram.

It is hoped to fill some of the gaps in our knowledge of the ecology of pingao in this thesis, especially of distribution, fruit seed and seedling ecology, and the relationship of selected environmental conditions to the degree of vigour, rate of growth and rate of dieback of *Desmoschoenus*.

CHAPTER II

DESCRIPTION AND TAXONOMY

2.1 TAXONOMY

Desmoschoenus is a monotypic genus of the family *Cyperaceae*. It is a member of the tribe *Scirpeae* because the glumes of each of its spikelets are spirally arranged and all its glumes are floriferous and hermaphrodite with the exception of the lowest glume of each spikelet, which is sterile. Although *Desmoschoenus* has no close affinities it is considered to resemble the 'prototype' of *Scirpus* (Koyama, 1958).

It seems that Dr Daniel Solander was the first to describe *Desmoschoenus* from collections made on Cook's first voyage to New Zealand in 1769-1770, (Hooker, 1963). He named it *Scirpus frondosus* but the manuscript was never published.

Achille Richard (1832) was the first to publish a formal description using the specimens collected on Dumont D'Urville's second voyage to New Zealand in 1827. He named it *Isolepis spiralis* and his observations translate, "The species is without contradiction one of the most notable of the genus *Isolepis*. It is so much removed from all the others by its appearance that it can't be compared to any of them as far as I know. But the characteristics of the flowers are evidently the same as the other species in the genus *Isolepis*." *Isolepis* is often since added to the genus *Scirpus* as section *Isolepis*. The difference between sections *Isolepis* and *Desmoschoenus* is that the former has lateral inflorescences which are composed of only one to three spikelets, whereas *Desmoschoenus* has a large compound terminal inflorescence.

Desmoschoenus was also described by Joseph Hooker in his *Flora Novae Zelandia* (1963) subsequent to his Antarctic expedition on the Erebus (1839-1843). He named it *Desmoschoenus spiralis,* considering it to be distinct enough to warrant its placement in a new genus.

A further description was later published by Dr. E. Steudel (1855) who created another new genus and called the plant *Anthophyllum urvillei,* but his description erroneously attributed *Desmoschoenus* with a bifid style and single flowered spikelets.

In 1878, Boeckeler classified *Desmoschoenus* as *Scirpus frondosus* using the name from Solander's earlier manuscripts. He noted that apart from the plants peculiar form it had the typical characteristics of the genus *Scirpus* with regard to its floral biology.

Koyama (1958), in his taxonomic study of the genus *Scirpus s.l.,* placed *S. frondosus* in section *Desmoschoenus* with *S. inanus* on the basis that they were the only species of *Scirpus* whose inflorescences were compound panicles. He considered inflorescence type an indispensible character in determining phylogeny and proposed that the paniculate structure of inflorescences in section *Desmoschoenus* was a primitive characteristic of the genus. He stated that

S. frondosus was primitive in other respects but did not give their nature.

An embryological investigation of the genus *Scirpus s.l.* made by Van der Veken (1965) has contributed much towards making more clear the relationship of *Desmoschoenus* to other species of *Scirpus*. He found that the genus could be divided into six groups depending on embryo type. Section *Desmoschoenus* was placed in the group with a *Cyperus*-type embryo. The embryological features that distinguish this group are the ellipsoid to narrowly turbinate shape of the embryo, the lateral position of the radicle, the basal position of the first leaf, and the fact that the germination slit at the top of the coleoptile runs parrallel to the orientation of the first leaf.

Scirpus frondosus was the only species in his section *Desmoschoenus*. It had characteristic embryological features of an ellipsoid-fusiform shaped embryo, a radicle cap situated well below the middle of the embryo with a well developed cotyledon notch, a relatively short coleoptile with a submedian germination slit, and a clearly differentiated second leaf (Figure 11). The embryo was also one of the largest of the 77 species of *Scirpus s.l.* studied. On the basis of its special embryology and form, Van der Veken suggested that section *Desmoschoenus* be made into a distinct genus.

Desmoschoenus was finally withdrawn from *Scirpus* and put into its own genus as *Desmoschoenus spiralis* (A.Rich.) Hook. f. by Elizabeth Edgar in the *Flora of New Zealand* Vol II, (1976).

The characteristic inflorescence, the scabrid stiff leaves, the much branching woody rhizome, and embryological evidence were given as the main reasons for this treatment.

2.2 DESCRIPTION

2.2.1 General Description

Desmoschoenus spiralis is a stout perennial sedge up to 70 cm tall with an extremely thick, woody, much branching rhizome which is either shortly creeping or vertical in growth. The rhizomes give off numerous tufts of stiff but flexible scabrid linear leaves tightly bound together at their bases by hollow-cylindrical resinous membranous sheaths. The laminae are orange-green in colour, curved, and fan out from the sheaved base, tapering gradually to a sharp trigonous tip. When the leaves decay the persistant fibrous strands of the sheaths clothe the rhizome. New roots grow from the rhizome through the leaf sheaths.

The inflorescence is terminal and borne atop a 30-90 cm long, stiff, flexible, cylindrical to trigonous culm. It is a contracted panicle composed of confluent clusters of sessile spikelets. Spikelets are comprised of 8-17 spirally arranged bracts which subtend spirally imbricate keeled glumes, all floriferous except the lowest one. Flowers are hermaphrodite. Three flattened membranous linear stamens arise separately from the ovary base. From the top of the ovary arises a single style which supports a trifid stigma. The fruit is an obovoid to oblanceolate, concavo-convex nut with a dark, smooth, impervious, shiny pericarp. Refer to Figure 1.

2.2.2 Habit

There are two main habit types apparent. A plant exhibits one or other depending on the environmental conditions, viz. sand deposition. This is discussed in

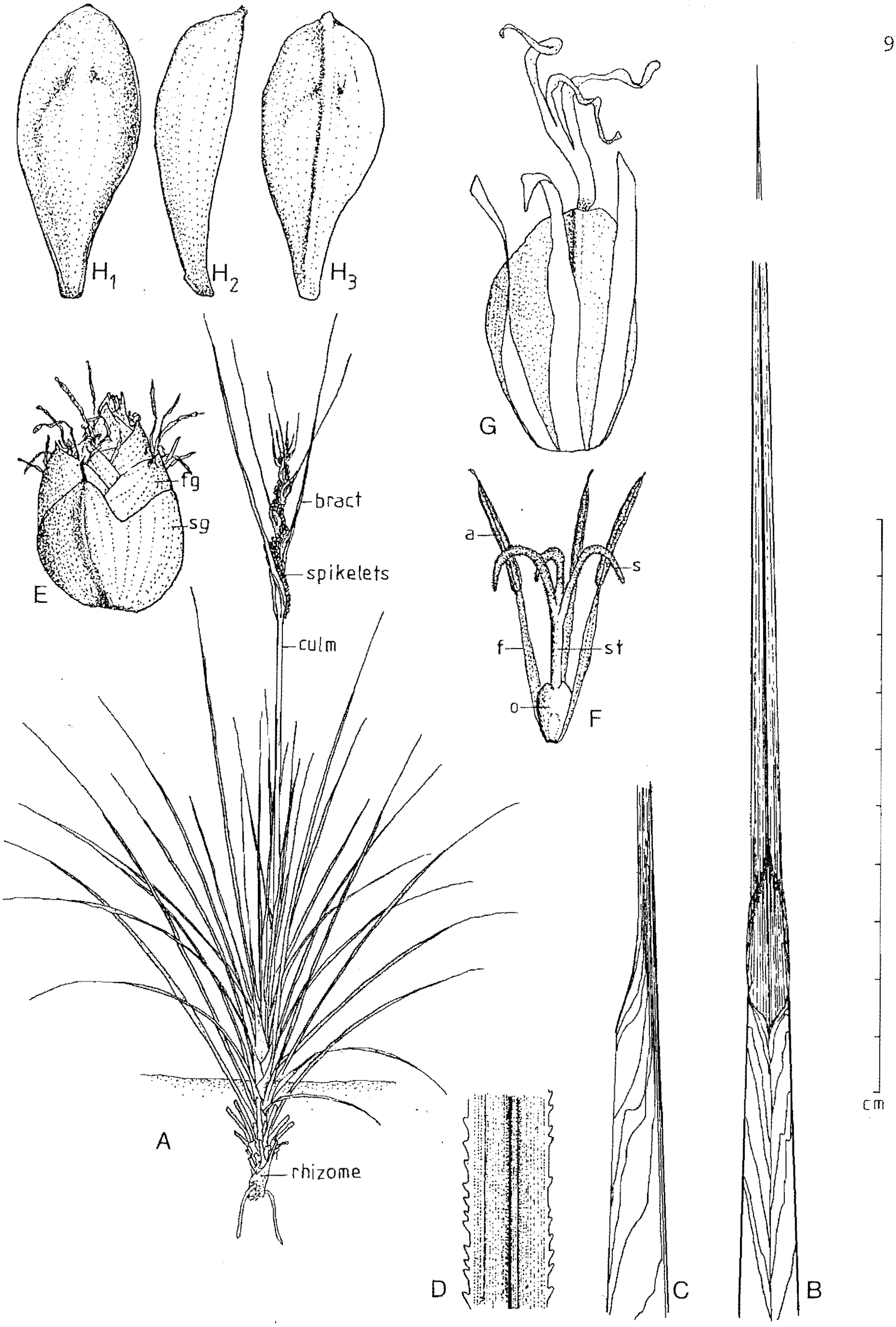


Figure 1. *Desmoschoenus spiralis*. A, habit (erect) and inflorescence, (x0.2); B, leaf (adaxial surface) showing hollow cylindrical membranous sheath and grooved lamina, (x1); C, sheath and lamina base (side view), (x1); D, lamina section magnified showing toothed margins, (x10); E, spikelet comprised of an outer sterile glume (sl) and floriferous glumes (fg) with exserted stamens and stigmas, (x6); F, flower without its glume, comprised of an ovary (o), style (st), trifid stigma (s), filaments (f), and anthers (a), (x15); G, developing fruit with persistant style, stigma and stamens, (x20); H, ripe fruit (nut), H_1 concave surface, H_2 side, H_3 convex surface, (x20).

Chapter VII. A continuum of growth forms exist between these two extremes.

2.2.2.1 Erect Habit. The rhizome is orientated vertically, (orthotropically), with the apex growing up through the sand. Growth is sympodial with new branches arising orthotropically from the axial leaf buds of the leaves at the base of the terminal inflorescence. The rhizome surfaces are undifferentiated, i.e. leaves are orientated spirally around the rhizome, side branches may develop from the axils of any leaf, and roots may emerge from any surface of the living rhizome. Leaves recurve only slightly. Refer to Figures 2 and 3.

2.2.2.2 Leader Habit. The rhizome is orientated horizontally, (plagiotropically), with the apex growing parallel to the sand surface. As far as can be ascertained, growth is monopodial; never has there been observed the main rhizome of any leader plant producing an inflorescence. Inflorescence production is restricted to the side branches. Because of its horizontal position the rhizome is dorsiventrally differentiated, i.e. side branches only develop from the rhizome's upper surface, and roots emerge only from the lower surface of the rhizome. Although the leaves are produced spirally around the rhizome they are not orientated spirally because leaves arising from the ventral surface grow upwards and outwards in the same manner as the dorsially produced leaves. Leaves are markedly recurved. In general, they have shorter laminae and internodes than leaves of plants with an erect growth form. Very stunted leader plants of pingao with extremely

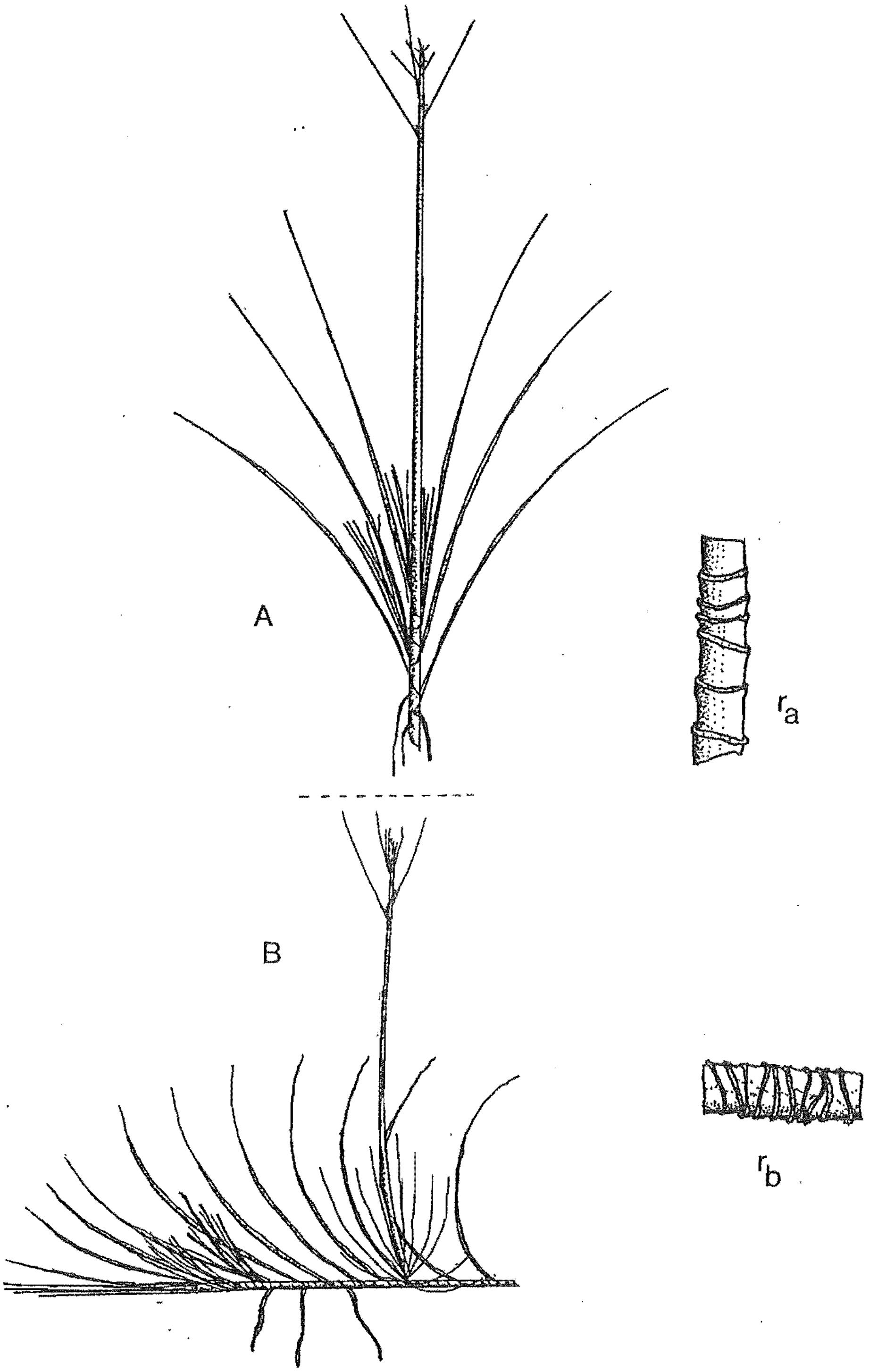


Figure 2. The erect (A) and leader (B) habits of *Desmoschoenus spiralis*. The rhizome, stripped of its leaves, is shown for the erect habit, (r_a), and the leader habit, (r_b).

Figure 3. Erect habit of pingao
(five cent piece indicates size)

Figure 4. Leader habit of pingao
(five cent piece indicates size)

short laminae and internodes have also been observed. Refer to Figures 2, 4 and 5.

2.2.3 The Rhizome

The rhizomes of pingao are about 1.5 cm diameter, terete to obtusely trigonous in cross section, and quite woody, being composed of many densely packed fibres. They are completely covered in the bases of old leaf sheaths which gives them a rope-like appearance. Dead rhizomes persist long after the plant is dead, (Figure 6). Elongation of the rhizome, in response to sand deposition, is restricted to the first few centimeters behind the apex. Root initiation occurs behind this zone of elongation.

As is common with most rhizomatous plants, rhizome extension occurs by apical growth (the distal end) and rotting takes place at the proximal end. When rotting reaches a side branch junction the individual plant becomes two. In this way a clonal population is formed, i.e. individuals that are physically separated but genetically the same. It is possible for large areas of land to be covered by a large number of these genetically identical plants.

Because of growth at one end and death at the other end, the plants are in effect mobile and can travel substantial distances over time. They are also potentially immortal, continuously renewing their vegetative parts, (Bell, 1976).

The pattern of rhizome growth of plants with erect habit was recorded from vertically sectioned dunes exposing

Figure 5. Stunted-leader habit of pingao (5 cent piece indicates size).

Figure 6. Persistant rhizome of a dead pingao plant with leader habit

the plants' subterranean organs, (Figure 7). An aerial view of a plant with leader growth was also recorded. Diagrams of each appear in Figure 8.

2.2.4 The Leaves

2.2.4.1 The Sheath. The dimensions of an average sheath are 8-10 cm long and 1-2 cm in diameter. The sheaths of each leaf in a tuft of pingao surround the sheaths of all younger leaves and protect the apex. They are non-photosynthetic. The part of the sheath continuous with the lamina midrib is opaque and is the sheath's thickest part while the rest of the sheath cylinder is made up of a very thin transparent membrane patterned with a network of red-brown veins. Upon dying the sheath turns dark brown and scarious. It persists around the rhizome and splits longitudinally as the tuft increases in girth. An aromatic resinous secretion covers all sheaths, and binds them tightly together. Its function is not known but it probably provides apex protection and may prevent the sheaths from drying out.

2.2.4.2 The Lamina. The lamina dimensions are (20) - 40 - (60) cm long and (2) - 4 - (6) mm wide. It has parallel venation which is continuous with the sheath. It is linear, concavo-convex in cross-section, and has a prominant midrib sometimes forming an abaxial keel which is usually denticulate in the same manner as the margins. Most of the lamina is composed of sclerenchyma which is responsible for their extremely fibrous nature. This first leaf of each tuft (and rarely the second leaf) is modified into a bract which comprises a sheath with either a much reduced lamina or more commonly no lamina.

Figure 7. Rhizome excavation to show rhizome and root patterns

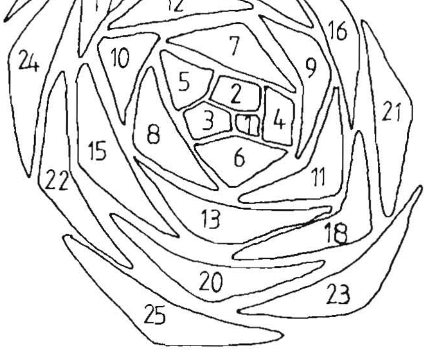
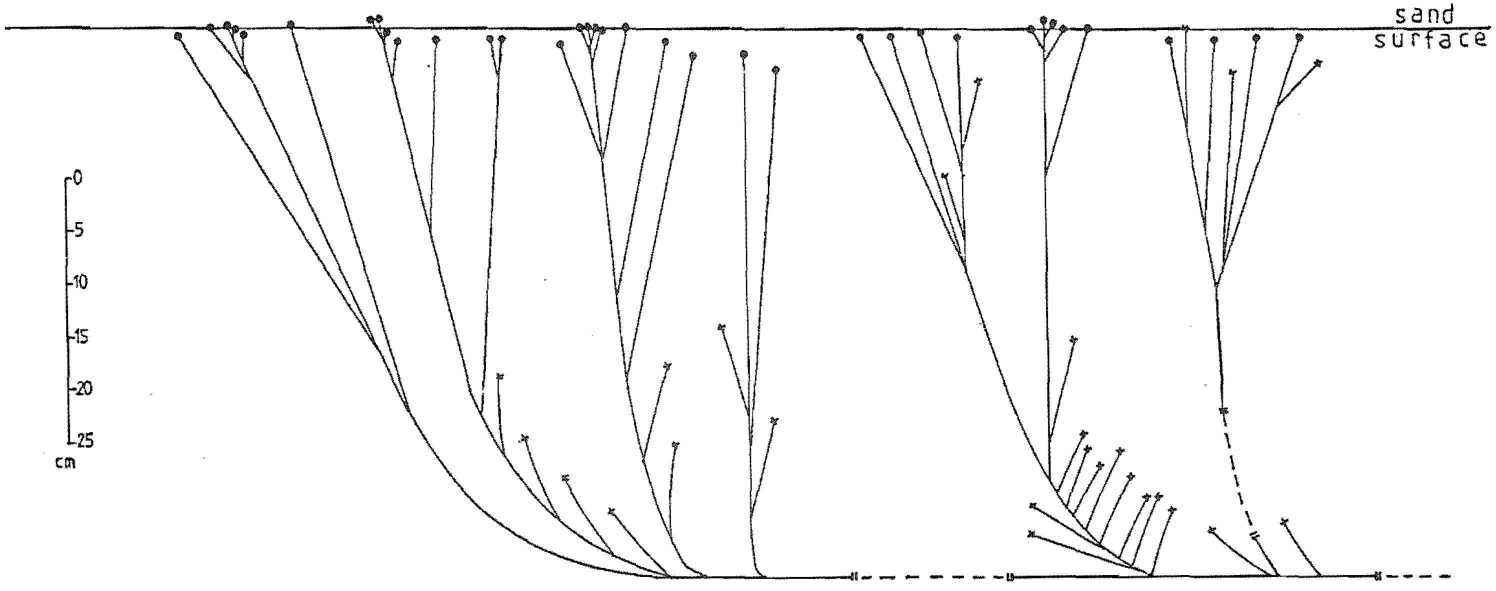


Figure 9. Cross-section of a tuft of pingao showing the position of consecutive leaves



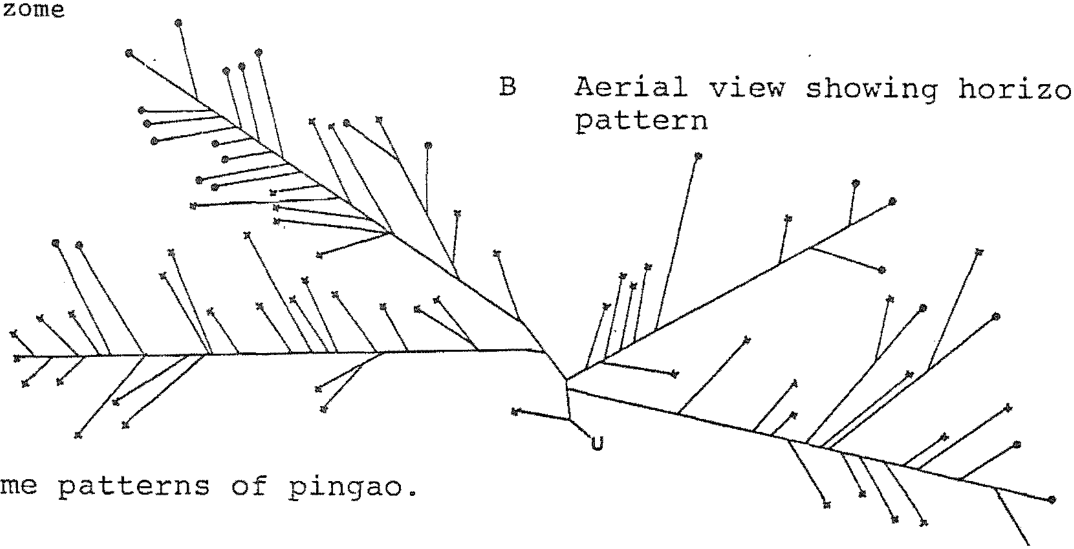
A Vertical profile showing erect rhizome pattern

● live tuft

* dead tuft

‖----‖ suspected rhizome

U rhizome goes underground



B Aerial view showing horizontal rhizome pattern

Figure 8. Rhizome patterns of pingao.

2.2.4.3 Development. New leaves are produced from the apex, lamina tip first and sheath last. Very little elongation occurs along the leaf itself. The young leaves are extremely tightly packed around the apex before the internodes between them increase in length. It is the pressure of young leaves against each other that is responsible for their ultimate shape. Figure 9 shows a tuft of leaves in cross-section and illustrate the effect of leaf to leaf pressure on leaf shape. Figure 9 also gives the phyllotaxis of pingao. It seems that the pattern of leaf orientation is repeated every 12 leaves produced over 5 revolutions.

2.2.5 The Roots

The roots are adventitious, arising behind the zone of internode elongation and emerging through the outer layer of sheaths. From the rhizome, they spread either horizontally or downwards in all directions forming a fibrous root system which binds the sand more effectively than would a tap root system. Individual roots are white, covered with root hairs, terete in cross-section, of lengths frequently in excess of three metres, and have an average width of 4 mm. As is consistant with roots of other cyperaceous plants, the cortex appears to die early and becomes soft and non-functional. After this occurs the endodermis acts as the protective layer around the stele.

2.2.6 The Inflorescence

The inflorescence of pingao is (7) - 20 - (30) cm in length and the axis is usually erect or slightly curved. It is borne above the leaves, the peduncle being continuous with the culm. It is made up of leaf-like bracts which are adnate to, and spirally arranged around the peduncle axis. They decrease in length from the inflorescence base to its tip. The lowest bract usually exceeds the inflorescence in height.

Inflorescence development begins with the rapid growth of the rhizome (8) - 13 - (17) internodes back from the apex. This internode becomes the culm. The growth is arrested of all partly developed leaves borne on top of the culm. These leaves become the bracts. Unlike leaves, the bracts are much reduced in length and their sheaths are open. The internodes of these bracts increase in length at the same time as culm growth.

Clusters of 4-5 mm long spikelets are borne in 1-3 rows around the base of the bracts where the bract sheaths join the peduncle, (Figure 10). The clusters around the lowest two bracts may comprise of up to 40 spikelets, but this number decreases with each successive bract. The bract at the apex of the inflorescence may only have 1-3 spikelets. Clusters may be separate between the lower bracts but confluent among the higher bracts.

Each spikelet is comprised of (5) - 9 - (14) flowers. Spikelets at the top of each cluster usually have more flowers than the lowest spikelets of each cluster. Each flower is comprised of a glume housing functional female and male reproductive structures. The flowers are spirally imbricate and are borne on very short pedicels arising from the rhachilla of each spikelet. The lowest glume of a spikelet is not floriferous. The flower at the

Figure 10. Detail of an inflorescence of pingao showing spirally arranged bracts subtending clusters of spikelets with exserted stigmas and stamens.

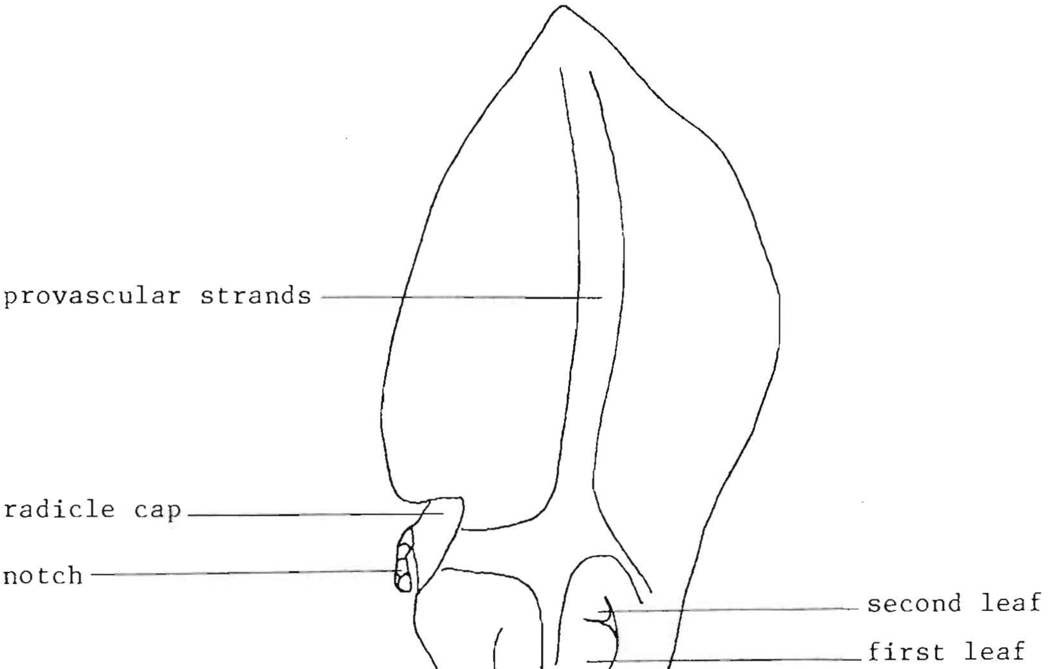


Figure 11. Longitudinal-section of the embryo of *Desmoschoenus spiralis,* (x200).

Adapted from van der Veken, (1965).

base of each spikelet is the oldest and the flower at the spikelet tip is the youngest.

Glumes are broad-ovate with truncate bases, and distinct venation. They sometimes have a keeled mid-rib which terminates in a short sharp tip (especially the lower glumes). They are chaffy, dry and are dark red-brown in colour. The glumes and the three stamens are hypogynous. The flattened scarious filaments arise between the ovary and the glume, supporting long thin anthers which hold yellow pollen. The stigma is three-armed. Each arm is tightly curled when exserted and has a granulate receptive surface.

Flowering is progynous, i.e. the stigmas are exserted and receptive (usually in late October) before anthesis occurs (usually in early November). The anther locules split longitudinally. Upon pollination the stamens, style, and stigma wither but remain associated with the developing fruit.

The fruit is comprised of a tough pericarp housing a single seed (i.e. a nut). Its average dimensions are 3.2 x 2.2 x 1.2 mm with an average weight of 1.83 mg. Its shape is determined by its position within the spikelet. Fruits from the spikelet base are obovoid while fruits from the spikelet apex are oblanceolate. It is concavo-convex in side-view. The colour of semi-mature fruits is light brown, but with a gradual increase in pigmentation due to exposure to the sun the mature fruit is dark-brown to black. The outside surface of the pericarp is smooth and shiny while the inside is covered with honeycombed reticulations.

The seed is positioned within the narrower end of the fruit (the staminal end) and has average dimensions of 2.0 x 1.3 x 1.2 mm and an average weight of 1.23 mg. It is oval to obovate, cream coloured and covered by a thin flaky testa.

The embryo is positioned within the narrower end of the seed and is disproportionately large, (Figure 11). This has already been described in detail in Section 2.1.

CHAPTER III

DISTRIBUTION

3.1 PAST DISTRIBUTION

Early botanical surveys of districts throughout New Zealand were concentrated between 1860 and 1920 and give an indication as to the extent of the past distribution and frequency of *Desmoschoenus spiralis*.

On an expedition around Northland, Cheeseman (1896) observed *Desmoschoenus* to be common on sand-hills throughout the district and noted its presence from Ahipara to Cape Maria van Diemen, Spirits Bay, Hukutere Hill and Tauroa Point. Carse (1910) noted its abundance on sand-dunes of the Mangonui County, and Buchanan and Kirk (1869) list pingao from Whangarei, Bay of Islands, Whangaroa, North Cape, Kaitaia and Hokianga districts, and Stephenson Island.

Kirk (1870) recorded its presence on Auckland's Isthmus and the Takapuna district, both areas being represented by a few individuals. Cheeseman (1871) recorded it as sparsely dotting the extensive sand-hills north of the Waikato River, and Carse (1902) found it as common on the sand-hills of the Mauku district, naming the Kariotahi Gap as an example. Kirk (1868) described it as abundant on the eastern dunes of Great Barrier Island and in 1896 records it for the East Cape district. Buchanan (1873) reported it from the sand-dunes of Mirimar Peninsula, Wellington.

In the South Island *Desmoschoenus* was present at Blind Bay (Clifford Bay - Marlborough) (Cheeseman 1881), and it was observed surmounting the sand-dunes from the Ure to the Clarence Rivers, with *Spinifex hirsutus* and *Ammophila arenaria* (marram), (Martin 1932). It was the most conspicuous plant along the coast from Westport to Cape Foulwind and was present on all coastal sand-hills in the Westport district (Townson, 1906). Hamilton collected it at Okarito in 1878. Laing (1919) reported it from Banks Peninsula, and it also occurred in the neighbourhood of Christchurch (Armstrong, 1870). Buchanan (1868) observed a 'tolerable abundance' on coastal sand-hills in the east and west of the Otago-Fiordland region, Petrie (1896) records it as abundant on sand-hills of Otago's south and east coasts, and Crosby-Smith (1913) reported it as common on sand-dunes from Fiordland to the Waikawa River on the south-east coast of Southland, and on Stewart Island. It covered unstable foredunes of Sealers Bay, Codfish Island (Popplewell, 1911) and was by far the most characteristic dune plant on Chatham Island (Mueller, 1864; Cockayne, 1902).

These accounts illustrate that in the past pingao was abundant in many districts and common on most of the coastal dune systems throughout New Zealand. The briefness of all the early reports may be taken as indicating such ubiquity of pingao that more detailed notes were not considered necessary by the authors.

3.2 PRESENT DISTRIBUTION

3.2.1 Methods

Provisional maps of pingao's present distribution have been constructed. Information was gathered from herbarium specimens, literature, and casual observations and surveys by the present author and other collaborators.

Herbarium records were obtained from the herbaria of the Botany Division DSIR Lincoln, the National Museum of New Zealand, Auckland Institute and Museum, and the Universities of Auckland, Waikato, Massey, Victoria, Canterbury and Otago.

The greatest sources of information were observations and surveys. The surveys were carried out along the coasts of much of Northland, Coromandel Peninsula, Bay of Plenty, the Waikato Harbour, North Canterbury, Fiordland, Stewart Island and Chatham Island. No surveys and very few observations were made on the East Coast of the North Island from East Cape to Cape Palliser.

Where possible, information for each locality included the herbarium number of observer's name, date of collection or observation, relative abundance, type of substrate, evidence of browsing, and presence/absence of marram, spinifex, *Ulex europaeus* (gorse), *Lupinus arboreus* (lupin), and *Cytisus scoparius* (broom).

Localities were mapped on 5,000 yard square maps of New Zealand. Locations where *Desmoschoenus* was found to be common to abundant have been distinguished from ones where it is infrequent, scattered or rare. Records before 1960 have been distinguished from records of 1960 or after. Where no date is available for a record it is assumed that *Desmoschoenus* is still present at that locality unless it is known that the record was made some time before 1960.

Larger scale maps have been made of pingao distribution along the coast of Pegasus Bay, North Canterbury.

3.2.2 Results and Discussion

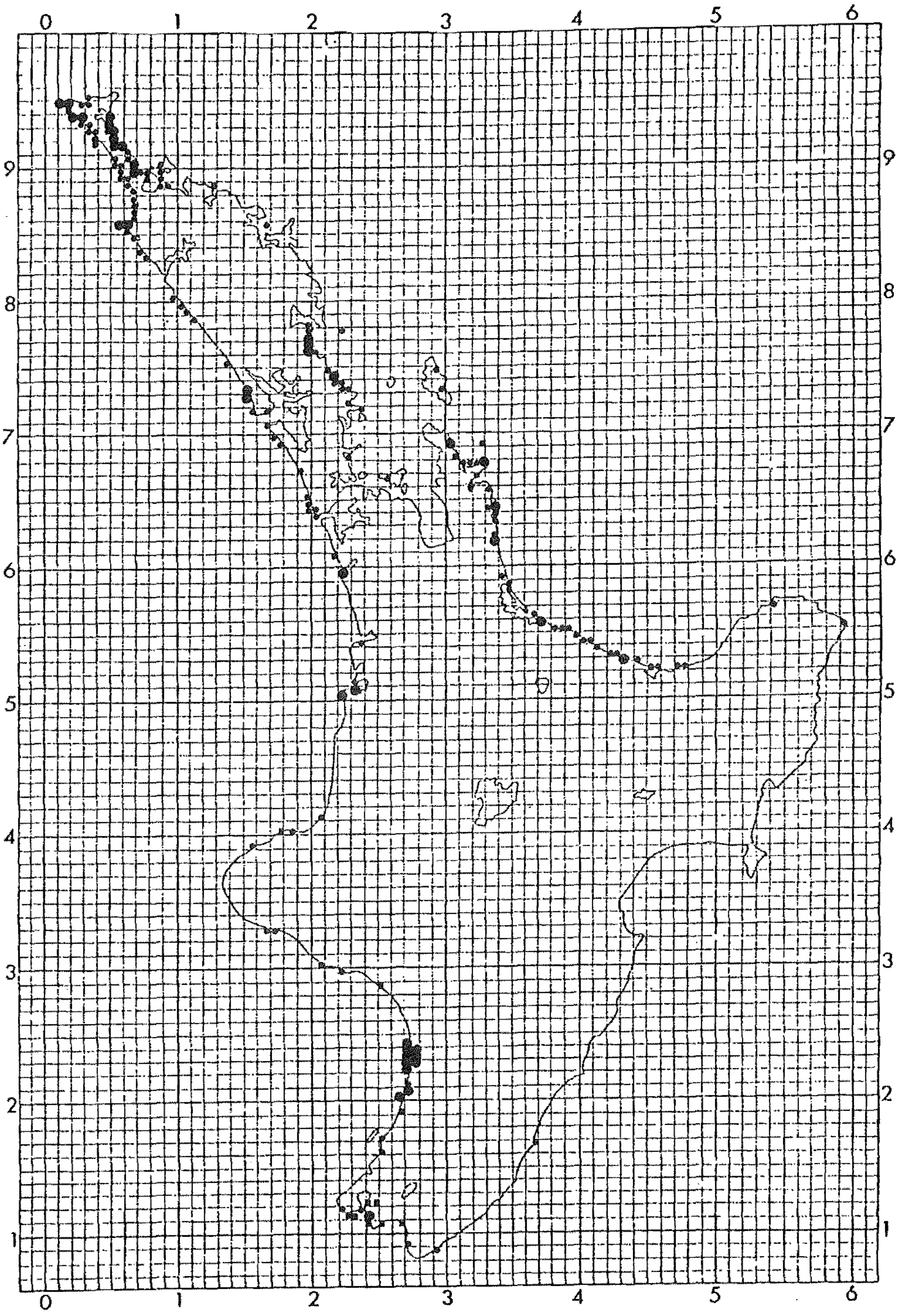
Detailed notes on the known occurrence and abundance of pingao along the New Zealand coastline are presented in Appendix I.

The distribution of pingao is shown in map form, Figures 12 and 13 . From this information the following results are presented.

Desmoschoenus occurs throughout New Zealand from North Cape to Stewart Island and Chatham Island 400 km east of the mainland. It is also recorded from the offshore islands of Great Mercury, Waiheke, Lady Alice (Hen and Chickens Group), Great Barrier and Moturua (Bay of Islands). With few exceptions it is entirely restricted to the coast. It is found up to 3 km inland from the Manawatu coast, 4 km inland at Masons Bay, Stewart Island, and 2-3 km inland along Ninety Mile Beach. The extensive sand country that spreads inland from the coast at these localities is responsible for pingao's inland occurrence. It is interesting to note that pingao occurs furtherest from the coast at the head of Lake McKerrow Fiordland, 19 km inland. The lake has been formed from a fiord, and it is presumed that pingao was present at the head of this fiord before the entrance was blocked.

For most of its distribution pingao is represented by small scattered colonies or solitary plants, although there are a few stretches of coastline where large numbers

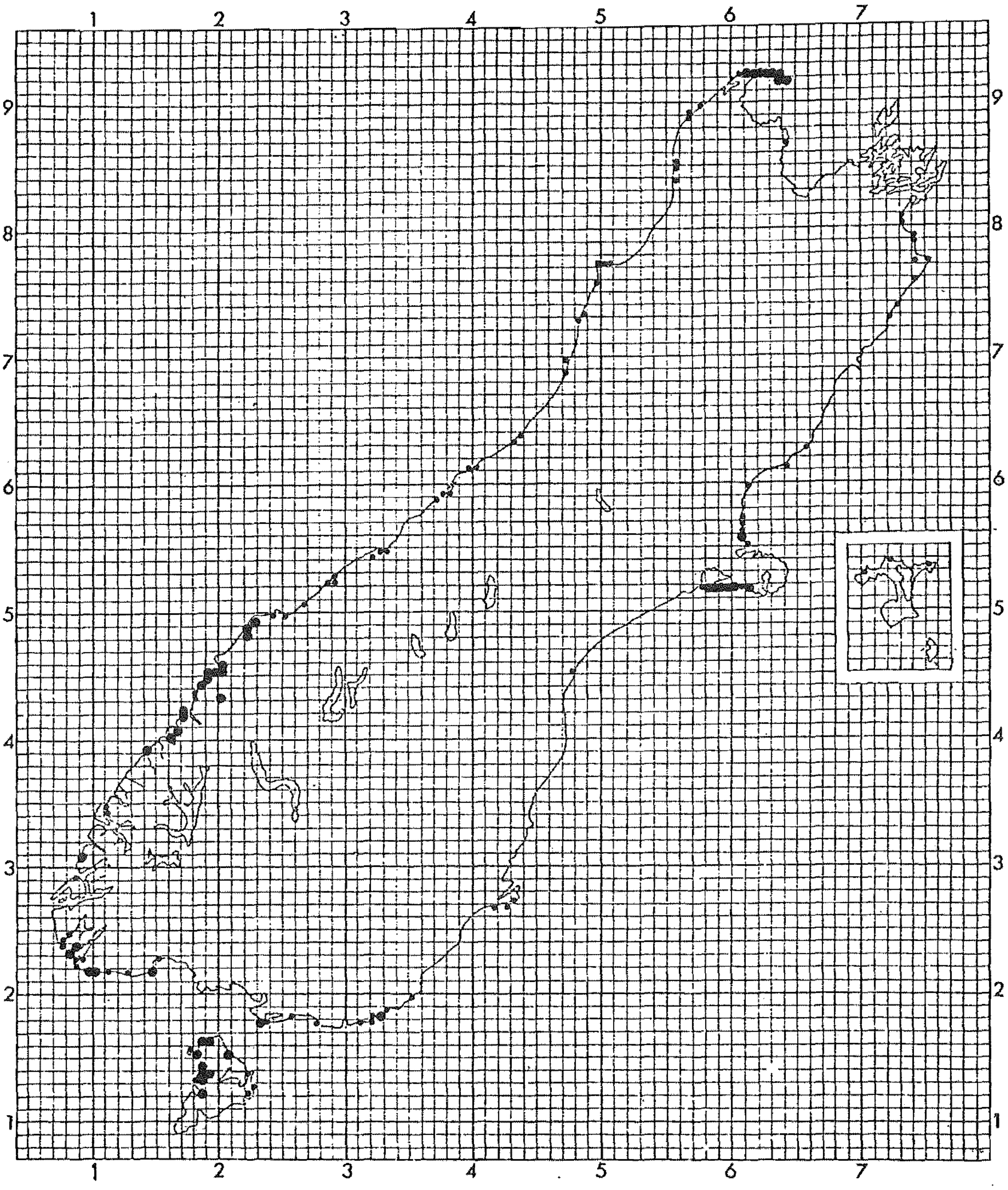
Figure 12. Distribution of *Desmoschoenus spiralis* in the North Island and offshore islands



Record after 1960: Uncommon to rare •
Common to abundant ●

Record prior to 1960 ▪

Figure 13. Distribution of *Desmoschoenus spiralis* in the South Island, Stewart Island, and Chatham Island.



Record after 1960: Uncommon to rare •
Common to abundant ●

Record prior to 1960 ▪

still exist. In the North Island these are parts of Northland (especially Northland Peninsula and Bream Bay - Pakiri beaches) and Whangamata (Coromandel), around Port Waikato and Kawhia Harbour, and throughout the Manawatu sand country. In the South Island pingao is still common to abundant along Farewell and Kaitorete Spits, some Fiordland beaches, and Tautuku Bay, East Southland. It is also an abundant plant on Stewart Island dunes. At such localities, introduced dune plants have either not yet established or comprise only a minor element of the coastal flora, and the influence of man on the dune ecosystem is minimal.

Notable absences are along the east coast of the North Island south of East Cape, much of the coast between Kawhia Harbour and New Plymouth, between Westport and Karamea, between Greymouth and Ross, the dunes north and south of Otago Peninsula and the coast west of Invercargill. A few of these absences may be due to lack of observation rather than lack of *Desmoschoenus*.

Desmoschoenus is typically found in exposed sites such as promontories, peninsulas, spits, long sweeping coastlines and shallowly indented bays. It is absent from sandy habitats within sheltered harbours, deeply indented bays, inlets and at the heads of sounds and fiords. Occasionally it is found growing on shingle substrates, such as at Cape Campbell and several Fiordland beaches. It has also been observed growing over the broken shells of middens on Ninety Mile beach. At most, if not all, of these sites such substrates are quite shallow and overlie sand in which pingao is rooting.

The former widespread distribution allied with the fragmentary nature of its present distribution, and the fact that large numbers of very small populations exist, indicate that *Desmoschoenus* exists in most localities now only as remnant populations. Absences of pingao from areas where it was recently common, (e.g. Kawhia Harbour), and frequent observations of the persistant rhizomes of dead plants adds weight to the assertion that numbers have been declining and that the trend is still continuing, (Given and Bartlett, 1979; Given, 1981). The rate at which pingao declines can be extremely rapid as the results from Aotea and Kawhia Harbours show, (Appendix I).

The extensive modification to, or destruction of, pingao's habitat is the reason for this decline. *Ammophila arenaria* (marram grass) introduction is the main reason for such modification. The increasing demand for agricultural land along coasts early this century and the development of coastal exotic forestry led to the planting of marram for the purpose of stabilizing dunes. As a result of these plantings, and because of natural increase both vegetatively and by seed, it is now the most ubiquitous plant of New Zealand's sandy coasts, typically forming extensive monocultures. In the surveys and observations it was recorded at over 40% of the localities where pingao was found, and is the dominant plant at most of these sites. Because presence/absence of marram was not recorded for many localities the true percentage is expected to be much higher. Marram is also the dominant sand binder at all localities where pingao is known to have become extinct. The possible mechanism by which marram displaces pingao is discussed in Section 6.3.6.

A good example of invasion of marram at the expense of pingao is found from various accounts of the vegetation of Otago Peninsula's sandy coasts. Before the introduction of marram the dune plants from the Taieri River mouth to Waitati north of Otago Peninsula were all indigenous. The common sand binder was pingao (Martin, 1956). After the introduction of marram, Martin (1924) states that it had become almost as common on Dunedin's dunes as in Europe, and more common than pingao. All that remains of pingao at the present are four small colonies.

Marram is still being planted either to prevent coastal erosion or, with lupin, to provide dune stability for exotic forestry. The dune system of Northland's Ninety Mile Beach is being afforested at a rate of up to 2,000 ha per year with the prospect of covering all but its most northern part (John Coster, NZFS, pers. comm.).

Introduced plants other than marram that are capable of invading and stabilizing dunes, include gorse, lupin, broom and *Elymus arenarius* (on Chatham Island). They have also contributed torwards pingao's decline, but not to the same extent as marram. Fires, trampling by cattle, habitat destruction by sand-mining, reclamation, off-shore sand-dredging, and the constant use of many sandy coasts for recreation have been noted in the surveys as being further threats to existing pingao populations. Browsing of pingao leaves was observed at many localities and is considered to be mainly caused by rabbits and hares. Although browsing was apparent of both mature plants and seedlings, it was never recorded as being heavy, and has no major part to play in limiting pingao distribution.

Pingao is usually the first plant encountered above high tide mark. It is most frequently found on the foredunes, entirley covering them, flanking their seaward faces or restricted to their toe slopes. It builds scattered hummocks of varying sizes on sand plains, deflation zones and amongst the hollows of mobile dunes. It is also found occupying dune slacks on small mounds above the level of surface water.

It was frequently observed in association with active blowout zones, and other areas where sand accumulates from eroding dunes. Small populations were frequently found at river mouths. Where marram is the dominant sand binder, moribund colonies of pingao have been occasionally observed at the interface of the dune system and the stable grassland behind it.

3.2.3 Limitations

Figures 12 and 13 can only be considered preliminary distribution maps. Inaccuracies may have occurred as a result of the following limitations.

1. Many observations and collections have been confined to localities that are of comparatively easy access. Such coasts are checked more frequently and thoroughly by casual observers. On the other hand, sandy beaches which are remote and/or difficult of access have not been visited to the same extent. By their very nature it is more likely that they will be inhabited by pingao. In the North Island more populations may be found along the eastern bays of North Cape, some of the bays between East Cape and Mahia

Peninsula and between Cape Kidnappers and Castlepoint, and the coastlines from Albatross Point to North Taranaki Bight and from the Turakina River to the Wanganui River. In the South Island further small populations may be found dotted along the Westland coastline.

2. Records that are undated or prior to 1960 give unreliable indications of pingao's present distribution.

3. Additional information such as plant abundance was mainly qualitative, and therefore subject to variation amongst observers.

4. In view of the fact that pingao has been observed to decline from a healthy population to local extinction in under ten years (Appendix I, Kawhia and Aotea Harbours), it is possible that other populations have also become extinct since being recently recorded.

5. Errors in mapping were possible of localities where pingao was limited to only part of a beach that extended for more than 5,000 yards and was recorded with no more precision than the name of the beach.

6. The past distribution of *Desmoschoenus* has been inadequately documented. Although it was recorded from most districts, very few specific localities have been given. Because of this many localities where pingao was once presence but is now extinct are unrecorded.

3.3 NORTH CANTERBURY COAST SURVEY

3.3.1 History of Pegasus Bay Dunes

Well developed dunes are more or less continuous along the length of Pegasus Bay, being interrupted only by river mouths, blowouts and wind channels.

As for most of the dunes in New Zealand, *Desmoschoenus* was once the dominant sand binder of this dune system. Pegg (1913) recorded it as being the most common of all plants on the sand-dunes at New Brighton, extremely common on New Brighton Spit opposite Shag Rock, and dominant on the Sumner foredunes. Laing (1919) recorded pingao from Sumner and Taylors Mistake.

Biggs (1947) gives a detailed account of the history of the dunes from the Waimakariri River mouth to Sumner. After the arrival of Europeans, in 1852 a dairy run was established on these dunes until 1880 when the New Brighton residential area was developed. The dunes from Waimairi to the Waimakariri River were grazed until the early 1900's and carried about 2,000 sheep. Continual grazing resulted in a general deterioration of the surface vegetation and sand began to drift inland. Pingao was eaten out and other dune plants succumbed to the increased sand instability. Twelve metre high wandering dunes developed which eventually travelled three kilometres inland.

To prevent further erosion marram and lupin were planted. Marram dunes grew at a rate of half a metre per year (King, 1905). Grazing was kept in check and pine trees were finally planted. In the 1930's artificial foredunes were built with fences and cuttings of *Leptospermum scoparium* (manuka). Marram was planted behind them. The same technique was used to create foredunes between Waimairi and South Brighton. The planted marram quickly established and replaced pingao in dominance.

The only dunes that did not have an artificial foredune created in front of them were south of South Brighton (Southshore) and north of Spencer Park. Pingao was most common on these dunes as late as the 1950's (Wall, 1953).

3.3.2 Results and Discussion

Detailed notes of a full pingao survey along the North Canterbury coast are presented in Appendix II. All pingao colonies are described and their locations are also mapped in Figures 14 to 17. The following results and discussion are presented from this information.

Today the Pegasus Bay dune system is almost entirely covered with marram grass. For most of their length, the seaward faces of the coastal dunes are eroding. Their steepness is characteristic of dunes built from marram (Ranwell, 1958). Storm-promoted erosion is partly responsible. The inland dunes are either completely stabilized by marram or have been planted over in plantations of *Pinus radiata*. *Desmoschoenus* is now very infrequent. It has disappeared from Taylors Mistake and Sumner. Small colonies have been found at Amberley Beach, the Waimakariri River spit north of Spencerville, Waimairi beach, from Central New Brighton to Southshore and at the end of New Brighton Spit. Pingao is still the dominant sand binder along 30 metres of coastal dunes at Southshore, (Figure 18).

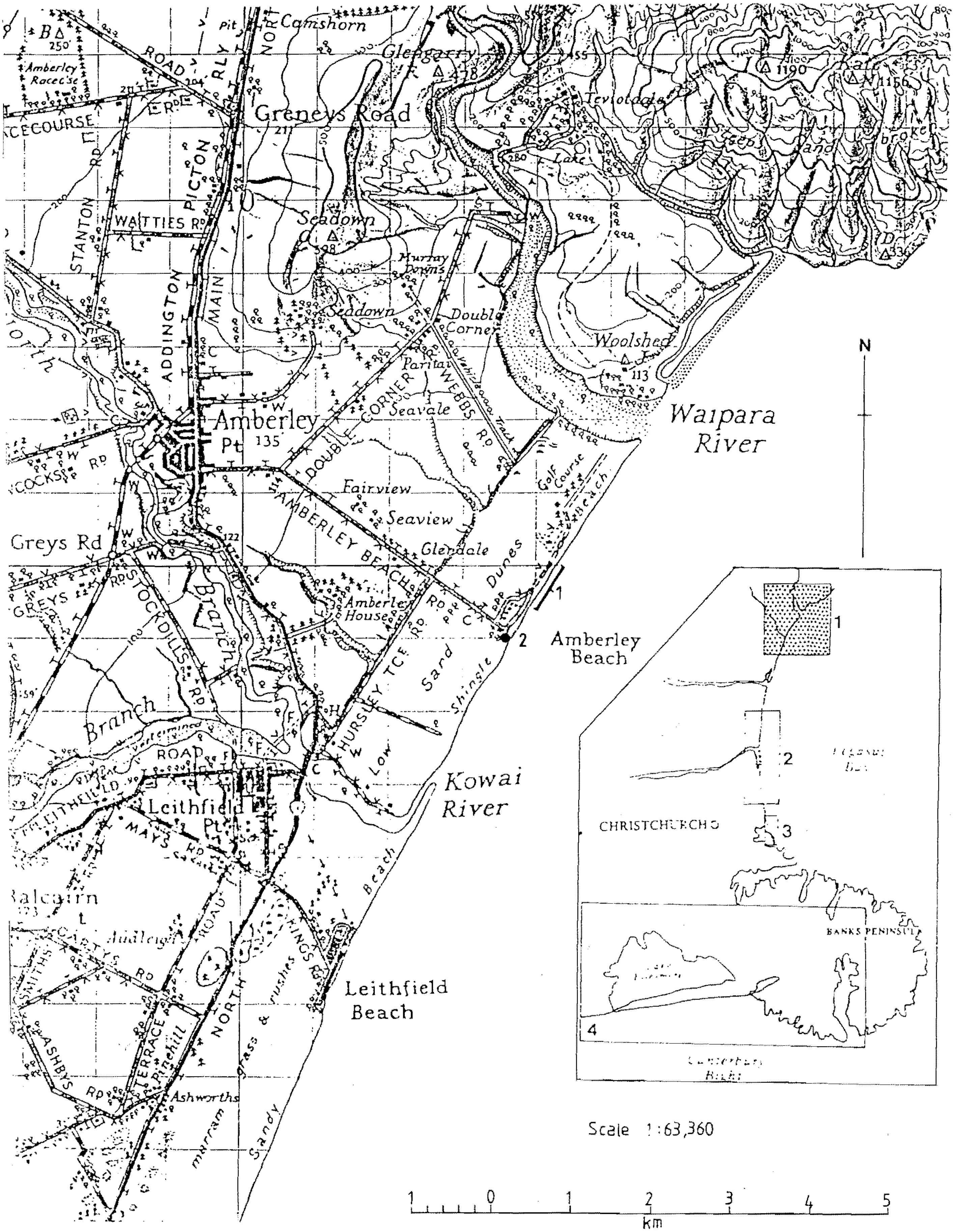
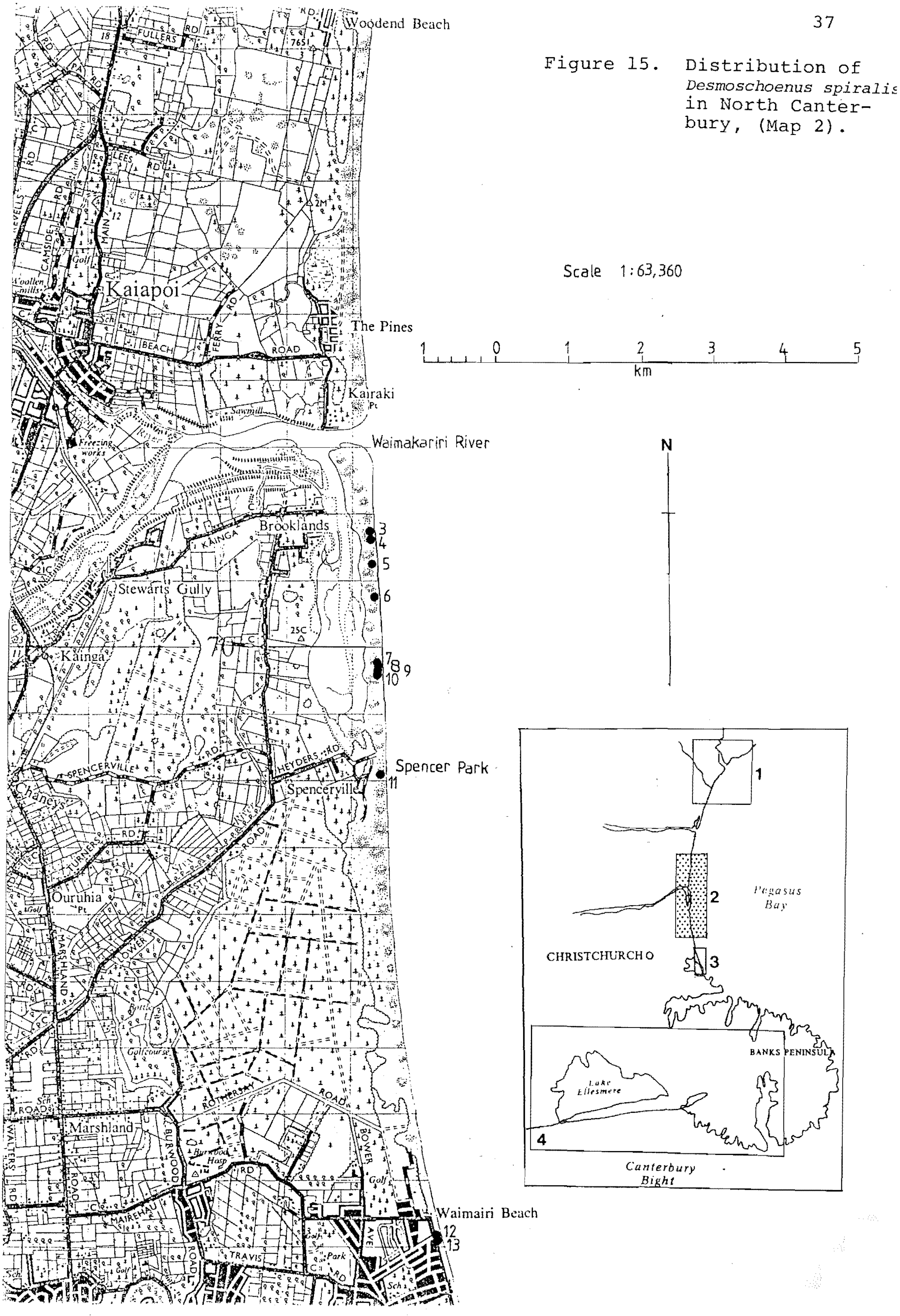


Figure 14. Distribution of *Desmoschoenus spiralis* in North Canterbury, (Map 1).

Figure 15. Distribution of *Desmoschoenus spiralis* in North Canterbury, (Map 2).



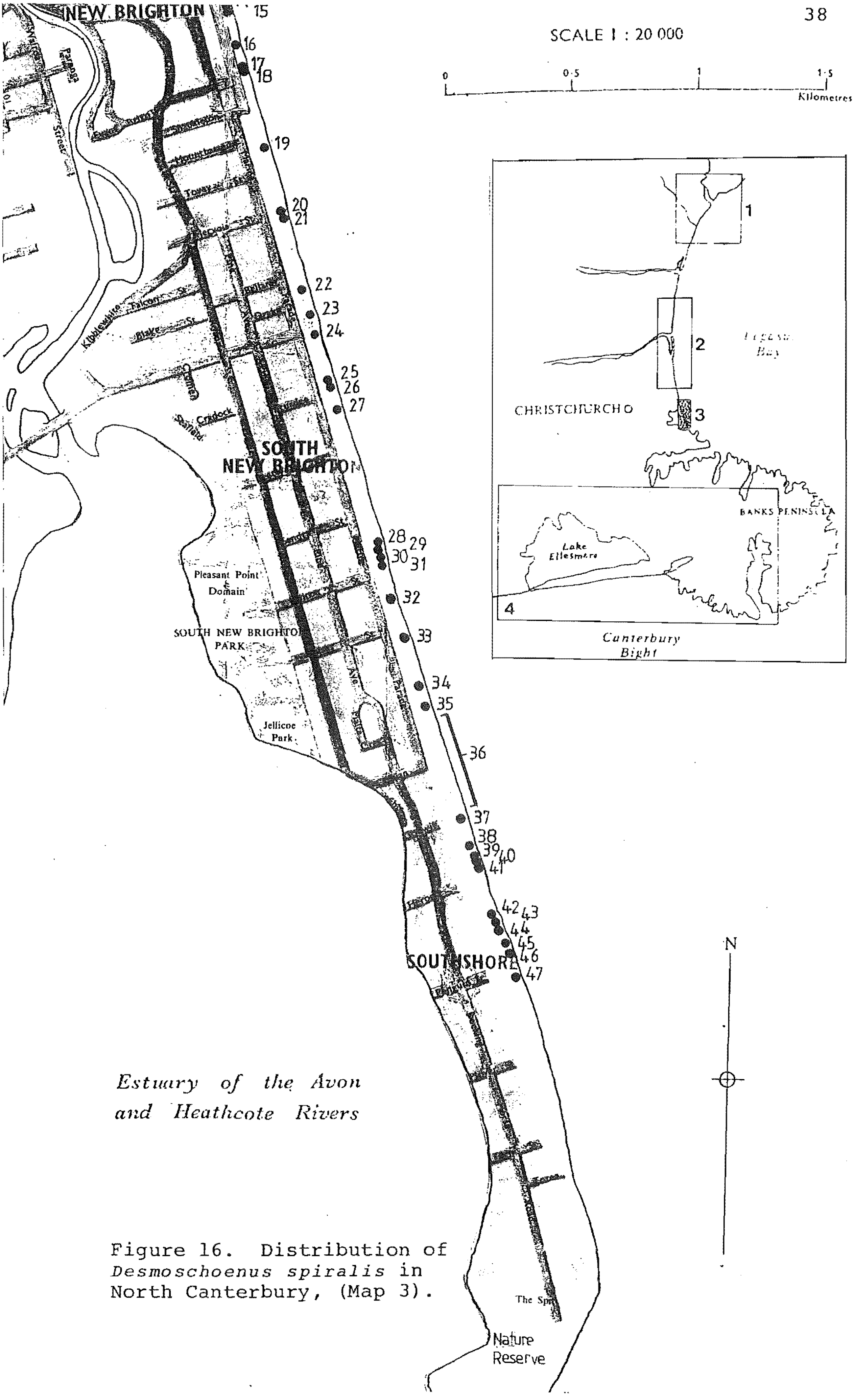


Figure 16. Distribution of *Desmoschoenus spiralis* in North Canterbury, (Map 3).

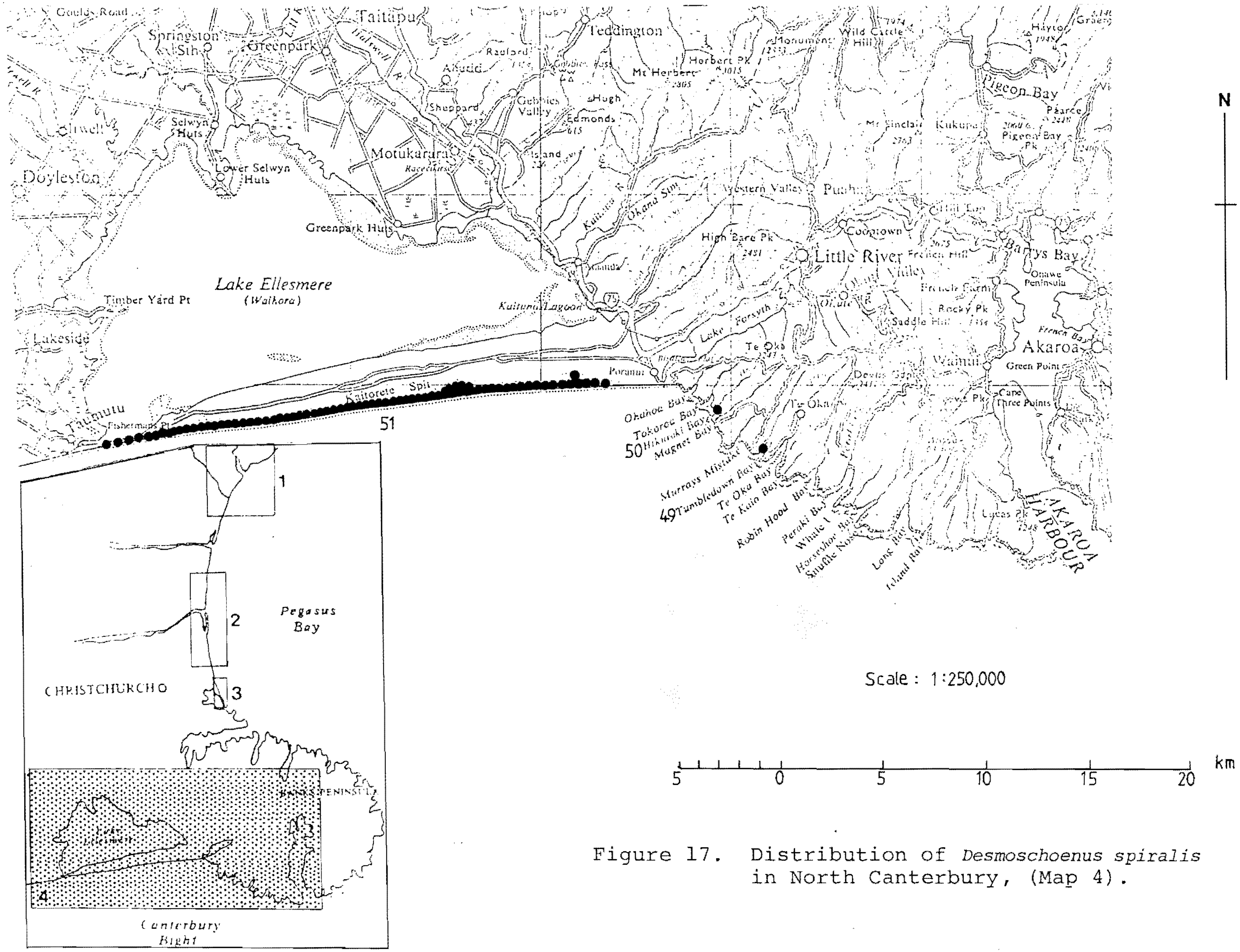


Figure 17. Distribution of *Desmoschoenus spiralis* in North Canterbury, (Map 4).

Figure 18. *Desmoschoenus*- dominant dune at Southshore, New Brighton. Marram and *Senecio elegans* also present

Nearly all the pingao colonies are restricted to the base or toes of the seaward faces of coastal dunes and are associated with blowouts and wind channels. It is at these places that drifting sand is available. Because of the very steep nature of the seaward dune faces, their upper slopes are being undermined. The sand from such erosion collects at the base of the dune where pingao is found. Wind channels are common throughout the coastal dunes and have, in some cases, developed into blowouts of varying sizes. Pingao is often dominant at such sites, and occupies a variety of stations. Healthy colonies were usually found on the seaward facing toe slopes of the dunes at either side of the blowouts. Occasionally, these colonies were continuous with plants further up the faces behind the toes. The upper plants were typically unhealthy. On the blowout depression, pingao was frequently observed covering small to large hummocks. It was also observed on some of the crests of dunes at the rear of the blowouts.

Plant vigour seems to be directly linked with the amount of available free sand. Plants that are not in the path of moving sand or are on deflating dunes are usually moribund and produce very few inflorescences. Such plants are usually associated with the persistent rhizomes of dead pingao. Pingao is also moribund at any interface that may occur between it and marram.

At Southshore where pingao is the locally dominant sand binder the dunes are of comparable height and steepness to the marram dominant dunes. The tufts of pingao are widely spaced, unlike the densely swarded marram, and give the dunes an open appearance. A small unhealthy population of pingao is restricted to a semi-stable hollow behind these coastal dunes and comprises the only occurrence of pingao along Pegasus Bay that does not have a coastal aspect.

In many cases the formation and development of wind tunnels and blowouts have been aided by their use as public thoroughfares to and from the beaches. Although *Desmoschoenus* does not occur along parts of the coast where there is heavy recreational use by the public (such as North and Central New Brighton), it is interesting to note that where it does occur, pingao is largely restricted to these thoroughfares. Such use seems to promote erosion enough to prevent colonization by marram, and maintain a favourable habitat for pingao. The recent erection of fences on the foredunes for the purpose of trapping sand and stabilizing active blowouts may, therefore, be detrimental to the long-term survival of the remaining colonies of pingao that are associated with these blowouts.

The bays surveyed on Banks Peninsula vary greatly in length, width and substrate type. *Desmoschoenus* was found only on the south facing coast at Hikuraki and Tumbledown Bays. Both are shallowly indented and exposed to southerly winds. The long-term prospects for the survival of the population at Hikuraki Bay are poor because of the constant trampling by cattle and gradual loss of habitat.

The dunes of Kaitorete Spit by far hold the largest population of *Desmoschoenus* in Canterbury. Their less intensive use in the past and their coarse sand has meant that these dunes did not pose as much of an erosion problem as the Pegasus Bay dunes and have therefore remained in a less modified state with only limited plantings of marram. Marram is only dominant on the dunes near the outlet of Lake Ellesmere, although it is well established at the sand mining site 8.5 km west of Poranui Point.

Unlike Pegasus Bay colonies, pingao is not restricted to the foredunes but occupies a wide range of stations within the dune system. It is dominant on the foredunes and reardunes, and occurs on sand plains, blowouts, amongst grassland and on ancient inland dunes.

As well as Appendix II, further information on the Kaitorete Spit dunes with respect to pingao distribution is given in Section 4.3.

CHAPTER IV

BACKGROUND - KAITORETE SPIT

4.1 INTRODUCTION

Fieldwork concerned with various aspects of the ecology of *Desmoschoenus* was carried out on Kaitorete Spit. The Spit is situated 30 km south of Christchurch, between latitude 43° 52' to 43° 48' S, and longitude 172° 21' to 172° 43' E, and runs approximately east-west from the southern part of Banks Peninsula to Taumutu township (Figure 19). It forms the southern shore to Lake Ellesmere and the northern shore of the Canterbury Bight. The Spit covers an area of 4855 ha. It is 28.5 km long and 3 km wide at its eastern end gradually tapering to only 100 m wide at its western end. It has a low lying topography averaging 5 m a.s.l, although some of the well developed dunes reach heights of up to 15 m a.s.l.

The geomorphology, natural history and the physical environment of Kaitorete Spit have been described by Wraight (1957), Burrows (1969), Armon (1970), Peace (1975) and Holland (1981).

4.2 GEOMORPHOLOGY

The Spit is technically a barrier - a continuous offshore gravel ridge joined to the mainland at both ends and separating Lake Ellesmere from the Pacific Ocean. This barrier began 6,000 - 7,000 years B.P. as a spit (Armon, 1970) which grew from its western end until it

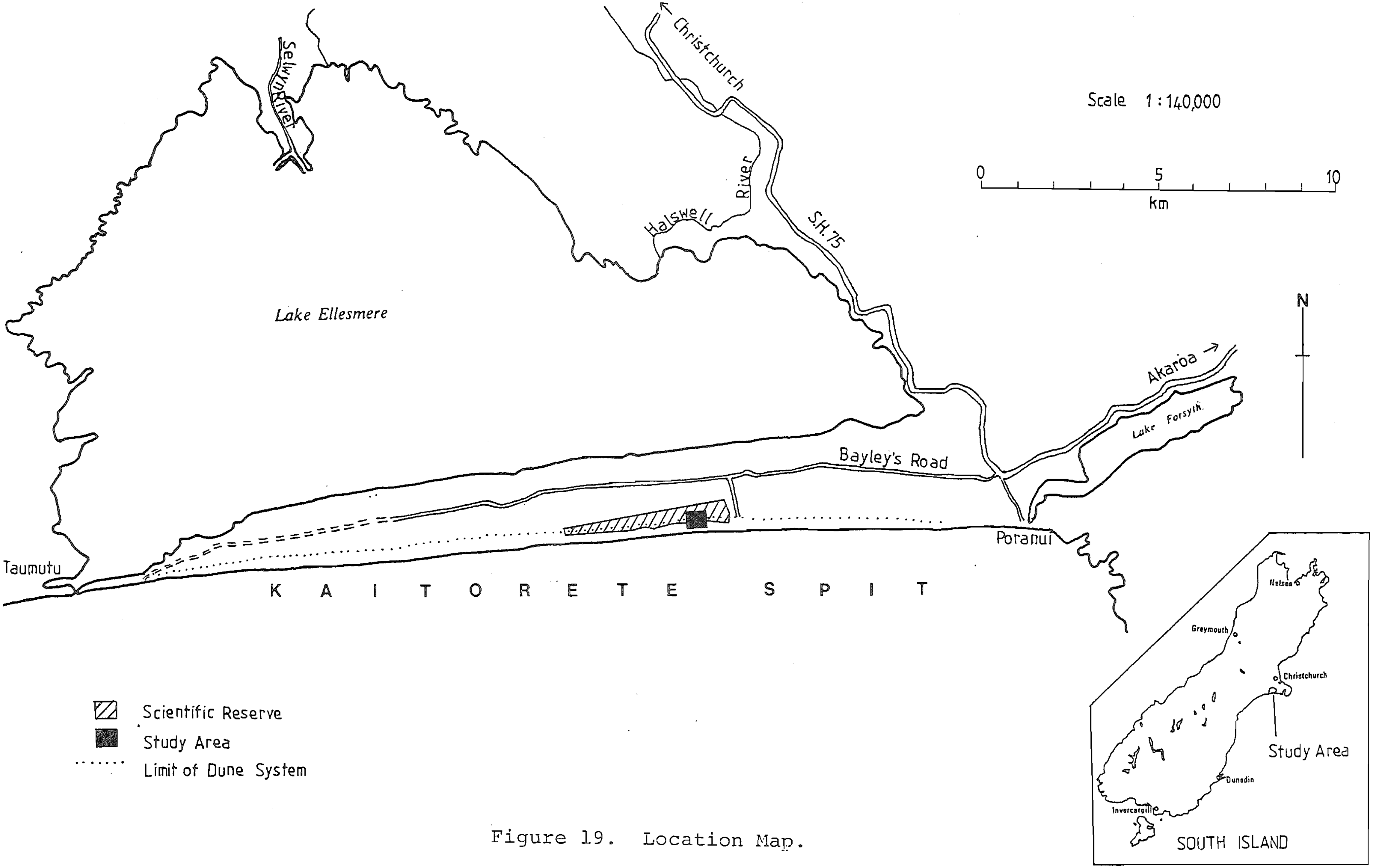


Figure 19. Location Map.

finally joined to Banks Peninsula in the east. As is typical of other barriers, its orientation lies at right-angles to the direction of wave approach, and is not influenced by the contours of the shoreline (Lewis, 1938).

The basement material consists of deposits of greywacke gravel that have been transported northwards by the prevailing north-east ocean drift. These deposits originate mainly from the coastal truncated margins of the Canterbury Plain fan gravels to the south, which in the last 5-7,000 years B.P. have undergone rapid erosion after the post glacial rise in sea level (Kirk *et al*, 1977). The gravel was deposited because the northward movement of these sediments was obstructed by Banks Peninsula.

Changes in the position and dimensions of the barrier in the past have been due to retrogradation and progradation. Coastal erosion is still occurring today at the western end of the Spit, resulting in the opening of Lake Ellesmere to the sea. Conversely, the eastern end is prograding, which has closed the sea access of Lake Forsyth.

4.3 THE DUNE SYSTEM

The sand dunes are restricted to the south side of the Spit. They begin 3 km west of Poranui Point and form a continuous narrow coastal fringe almost to Taumutu, terminating at the mouth of Lake Ellesmere.

Dune building began about 2,000 years B.P. (Armon, 1970). Because of the limited supply of sand, the dunes were initially confined to the western end of the Spit, but formation continued eastward as a result of the erosion of gradually accumulated sand from the former. The most well developed dunes are 8 km east of Taumutu. From either side of them the height and width of the dune system gradually decreases along the rest of the Spit.

The structure of the dune system appears quite complex and irregular, although definite zones running parallel to the shoreline are discernable. Behind the foreshore is a strand line of coarse sand and gravel covered by driftwood. Adjoining this is a narrow gently inclined foredune ridge of coarse sand largely covered in *Desmoschoenus*. It seems that this is where most of the sand that is washed up on the beach is deposited. Towards the Spit's western end the sea has eroded the foredune, creating a steeper truncated coastal face.

Behind the foredune is a system of parabolic dunes, and associated deflation hollows (blowouts). Arms of the parabolic dunes run transversely from the foredune in the same direction as the onshore southwest wind, where they connect with a hindshore dune ridge (reardune) which runs parallel to the shoreline. These arms separate a series of blowouts that occur between the foredunes and reardunes. The reardunes are the highest in the dune system. Most of them have a gentle slope and are more stable than the foredunes. They are predominantly covered in *Desmoschoenus* but also have *Muehlenbeckia complexa* and *Carmichaelia appressa* frequently growing on them.

Figure 20. Foredune, Kaitorete Spit dunes, looking east

Figure 21. Blowout and eroding transverse dune Kaitorete Spit dunes, looking south-east

Figure 22. Reardunes and blowout, Kaitorete Spit dunes, looking east

Figure 23. Grassland and remnant dunes in the distance, Kaitorete Spit dunes, looking north-west

The blowouts have been largely denuded of sand, which has exposed the flat rounded stones of the Spit's basement. *Carex pumila, Raoulia australis* and *Scleranthus biflorus* are common blowout plants. Occasional solitary clumps of pingao also occur. Unlike most other dune systems there are no slacks (wet depressions) associated with these blowouts. This is because the gravel basement arrests deflation well above the water table.

A broken line of remnant dunes, 2-3 m high, dot the grassland to the north of the main line of reardunes. They are low in profile and probably represent the earliest line of dunes formed. Their vegetation cover is typically xerophytic including such plants as *Pteridium esculentum* (bracken), *Muehlenbeckia complexa, M. astonii, Clematis afoliata, Rubus squarrosus, Carmichaelia violacea* and *Hymenanthera crassifolia*. Between the rear dunes and the remnant dunes is either a strip of grassland or a sand plain composed of fine sand that has been blown landward. Small colonies or solitary plants of pingao occur on these landforms, but are rare.

Although the dunes are generally quite stable, areas of active sand movement exist. Wind channelling is evident on both foredunes and reardunes. The sand that is displaced from such channels is deposited on the lee side of the adjacent dunes. Where large channels have breached the reardunes sand has been deposited as narrow tongues on the adjoining grassland.

4.4 THE PHYSICAL ENVIRONMENT OF THE DUNES

Investigations of the soils and climate of the Kaitorete Spit dune system have been conducted by Wraight

(1957) and Peace (1975) respectively and are summarized below.

4.4.1 Sand and Soils

The dunes are composed of Kairaki sand. It is unusually coarse. About 80% have a particle size of 2 - 0.2 mm diameter. Due to the winnowing effect of the wind, slightly finer grained sand is found on the rear dunes than on the foredunes. There is little or no topsoil differentiation, with signs of A horizon development apparent on only the rear and remnant dunes, (Kairaki Brown Sand).

Poor soil development is largely due to the prevalence of semi-arid climatic conditions. The resultant sparse cover of xerophytic vegetation and the paucity of soil invertebrates and saprophytes are not conducive to the production and breakdown of organic matter. Preliminary investigations by Wraight (1957) and Burrows (1969) have indicated that the nutrient status of the dune soils range from 'low' on the younger coastal dunes to 'medium' on the older inland dunes. The most deficient of the major nutrients is nitrogen. Although salt spray is carried onto the dune system by onshore winds the amount of salt present in the sand moisture is negligible (refer to Section 6.4.3).

4.4.2 Water Relations

The Spit receives an average of 515 mm of rain per year with minimums as low as 385 mm. These are comparable to figures for the semi-arid parts of Central Otago. Much of the precipitation falls as light showers. Generally there is more rain during winter than summer.

Summer droughts are common. The amount of rainfall is exceeded by high rates of potential evaporation for all months except June and July and sometimes May and August. The lowest rate of evaporation is on the foredunes. Vapour pressure deficits higher than 0.5 mm prevail for at least 13 hours per day during summer, and several hours per day in autumn. During winter, diurnal changes in relative humidity are usually between 95-65% but in summer this range increases to 90-40%. Extremes of less than 20% have been recorded.

The accumulation of litter at the sand surface, (as on the reardunes), tends to intercept rainwater and restrict infiltration. Conversely, where litter is incorporated within the substrate, as for the top 5 cm of the remnant dunes, the soil's water holding capacity is increased. For this reason the amount of soil moisture decreases below 5 cm on the remnant dunes while at all other sites there is an increasing moisture gradient with increasing depth.

Field capacities over the whole of the dune system are very low due to the large pore size of the sand, but the water that is present is not bound to the same extent as soils with high organic matter or clay content, and is therefore more freely available to plants.

High transpiration rates in summer, especially of the vegetation on the remnant dunes, have an important effect in reducing soil moisture. The blowouts retain more moisture than other sites despite also having the highest evaporation rate. This may be attributable to the absence of rainwater interception and run-off, and the lack of plants to remove water by transpiration.

Water vapour movements which are responsible for causing internal and external dew formation are very important in contributing to the water content within the dunes (Lush, 1948). Dew is formed by the condensation of moisture from a warm air mass onto the cooler sandy substrate. It is also formed within the dunes by an upward movement of water vapour to drier warmer strata. The vapour condenses as these layers cool at night. Such phenomena occur frequently and are especially common during the summer months.

4.4.3 Temperature

The dunes experience a large seasonal range in air temperatures. A winter minimum of -7.5°C and a summer maximum of 37°C have been recorded. Surface temperatures are even more severe with 52°C being recorded on the north facing slopes of the reardunes. Such extremes are more typical of the rear and remnant dunes than the foredunes, temperatures for the latter being slightly ameliorated by sea breezes. Temperatures below the sand surface have the smallest range, and this range decreases with increasing depth.

4.4.4 Wind

The dunes have a relatively high mean wind reading of 155 km per day. Prevailing winds are from the northeast. However, the southwest wind seems to be the most important for it is responsible for the orientation of the parabolic dunes and wind channels, and for the influx of new sand to the system. Gale force winds, although infrequent, are either from this direction or from the northwest. Seasonal differences are also noticeable. May, June and July have the lowest totals of wind run dominated by winds from the south and southwest, while for the rest of the year, especially during early summer, the highest totals have been recorded of winds predominantly from the northerly quarter.

Due to the sand's coarse grain size, winds must reach 4 or higher on the Beaufort Scale before sand movement occurs. The amount of sand movement follows a decreasing gradient from the foredunes to the reardunes. There is no appreciable sand movement on the grassland, sand-plain or remnant dunes because of their relatively sheltered and stable nature. Strong onshore winds frequently carry saltspray. Although some of this reaches the south faces of the reardunes most of it is deposited on the foredune especially near the strand interface.

Low nutrient status, rainfall and waterholding capacity, high potential evaporation, a wide range of temperatures both diurnally and seasonally, relative windiness and a semi-stable substrate all contribute to the distinct character of the Kaitorete Spit dunes. It is a truly xerophytic environment and one to which *Desmoschoenus spiralis* is suited.

4.4.5 Comparison of the Climate During the Period of Fieldwork with the Climate of Previous Seasons

The closest meteorological station to the Spit is

21 km north, at Lincoln College. Peace (1975) found, as a result of her climatological investigations, that the climate of the Spit and Lincoln were similar with the exception of rainfall which was 20% lower at the Spit. Temperatures were comparable and wind run was only 4.5% greater at the Spit than at Lincoln. Potential evaporation figures are expected to be higher at the Spit than at Lincoln. To find out whether the climate at the Spit for the duration of fieldwork (December 1980 to the beginning of April 1982) was similar to the climate of previous seasons, climatological data taken at Lincoln from September 1980 to March 1982 were compared with Lincoln's average monthly records.

Results: Figures 24, 25 and 26 show climatological data from the Lincoln meteorological station giving both the monthly records (continuous lines) and the average monthly records (broken lines) for mean wind run, rainfall, and mean temperature respectively. Figure 27 shows the monthly and average monthly potential evaporation at Lincoln.

The monthly mean temperatures were very similar to the average monthly means. The summers of 1980-81 and 1981-82 were both over 1°C warmer than usual. Also February's temperatures for both years were as high or higher than January's temperatures instead of being slightly lower. The summer of 1981-82 was longer than usual with December having a mean temperature 2°C higher than the average monthly mean, and March being 1.3°C higher than average. Winter 1982 was later than usual with the lowest temperatures occurring in August instead of July.

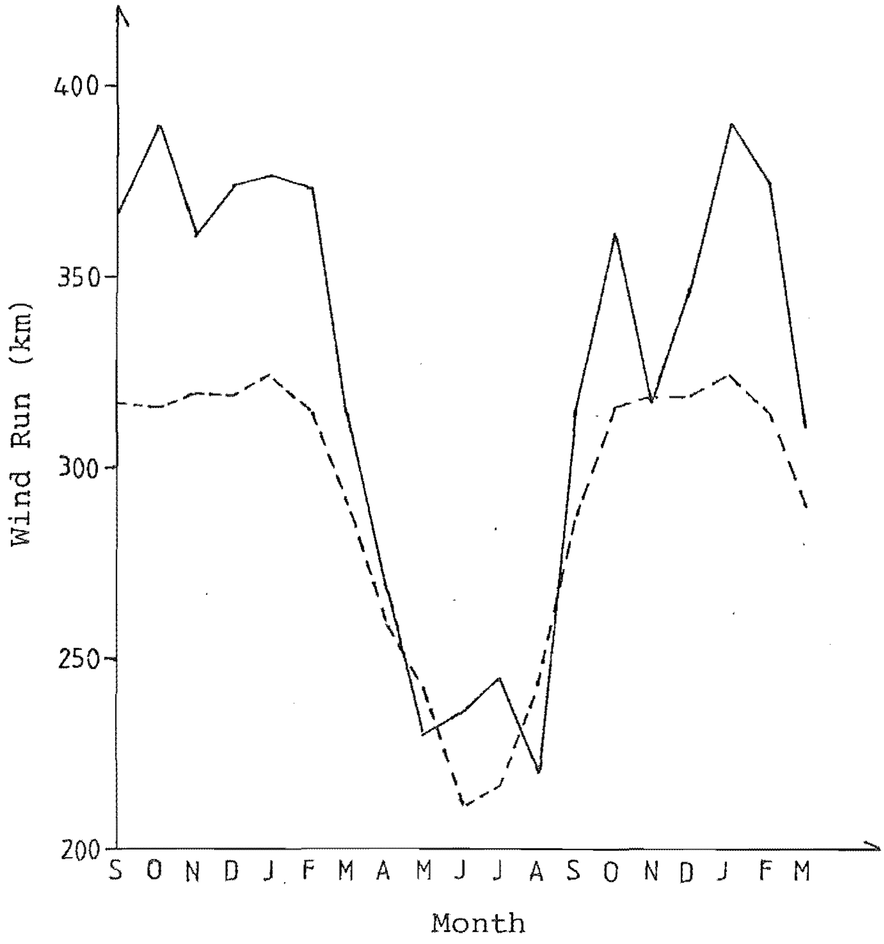


Figure 24. Monthly Mean Wind Run, Lincoln, September 1980 to March 1982 ——, and Average Monthly Mean Wind Run, Lincoln, 1928-1979 – – –

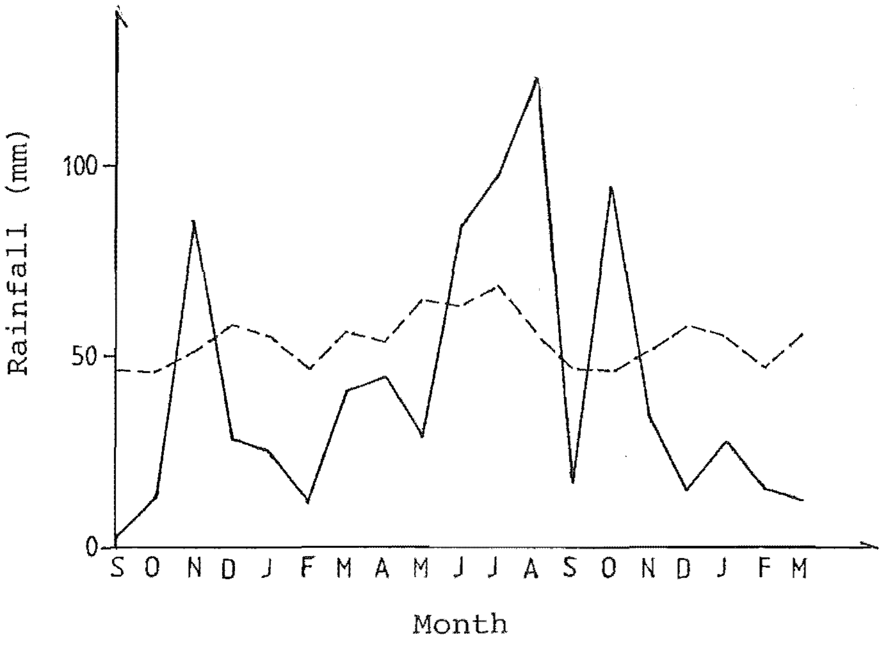


Figure 25. Monthly Rainfall, Lincoln, September 1980 to March 1982 ——, and Average Monthly Rainfall, Lincoln, 1881-1979 – – –

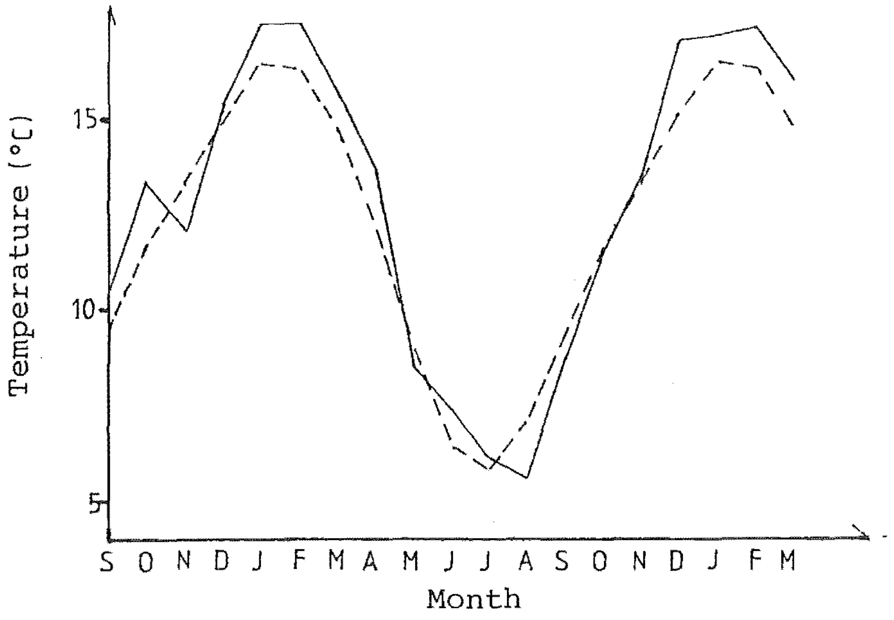


Figure 26. Monthly Temperature, Lincoln, September 1980 to March 1982 ———, and Average Monthly Mean Temperature, Lincoln, 1881-1979 — — — —

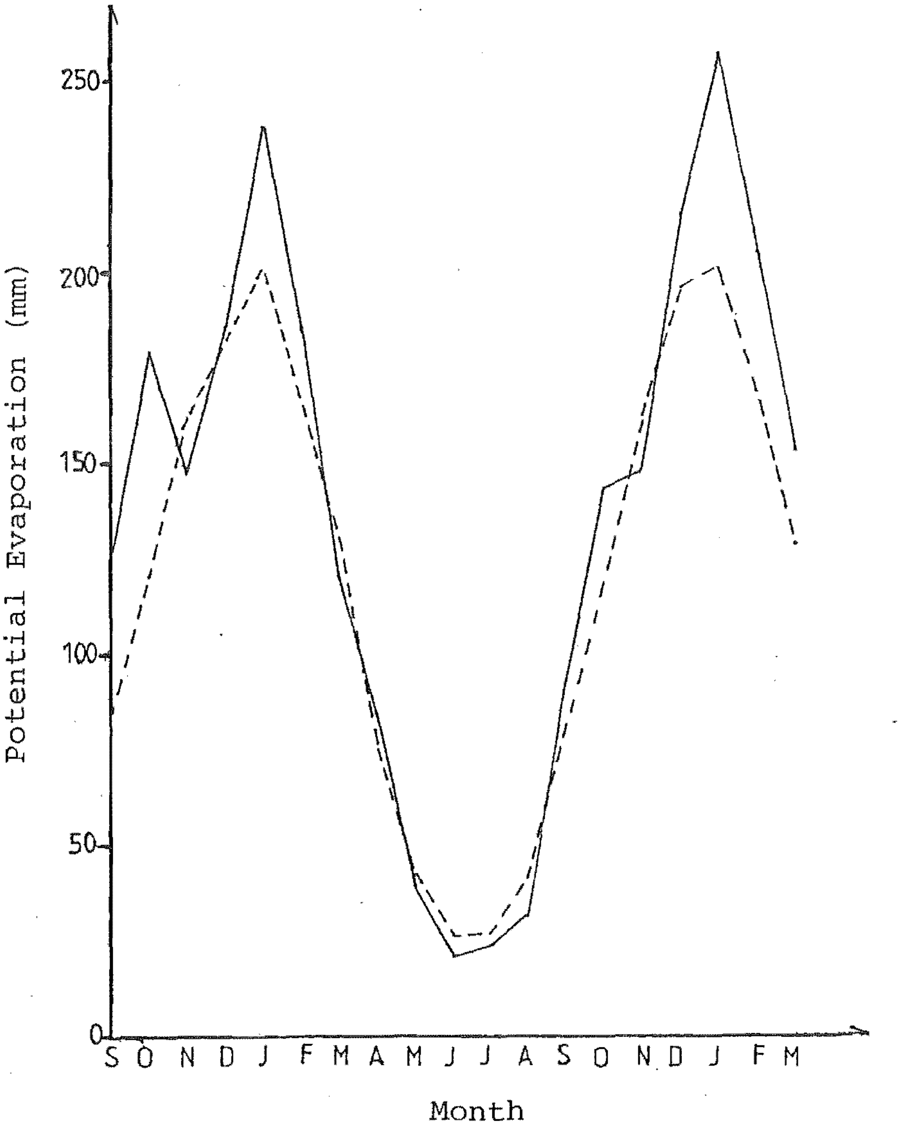


Figure 27. Monthly Potential Evaporation, Lincoln, September 1980 to March 1982 ———, and Average Monthly Potential Evaporation, Lincoln, 1964-1979 — — —

Monthly potential evaporation showed similar trends to the average monthly totals. Evaporation was higher during the summer of both seasons, especially summer 1981-82, when January's P.E. was 56 mm over the 201 mm average.

Although the monthly mean wind run showed the same trends as the average monthly means, windier conditions than usual were experienced for all months except May, August and November 1981. Wind run was greatest during spring and summer of both seasons with the monthly means being approximately 50 km higher than average. Despite the fact that there was more wind run than usual, there were no storms during the period of fieldwork. Between Setptember 1980 and March 1982 'strong winds' (6 on the Beaufort Wind Scale) were recorded for only 12 days and 'near gales' (7 on the B.W.S.) for 3 days (22/9/80, 26/9/80 and 27/1/82, all nor'westers). On only one day (22/11/80) did wind run exceed 700 km, (N.Z. Met. Service).

Monthly rainfall deviated much from the average monthly totals due to its inherently variable nature from year to year. Winter 1981 had over 60% more rain than usual. The summer of 1980-81 had 2.4 times less rain than usual and the summer of 1981-82 had 2.7 times less rain than usual. March 1982 ended the driest four month period recorded at Lincoln College since weather observations began there in 1881 ('The Press', 14/4/82).

In conclusion, deviations from the climate averages during the months of fieldwork were such that the winter was wetter, windier and later than usual for Lincoln, the summers were longer, warmer drier and windier than usual for Lincoln, and that it is reasonable to assume the above is also true for the Spit.

4.5 THE STUDY AREA

The well developed dune system within, and south of the Kaitorete Spit Scientific Reserve was chosen as a study area. It is situated at grid reference S94/5965197 (NZMS1), 9.5 km west of Poranui (Figure 19).

The study area exhibits the typical foredune to ancient dune sequence and is representative of the Kaitorete dunes in general. *Desmoschoenus* is the main plant cover over most of these landform units, occupying a wide variety of microstations and being subjected, in varying degrees, to a range of environmental factors.

The area is reasonably accessible, being 0.8 km west of the public road servicing the sand quarry to the east of the reserve. At the same time, chances of human interference were slight. Visitors to this part of the Spit, and indeed to most of the Spit, are few in number and restrict themselves mainly to the foreshore.

4.5.1 The Sites

The study area itself is 450 m^2 and comprises 14 sites, A to N, (Refer to Figure 28). The nature of the fieldwork was such that the sites could remain undetected to the casual observer. Sites A, B, C, D and N occur on the foredune, B being on the lee side of a transverse dune. Sites E, F and G occur on the reardunes. E and G are north-facing and F is south-facing. Sites H and I are small

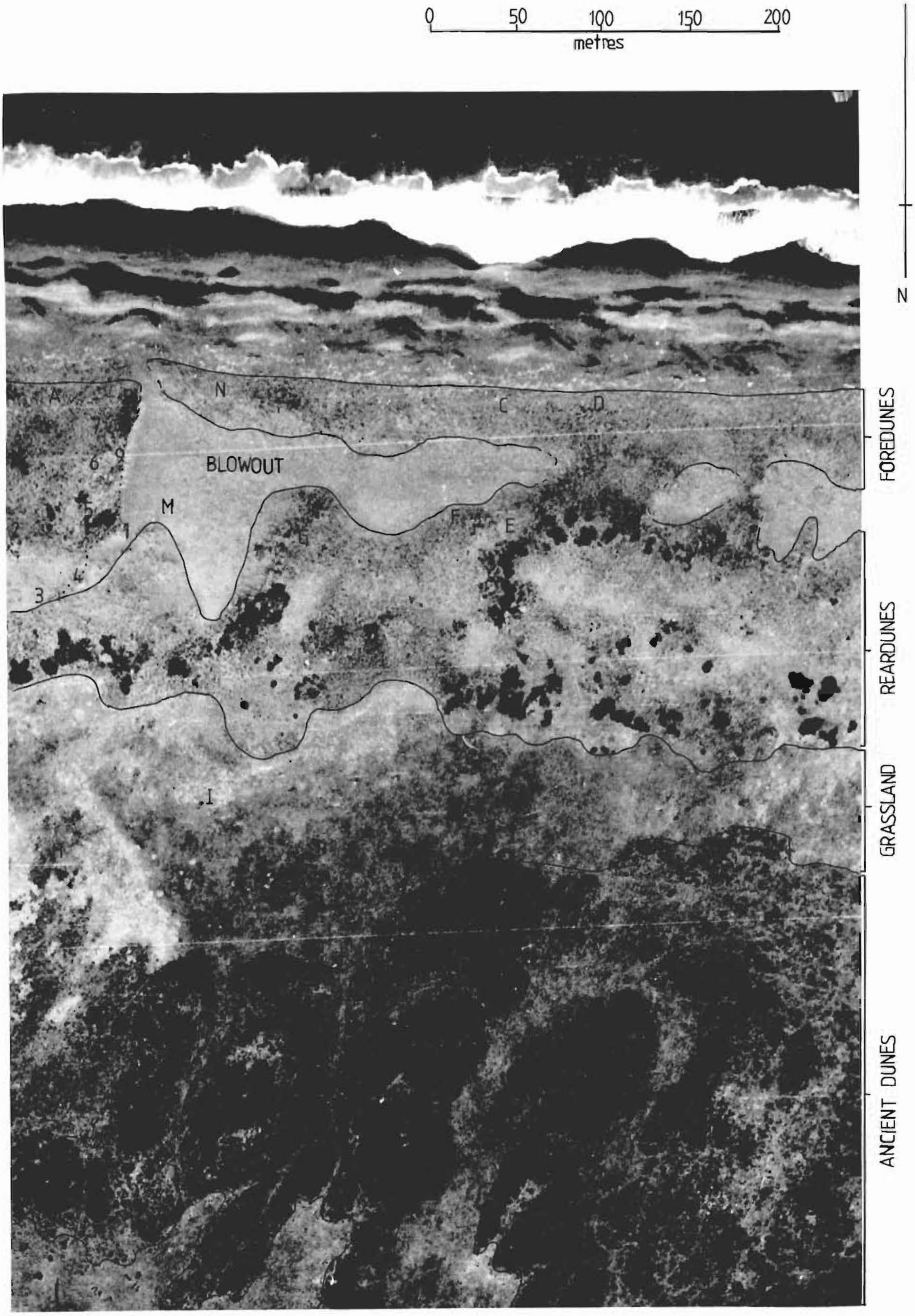


FIGURE 28 The Study Area

.... ridge of eroding transverse dune colonies of pingao occurring on shallow sand mounds on the grassland. Site I is divided into subsites I_s and I_{ns}. Site J occurs on the grassland, and sites K and L occur on the remnant dunes. Site M is on a blowout at the toe of the transverse dune.

4.5.2 The Investigations

Quantitative analyses of pingao populations were carried out at sites A to I. Growth analyses, phenological observations, and measurements of soil water content and movement of sand were carried out at sites A, C, E, G, and H. Soil water content measurements were also taken at sites I, J, K and L. Stakes 1 to 9 were positioned around the eroding transverse dune to monitor sand movement. A sand burial experiment was carried out at site N and a sand accumulation experiment was carried out at site I. Seedlings studies were carried out at site M. (Refer to Tables 1 and 2, and Figure 28).

Table 1. Sites of Investigations

Site	Quantitative Analysis	Growth Analysis	Soil Water Content	Sand Movement	Salt Content	Burial, or Accumulation of sand	Seedling Studies
A	✓	✓	✓	✓	✓		
B	✓						
C	✓	✓	✓	✓			
D	✓						
E	✓	✓	✓	✓	✓		
F	✓						
G	✓	✓	✓	✓			
H	✓	✓	✓	✓			
I	✓		✓	✓		✓	
J			✓				
K			✓				
L			✓				
M							✓
N						✓	

Table 2. Stake Positions

Stake	Position
1	windward side, base of transverse dune
2	leeside, 50 m from transverse dune crest
3	leeside, 10 m from transverse dune crest
4	crest of transverse dune
5	leeside, 10 m from transverse dune crest
6	
7	
8	leeside, 100 cm from transverse dune crest
9	

CHAPTER V

FRUIT, SEED AND SEEDLING ECOLOGY

5.1 INTRODUCTION

This chapter deals with the dispersal of the fruit of *Desmoschoenus spiralis*, the predation, viability and factors controlling germination of its seeds, and aspects of the ecology of its seedlings.

5.2 DISPERSAL

5.2.1 Adaptations for Wind Dispersal (Anemochory)

Wind is the only known agent responsible for the dissemination of *Desmoschoenus* fruit from the parent. This is achieved by jactitation (Ridley 1930), a mechanism involving the passing of wind past a seed-bearing structure causing the seed to be thrown from it.

Throughout flowering and fruiting the culm elongates from its base in the centre of leaf tufts. The glumes and fruit dissociate from the spikelet rhachillae upon maturing but persist on the inflorescence as loose clusters of spirally arranged spikelets. At this stage the culm has elongated to the extent that the fruit are borne well above the leaves and are exposed to the wind. The bracts subtending the spikelet clusters ascend and exceed the inflorescence apex. They are spirally arranged around the axis and this formation acts as a wind trap. Due to the rigidity of the culm, the whole reproductive structure is jerked back and forth upon the passing of wind through the bracts, resulting in the loose fruit being thrown from it. The glumes usually fall separately and therefore do not play any role in dispersal.

A seed shadow is generated around each inflorescence, as the majority of fruit fall within a few metres of the parent and collect in sheltered sand hollows or amongst neighbouring tufts with other litter. Fruit thrown onto open sand, though, may be further dispersed by wind.

The average weight of the fruit of *Desmoschoenus* is 1.83 mg, (N = 50). Its weight is comparable to the diaspores of *Papaver dubium* (1.35 mg), *Casuarina equisetifolia* (1.42 mg), and lighter than *Eucalyptus globulus* (3.03 mg) all three of which are wind dispersed (Ridley 1930). The fruit is of large size for its weight, having an average surface area of 16.4 mm^2, and a surface area to weight ratio of 9.0 $mm^2 . mg^{-1}$.

The outer surface of the pericarp is very smooth and its hemispherical shape causes little friction. The exposed nature of the dune environment, coupled with the smooth relief of sandplains and foreshore make it possible for fruit to be disseminated by wind over large distances within the dune system. Although these dune characteristics are not developed to the same extent on Kaitorete Spit as on other dune systems, pingao fruits have been observed 28.5 m from their nearest seed source. It may be assumed that fruit travel even larger distances. Such distances are sufficient to enable dispersal of fruit to areas which may arise within the dune system that are suitable for seed germination. Although wind dispersal is non-directive, the production of a large number of seeds each year compensates for the non-establishment of seeds blown to unfavourable habitats and increases the chance that some seeds will find a "safe site" (Stebbins 1971).

5.2.2 Adaptations for Dispersal by Sea (Hydrochory)

Desmoschoenus fruit has been found at high tide mark at Kaitorete Spit. This observation, coupled with the fact that pingao has a widespread New Zealand distribution, suggests that its fruit may be dispersed long distances by sea.

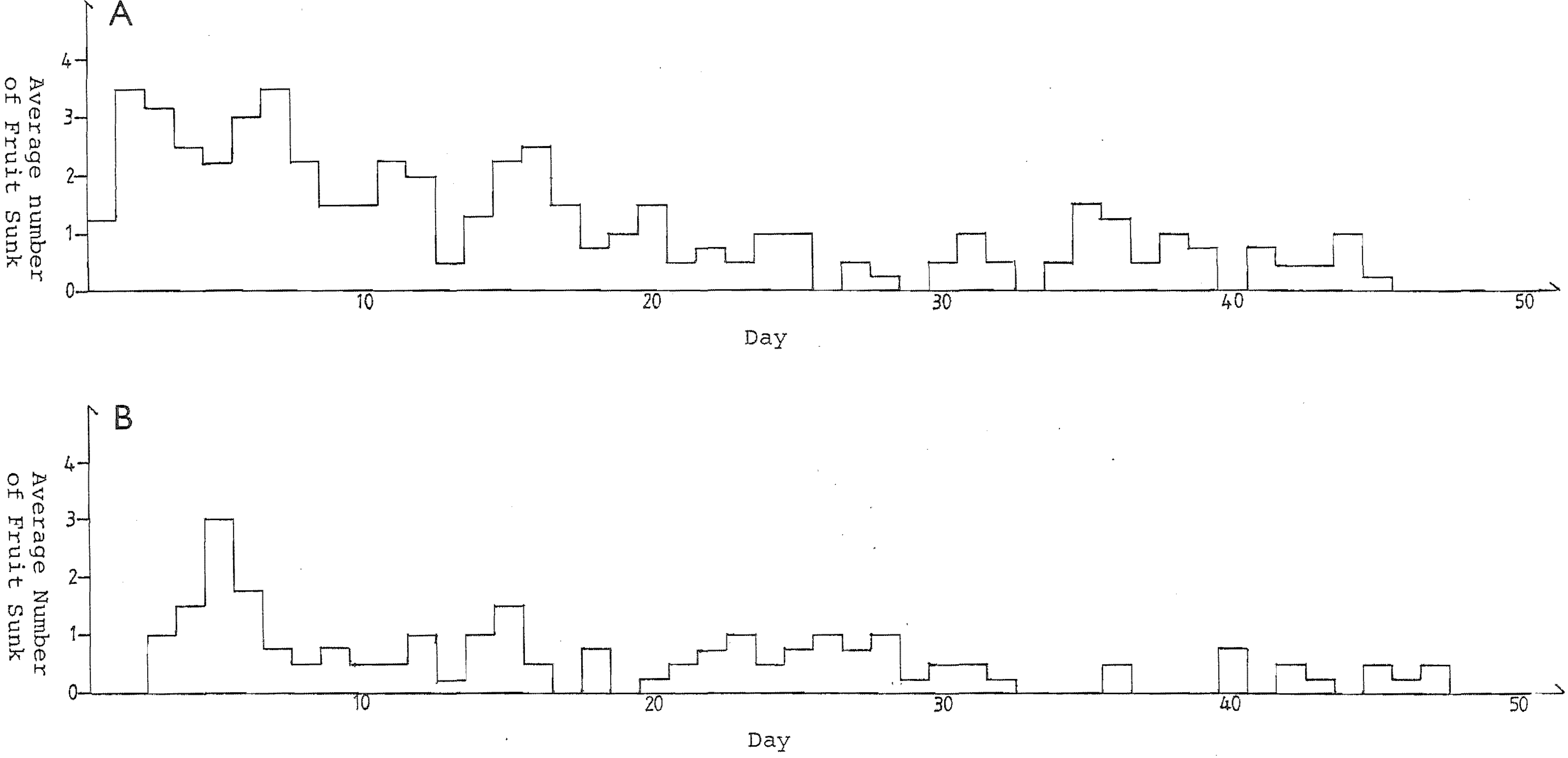
Floatation experiments were carried out to determine how long *Desmoschoenus* fruit is able to float on freshwater and seawater, and whether the seed is viable at the end of these treatments.

Method and Materials. Fresh fruits were used in 50 ml vials containing 25 mls each of either freshwater or seawater. Each medium had four replicates and each vial contained 80 seeds. Vials were intermittantly shaken for a total of 30 minutes per day (Kerin and Evanari, 1974) to better simulate natural conditions. A daily record was kept of the fruit that sank. Care was taken to ensure that the vials were not air tight and that the experiment was operating under normal atmospheric pressure. The experiment was stopped after 50 days. Two replicates of the floating and sunk seed of both treatments were tested for seed viability (for method see Section 5.4.2.2). The other two replicates of both treatments were incubated in an attempt to germinate the seeds (Section 5.4.2.1.g).

Results and Discussion. The average specific density of the fruit is 0.38 g. cm^{-3}. It is therefore 2.6 times less dense than freshwater and 2.7 times less dense than seawater. The main reason for this lies in the fact that between the seed and pericarp there is a large air space, which accounts for an average of 62.6% of the volume of the fruit. The pericarp is hard and impermeable. It completely encloses the seed and protects it from physical damage and the effects of seawater.

For both fresh and seawater treatments, floating ability decreased with time. The fruit slowly imbibed water and sank (Figures 29 & 30). During the first 12 days the rate of sinking for both treatments was highest. It decreased gradually, until towards the end of the experiment no further sinking was observed. The lag at the beginning of the experiment, which was longer in the case of the fruit floating in seawater, is assumed to be the time required for water to be absorbed before sinking occurred.

The rate of sinking was slower for fruit in seawater than for the freshwater fruit. 66.9% of the seawater fruit remained floating at 50 days compared with 31.3% of the fruit still afloat in freshwater. It is suggested that the difference in the densities of seawater and freshwater are responsible for the difference in floatation results. Splitting of the pericarp as a result of shaking was not observed, although some splitting is likely in natural conditions as a result of wave action.



4 replicates each of 80 fruits
for both treatments

Figure 29. Average number of fruit sunk over 50 days in (A) freshwater and (B) seawater.

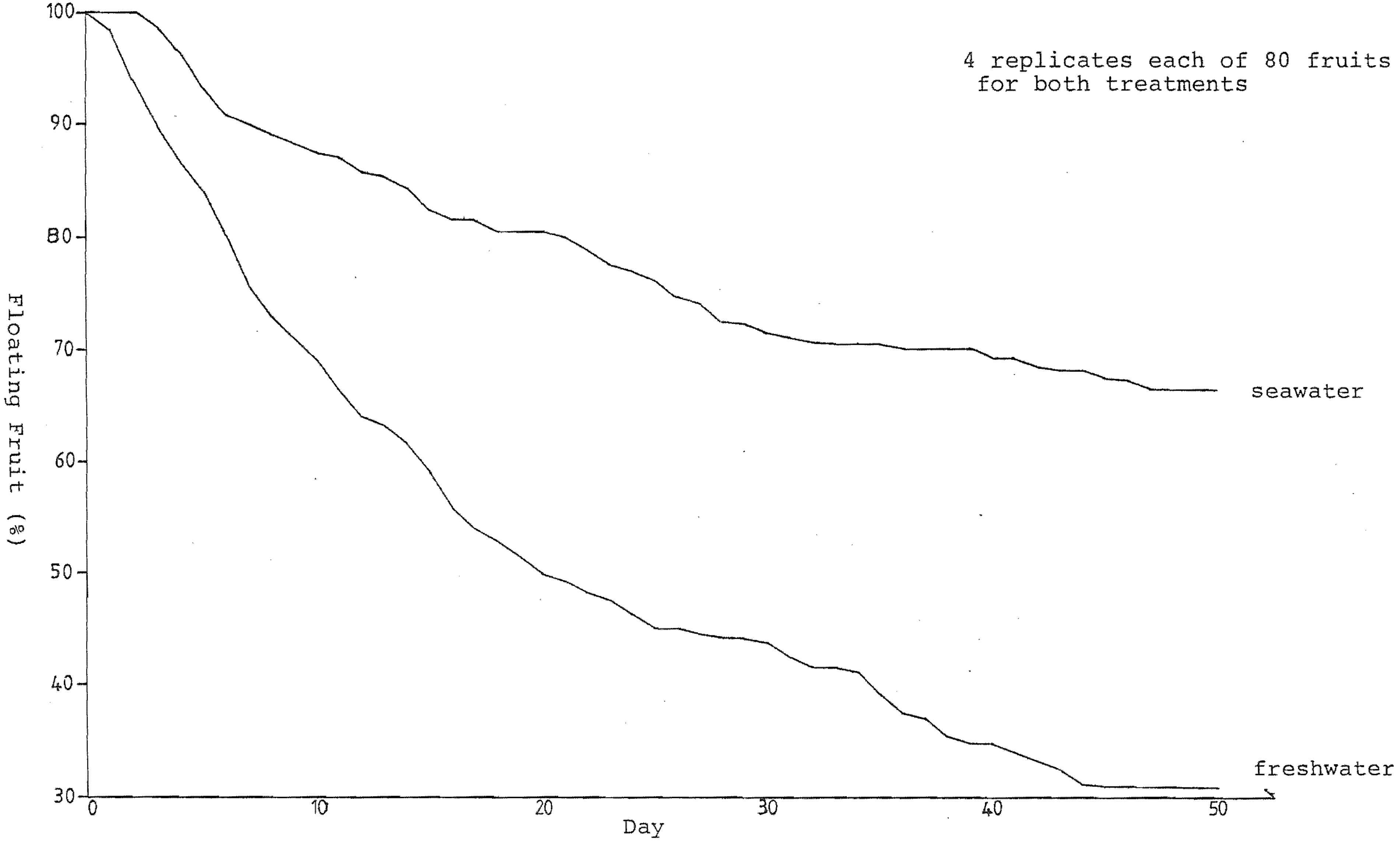


Figure 30. Duration of fruit floatation expressed as a percentage

Although the experiment was stopped after 50 days, it is expected that some fruit are capable of floating for a longer time span. Brodie (1960) states, with reference to ocean currents around New Zealand, that the top few centimetres of seawater travel approximately in the direction of the gradient wind and at 2.2% of its velocity. The fastest drift he recorded was 16.3 km per day, although most of his drift cards covered an average distance of 6.4 km per day (the average interval being 60 days). With favourable offshore winds, it would therefore be possible for some fruit of *Desmoschoenus spiralis* to cover distances of ocean in excess of 320 km.

The viability of floatation experiment seeds and accompanying *t* tests are presented in Appendix III, Tables 24 and 25. The highest viabilities were found of seeds that were still afloat after 50 days. The *t* tests confirm that the viabilities of freshwater and seawater unsunk seeds were significantly greater than the viabilities of freshwater and seawater sunken seeds. The freshwater and seawater floating seeds were 51.6% and 49.1% viable respectively. From observations during fruit dissection it seems that most of the inviability was caused by water entering some of the floating fruit which over time had rotted the seeds. Of the freshwater and seawater sunken seeds 17.9% and 12.4% respectively were viable. Most of the sunken fruit that contained viable seeds were waterlogged but it seems that the chaffy seed testa is only semi-permeable to water which would temporarily retain the seeds' viability. Inviability of the sunken seeds was due to rotting.

5.3 SEED PREDATION

Fruit was collected at Site A on 14 April 1981 and 1 August 1981 from sand hollows and around the bases of pingao tufts, where fallen fruit had accumulated. From both collections 10 samples of 100 fruit were counted to determine the percentage of fruit that had been robbed, by insects, of their seeds. Of the fruit collected in April, 26.5% had had seed removed from them. Of the fruit collected in October, 95.0% had been robbed. Insect exoskeletons found amongst the fruit and glumes were unidentified. Some of these insects may be assumed to be responsible for the predation.

As Janzen (1971) states, seed predation by insects is a highly structured event and has co-evolved at the chemical, spatial and temporal levels. The seeds' high nutritive value, the abundance of fruit produced per square metre, (Section 6.2.5.2) and the accumulation of much fruit in sheltered places, provides insects with a large seasonal food source that can be easily utilized. The chance of predation is extremely high for seeds whose fruits collect in 'seed sinks' sheltered from the wind. As the above results show, seven months after fruit shed only 5% of the seeds in such sinks remained uneaten. Escape from predation is more likely if the fruits are widely disseminated. The greater the area over which the fruit is able to disperse, the less chance there will be that they will accumulate in large numbers in any one place. Solitary pingao fruits are extremely inconspicuous amongst the sand. Only when they are close to the parent in conspicuous 'seed sinks' do the fruit lend themselves to predation.

Predation by insects has never been observed while fruits are still on the inflorescence. Instead, flocks of goldfinches *(Carduelis carduelis)* have been seen alighting on the seed heads and feeding on the fruit. They have been noticed foraging amongst the sand dunes from February to May during which time the fruit are ripening and being shed.

Pipits *(Anthus novaeseelandiae)* and skylarks *(Alauda arvensis)* have also occasionally been seen feeding while perched on the fruiting heads of pingao, but it is unknown whether seed predation or insect gleaning was occurring. Pipits are largely insectivorous while skylarks are largely graminiferous. The latter include, as a major part of their diet, cyperaceous seeds especially in autumn and winter (Garrick, 1981). This suggests that skylarks may feed on *Desmoschoenus* seed when it is available.

5.4 SEED GERMINATION AND VIABILITY

5.4.1 Introduction

Seed germination and seedling establishment are the most critical times in the life cycle of most plants. Nearly all mortality suffered by seedlings occurs during the first year of life (Stebbins, 1981). It is therefore advantageous for the survival of a species that the germination of seed is regulated to coincide with the onset of conditions favourable for seedling development. To this end many seeds exhibit some form of dormancy mechanism.

Quiescence, which is not a true dormant state (Villiers, 1975) occurs in most seeds, germination being prevented by the absence of one or more of the basic conditions required for normal growth (i.e. warm temperature, adequate water and aeration). True dormancy, however, can result from one, or a combination, of the following.

Properties of the tissue surrounding the embryo:

i. mechanical resistance of the testa or pericarp to embryo growth,
ii. impermeability of the outer coats to water and/or gases,
iii. chemical inhibitors within the outer coat.

Properties of the embryo itself:

i. immaturity of the embryo,
ii. metabolic block within the embryo.

The breaking or removal of the outer coat is well known frequently to promote germination (Toole *et al*, 1956; Koller, 1964). Other methods of destroying the integrity of the pericarp or testa include freezing (Yeo and Dow, 1978) and physical or chemical scarification (Rolston, 1978; Maguire, 1976). Artificial abrasion of the outer coat of some cyperaceous species increases the germination percentage (Jermy and Tutin, 1968).

Physiological dormancy, resulting from a metabolic state of the embryo that prevents germination, is known in some species to be overcome by treatment with growth regulating hormones. It is generally accepted that such dormancy is controlled by the balance between hormones which impose dormancy and hormones that stimulate active growth (Frankland and Wareing, 1966; Addicott and Lyon, 1969; Mayer-Pokeljoff and Mayber, 1975). Gibberelic acids have been detected in germinating seeds (Phinney and West, 1960), and treatment of dormant seeds with GA_3 is known in many cases to decrease any after-ripening period that may be present (Stokes, 1965), and also promote germination (Edwards, 1976; Jarvis and Wilson, 1977; Maguire, 1980). GA_3 is also known to promote the germination of certain light requiring seeds (Lang, 1965; Koller *et al,* 1964) and seeds that otherwise require either chilling or high temperatures (Stokes, 1965; Mayer-Pokeljoff and Mayber, 1975; Wareing *et al,* 1973).

The absence or presence of light is necessary to break physiological dormancy in certain seeds (Wesson and Wareing, 1969; Smith, 1973), the light requirement for the germination of a species usually being consistent with their ecology (Gringe and Jarvis, 1975). The seeds of many species of sandy habitats are negatively photoblastic (Kerin and Evenari, 1974; Barbour, 1970; Batanouny and Ziegler, 1971; Harty and McDonald, 1975) which suggests that seeds can only germinate after being buried to a certain depth by sand. The ecological advantage of such a dormancy mechanism is that seeds will germinate in the moist region below the hot dry layer.

Dormancy may also be overcome in seeds which are after-ripened by subjection, in the imbibed state, to low temperatures (Yeo and Dow, 1978). The physiological changes which occur during after-ripening are such that they proceed most rapidly at temperatures slightly above freezing point (Stokes, 1965).

Both coat imposed dormancy mechanisms and embryo related dormancy mechanisms often occur in combination. The pericarp and/or testa must undergo physical change and the embryo physiological change before germination occurs. Each of those mechanisms may be independent or interdependent, and may occur synchronously or consecutively (Vegis, 1962).

With these factors in mind, an attempt was made to determine whether or not *Desmoschoenus spiralis* seed exhibits dormancy, and if so, the type of dormancy mechanism that is operating and the factors affecting it. It is hoped that this will give an insight into the factors responsible for the breaking of dormancy *in situ*.

5.4.2 Method and Materials

Fallen mature fruit of *Desmoschoenus spiralis* was collected from Kaitorete Spit on 4 April 1982 and stored dry in a paper bag at room temperature. Germination was tested in 9 cm diameter petri dishes containing Whatmans No.1 filter paper over a thin covering of washed white sand and moistened with distilled water (Figure 31). Moist conditions were maintained by the further addition of distilled water when necessary. There were two replicates of each treatment and control with 50 fruits per petri dish. All fruits were surface sterilized with a rinse of 3% sodium hypochlorite solution followed by a thorough rinse with distilled water before incubation.

Incubation was conducted in a growth room with a controlled temperature of 20^{o}C, a photoperiod of 16 hours day and 8 hours night, and photosynthetically active radiation of 190 microeinsteins. m^{-2}. sec^{-1}. Fruits were checked every two days for the first two weeks and once a week thereafter. Germination was considered to have taken place when the coleoptile had emerged. Seeds that had germinated

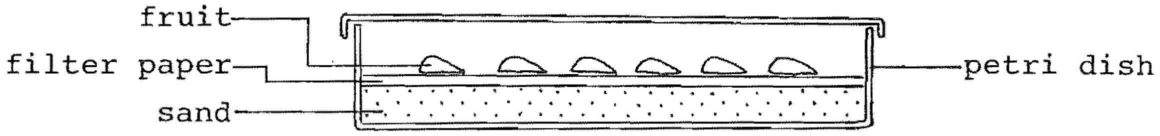


Figure 31. Incubation of pingao fruit

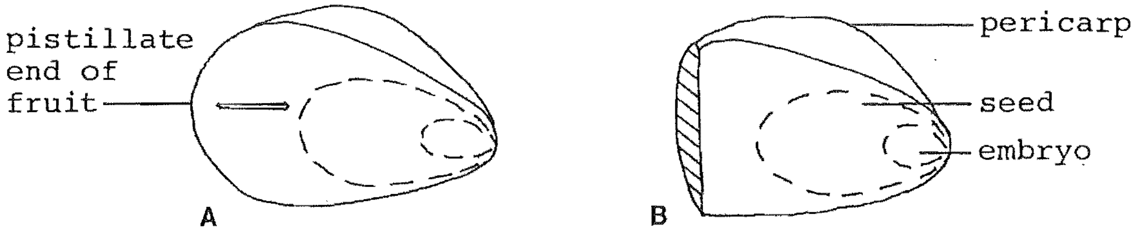


Figure 32. A. Slit pericarp. B. Nicked pericarp.

were moved and attempts were made at growing them. Incubation was discontinued after 63 days.

5.4.2.1 Germination Treatment

(a) Physical Scarification. The effect of physically scarifying the testa was investigated. Physical methods were -

(i) abrasion of the seed coat with sand,
(ii) mechanical rupturing of the seed coat, and
(iii) freezing.

(i) 50 g of fine white sand were placed in a mortar and pestil with *Desmoschoenus* fruit, and very lightly stirred for five minutes until the shine on the pericarp surface was removed.

(ii) Pericarps were ruptured by either applying a minute longitudinal slit along the flat surface of the pistillate end of the fruit, or by completely removing the pistillate end of the pericarp (i.e. nicked), (Figure 32).

(iii) Fruit was frozen net at -10°C for 4 weeks to test its effectiveness in promoting germination by weakening or injuring the testa.

(b) Chemical scarification. Chemicals used to scarify pingao fruit included either a 5% solution of sodium hypochlorite, or a 36% solution of hydrochloric acid. Each replicate was placed in a 100 ml beaker with a 25 ml perforated enamel crucible inverted over it. The solutions were poured into the beakers until the crucibles were submerged. The crucibles were lightly tapped to release trapped air bubbles. This method overcame problems of fruit floatation and therefore the problem of uneven exposure of fruit surfaces to chemicals. Fruits were immersed for 10 minutes or 1 hour in HCl, or for 24 hours in sodium hypochlorite. While soaking in HCl the system was regulated at about 21°C by use of a cold water bath. After soaking, the fruits were rinsed thoroughly with distilled water.

(c) Pericarp Removal. The possibility of physical restriction to embryo development and/or chemical inhibition of germination by the pericarp was investigated by completely removing the pericarp with scalpel and tweezers. Extreme care was taken not to injure the seeds.

(d) Chilling. Fruit were chilled to test for the presence of physiological dormancy. Both intact fruit and sand scarified fruit were cool stored wet and dark for 2 months at 4°C, and then incubated. The pre-treatment of sand scarification negated any effect the pericarp may have had in preventing moisture availability to the seed.

(e) Hormone Treatment. Fruits were incubated with a 10^{-3} M solution of GA_3 as the initial moistening agent. Further moisture additions were made with distilled water. Sand scarified fruits were also subjected to 10^{-3} M GA_3 treatment.

(f) Dark Treatment. In an effort to determine whether germination of pingao seed is inhibited by light, variously treated fruits were incubated in petri dishes enclosed in tin foil. Pre-treatments included, (i) control, (ii) sand scarification, (iii) 2 months cool storage wet, (v) 10^{-3} M GA_3 and (vi) sand abrasion followed by 10^{-3} M GA_3.

(g) Floatation Treatments. Fruit which had remained afloat in seawater and freshwater for 50 days were also incubated in an attempt to see whether such conditions promoted germination.

(h) Dry Stored. Fruit that had been stored dry for six months, and slit six month old seed were incubated to see whether natural after-ripening was necessary for germination. Jermy and Tutin (1968) note that for most Carex species, seeds require an after-ripening period of 3-12 months.

5.4.2.2 Viability

Seed viability tests were performed with tetrazolium (2:3:5 triphenyl-tetrazolium chloride) closely following the method of Moore, 1973. The tests were carried out on freshly collected seed, six month old seed, and 10 month old seed. Pericarps were removed and the end of the seeds opposite the embryo was nicked to facilitate the uptake of tetrazolium. Two replicates of 50 seeds each were treated in a 1% tetrazolium solution on Whatman No.1 filter paper for 24 hours at room temperature. Throughout the viability testing the tetrazolium solution was kept in the dark to prevent light turning the solution pink. Embryos were teased out from the surrounding endosperm tissue with the use of a stereomicroscope. Seeds were considered viable if the embryos stained bright pink.

Replicates of seeds from the floatation experiment also had their viabilities tested.

5.4.3 Results and Discussion

The effects of the various treatments on the germination of *Desmoschoenus* seed is presented in Table 3. Of the 25 treatments, sand scarification and scarification with conc. HCl for one hour (both in light conditions) gave the highest germination successes of 9% and 7% respectively. Overall, there was a very low germination percentage with all other treatments lying between 0% and 6%. Most of the seeds that germinated did so during the second, third and fourth weeks of incubation, the highest rate being in the third week. Only one seed germinated during the five weeks incubation period after the first month.

Unlike some sand dune species, pingao seeds are not negatively phototropic. Even combinations of treatments in the dark did not promote germination. In fact the germination percentage of some dark treatments was less than the same treatments in light conditions.

Brown exudate accumulated on the filter paper under all fruit that had undergone pericarp treatments (excluding pericarp bleaching with sodium hypochlorite, and pericarp removal). The exudate is a pigment which is produced within the pericarp as a response to sunlight. When the exocarp is damaged water is able to permeate into the fruit and the

Table 3. Effect of Various Treatments on the Germination of Pingao Seed (replicates combined, 2N = 100)

treatment in dark

	Treatment	WEEKS 1	2	3	4	5	6	7	8	9	% Total	Brown exudate
1	Control										$^{0}/_{0}$	$^{x}/_{x}$
2	Sand scarification		$^{6}/_{1}$	$^{3}/_{3}$							$^{9}/_{4}$	$^{\checkmark}/_{\checkmark}$
3	Pericarp slitting				1						1	✓
4	Pericarp nicking										0	✓
5	Pericarp removal				2						2	x
6	Frozen wet				2		1				3	x
7	HCl (10 mins)				1						1	✓
8	HCl (1 hour)		3	3	1						7	✓
9	Sodium hypochlorite		3		1						4	x
10	GA_3										$^{0}/_{0}$	$^{x}/_{x}$
11	Sand scarified, GA_3		$^{0}/_{1}$	$^{3}/_{1}$	$^{1}/_{0}$						$^{4}/_{2}$	$^{\checkmark}/_{\checkmark}$
12	Chilled wet										$^{0}/_{0}$	$^{x}/_{x}$
13	Sand scarified, chilled wet		$^{1}/_{0}$	$^{2}/_{1}$	$^{3}/_{1}$						$^{6}/_{2}$	$^{\checkmark}/_{\checkmark}$
14	6 month old seed										0	x
15	Slit. 6 month old seed			1							1	✓
16	Freshwater unsunk										0	x
17	Freshwater sunk										0	x
18	Seawater unsunk		1								1	x
19	Seawater sunk										0	x
	TOTAL	0	15	17	14	0	1	0	0	0		

pigment is able to leach out. Removal of the pigment by excising the pericarp or by bleaching did not increase germination significantly. It does not seem to be responsible for inhibiting germination.

Fruit that were scarified gave the highest germination percentages which indicates that the pericarp is at least in part responsible for seed dormancy, almost certainly by preventing entry of water and gases to the seed. Chemical and physical scarification simulates the natural breakdown process of the pericarp by wind and sand. At the same time, it is important to note that fruit slitting and nicking, although enabling the access of water to the seed, did not promote germination. The reason for this is unclear.

Gibberelic acid did not break dormancy nor did pre-chilling the fruit for two months. Fruit dry stored for six months before incubation, even when slit, did not promote germination, and seeds incubated after the floatation experiments showed no significant increase in germination from the control, (Appendix III, Table 22). It is worthy of note that the seed of a fruit that remained afloat in seawater for 50 days, germinated during the third week of incubation.

Low germination cannot be attributed to low seed viability, (Appendix III, Table 23). Viability of fresh seed is very high with 89% having the potential for germination. Viability slowly decreases with seed age to 82% after six months and 66% after 10 months dry storage. Probably half of the seeds are viable for up to a year.

Low germination percentages of all treatments and combinations indicates that dormancy is influenced by either another factor (e.g. temperature, testa impermeability) and/or a combination of factors that have not been tested (e.g. after-ripening + scarification, scarification + GA_3). Temperature was the only major factor not tested. It may happen that high temperatures such as those experienced by fruit on the dunes during summer, are responsible for releasing seeds from dormancy (Capon and van Asdall, 1967). Nevertheless, attempts at germinating *Desmoschoenus* seed at 30°C under controlled conditions were met with limited success (Margaret Bulfin, Botany Division, D.S.I.R., Lincoln, pers.comm.).

5.5 SEEDLING ECOLOGY

5.5.1 Method and Materials

The dune system within the study area was surveyed for *Desmoschoenus* seedlings. A 10 m x 10 m plot, M, was set up at the base of an eroding transverse dune where seedlings were found to be most frequent, (Figure 28).

All seedlings that occurred within the quadrat were mapped and labelled, A to V. All tufts comprising each seedling were also labelled. Each tuft was monitored, from December 1980 to the end of January 1982, for leaf production, new tuft production, tuft death and tuft browsing, trampling, undermining and burial by animals.

Instant recognition of the month in which a particular leaf was produced was possible by using oil paints as an identification aid. At the end of every month leaves that had emerged during that month were painted on their tips in a colour that was specific to that month.

The same plot was used to monitor the emergence of new seedlings. From September 1981 to the end of February 1982 a monthly detailed search of the plot was undertaken to find emergent seedlings from recently germinated seed. Seedlings that were found were monitored at monthly intervals for leaf production, mortality and interference by animals.

5.5.2 Results and Discussion

A survey of the study site revealed that seedlings were extremely rare. This observation was further substantiated by two subsequent field checks along the rest of Kaitorete Spit.

Seedlings were restricted to two zones within the study area,

(a) the strand zone between the foreshore and foredunes,

(b) a zone at the edge of a large blowout along the base of an eroding transverse dune.

Their occurrence was very sporadic throughout the former zone but they were frequent enough within the latter zone to enable a detailed study of their dynamics.

Esler (1969) points out that moist habitats such as sand plains and the bases of transverse dune slip faces provide suitable conditions for the seedlings of pingao. He also states that *Desmoschoenus* is dependent on a high water-table for germination of its seeds. Although there is nowhere on the spit where the water table exceeds the gravel basement, moisture close to the sand surface seems to be the main factor determining where seedlings are found, such as at zones (a) and (b). Seedlings have been occasionally seen growing out of cushions of *Raoulia australis* for the same reason - moisture within the cushion was adequate to promote seed germination.

Seedlings of the strand zone have little chance of establishment as high tides such as those caused by storm surges are effective in causing their death. A field check in November 1982 revealed that a high tide during the previous winter had stripped away sand from the roots of the strand zone seedlings. Death resulted from subsequent desiccation.

A total of 22 established seedlings were found to exist within the 10 m x 10 m plot. Two of these had only recently emerged and were each comprised of only one tuft, but the majority were over one year old and were made up of several tufts.

Browsing frequency, and leaf and tuft production of these seedlings are presented in Tables 4 and 5 and in Appendix III, Table 26).

Animal interference included trampling, uprooting and burial by sheep, but these events were nowhere near as frequent as browsing by hares or rabbits. Browsing occurred more or less constantly throughout the year except during August and September when none was recorded. Browsing was most severe during March, May, October, November and December 1981. With the exception of December, the leaf production over these five months decreased noticeably. It therefore appears that leaf production was temporarily reduced as a result of browsing. Despite these sudden decreases there is a seasonal trend apparent in the numbers of leaves produced. Most of the leaves emerge during summer (one to three per

Table 4 Seedling Growth and Death in Relation to Browsing, Site M. (December 1980 to January 1982). N (tufts) = 85

					MONTH										
	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Total
New Tufts Produced	-	2	1	1						4	2	3	7	4	24
Leaves Produced	33	44	77	41	45	6	13	11	12	67	55	37	89	80	610
Tufts Browsed*	2	2	7	26	4	15	9	1			11	19	11	2	109
Tuft Deaths		1	4	3	6	2				1		5	3		25
Tuft Deaths after Browsing		1	4	3	6	2						3	2		21

* not including the 12 tufts recently browsed before monitoring

Table 5 Old and New Tufts in Relation to Browsing Frequency, Site M. (December 1980 to January 1982).

	Not Browsed		Browsed Once		Browsed Twice		Browsed Three Times		Browsed Four Times		Total Browsed		Total
		%		%		%		%		%		%	
Old Tufts	2	(3.3)	30	(49.2)	12	(19.7)	10	(16.4)	7	(11.5)	59	(96.7)	61
New Tufts	18	(75.0)	4	(16.6)	1	(4.2)	1	(4.2)	0	(0)	6	(25.0)	24
Total	20	(23.5)	34	(40.0)	13	(15.3)	11	(12.9)	7	(8.2)	65	(76.5)	85

month for most tufts) and no leaves are produced over winter for most tufts. This is consistent with leaf production trends for adult tufts (Figure 45).

New leaf production is also seasonally determined beginning at the start of spring and continuing through to autumn. Browsing does not noticeably affect the degree of tufting; seedlings both browsed and unbrowsed were made up of a similar number of tufts (e.g. seedlings L and R, U and V). Instead, the degree of tufting seems to be a function of seedling age.

Although the number of tufts that died over the period of monitoring was similar to the number of new tufts produced over this period, (25 and 24 respectively), it can only be speculated that an equilibrium exists between tuft mortality and recruitment.

Of the 65 tufts browsed, 21 (32%) died before any new leaves were produced and in most cases death occurred within a month of being browsed. Only four other tufts died during the time that they were monitored. So although just under one third of the browsed tufts died subsequent to browsing, these deaths accounted for most of the total deaths. It is assumed that the deaths of the browsed tufts were a direct result of browsing.

At the end of 14 months only two of the 22 seedlings and 20 of the 85 tufts had not been browsed; 18 of these tufts were new and so most had only been subject to browsing for a few months. Of the 61 tufts present when monitoring began, 59 ended up being browsed. This is consistent with observations of seedlings outside plot M. Most showed signs of browsing.

Seedlings that were proximate to each other were often browsed at the same time (e.g. seedlings B, C and E, K and L). It seems that their closeness has meant that their chances of being browsed are not independent and that the browser is likely to graze more than one of the seedlings. Nevertheless, the frequency of browsing varied considerably among the 22 seedlings, and frequently among tufts of each seedling. This is not due to discrimination by the browser as much as the inconspicuousness of some seedlings (especially seedlings comprising of only one tuft), and the small size or inaccessibility of some tufts. Forty per cent of the tufts were browsed only once during the period of monitoring, 15.3% were browsed twice, 12.9% three times, and 8.2% four times.

The severity of browsing also varied considerably among tufts and even among leaves within the same tuft. Many leaves were cropped below the lamina-sheath interface, while some were only lightly grazed leaving most of the lamina intact, (Figure 33).

It seems that for established seedlings such as these, their survival is largely dependent upon the rate and severity of browsing. Also, regular cropping ensures that there is very little increase in biomass and that the seedling retains its tightly tufted form and low stature. Although the seedlings were only monitored for 14 months, the results indicate that due to constant browsing pressure the chance of any seedling reaching maturity is slight.

Figure 33. A seedling with all of its tufts browsed, site M.

Figure 34. Four month old seedling. The single tuft and thin laminae make it inconspicuous

Table 6 presents the months of emergence, leaf production rates and mortality of newly germinated seedlings within plot M over the spring and summer of 1981-82. Thirty seedlings emerged in total, whereas only two emerged the previous season (seedlings U and V). Obviously the rate of seedling emergence varies considerably from year to year.

Seedlings emerged from October to January with peak emergence in November. By the end of February only 16 remained alive (53%). The mortality of the seedlings that emerged in November was 31%, much less than the mortality of seedlings that emerged in October and December (62.5% and 80.0% respectively).

Apart from the two seedlings that died as a result of trampling by sheep, it is not known what caused these deaths. No water availability measurements were made around these seedlings but it is most likely that inaccessibility to sufficient water for many seedlings was responsible for their deaths. Their extremely fine needle-like leaves account for their inconspicuousness which is the main reason why none were browsed over the six months, (Figure 34).

Most new seedlings produced only one leaf per month, usually no longer than 5 cm. On the other hand, they had very long root systems comprising two to five adventitious roots up to 20 cm in length and associated fibrous roots.

Table 6 Leaf Production and Mortality of Newly Germinated Seedlings, Site M.(September 1981 - February 1982).

Seedlings			MONTH				Survivors
	Sept	Oct	Nov	Dec	Jan	Feb	
1		1	1	D			x
2		1	1	2	D I		x
3		1	2	1	D		x
4		1	1	1	1		✓
5		1	1	1	D		x
6		1	D I				x
7		1	2 IV		2		✓
8		1	1	1	1		✓
9			1				✓
10			1	2		1	✓
11			1	1	D		x
12			1		2	D	x
13			1	1	1	D	x
14			1	1		1	✓
15			1	1	D		x
16			1			1	✓
17			1	1	1		✓
18			1	1			✓
19			1	1			✓
20			1	D			x
21			1	2		1	✓
22			2	2	1	1	✓
23			1	2	1	1	✓
24			2	1	1		✓
25				2	D		x
26				1	D		x
27				2		1	✓
28				2	1	D	x
29				2	D		x
30					1		✓

CHAPTER VI

COMPARATIVE ANALYSIS

6.1 INTRODUCTION

It has been observed that *Desmoschoenus* populations on the reardunes and grassland appear to differ in many respects from foredune populations. Plants of the former zones seem generally less robust than plants of the latter zone. Density, habit and dispersion of tufts also seem to vary among these zones.

Quantitative studies of such phenomena as well as an investigation of aspects of the growth of *Desmoschoenus,* at each zone, are presented in this chapter. An investigation of selected environmental factors at each zone is also presented in an attempt to explain differences among the quantitative and growth analyses.

6.2 QUANTITATIVE ANALYSIS

6.2.1 Introduction

Four sites A, B, C and D were chosen on the foredunes, sites E, F and G were chosen on the reardunes and site H (Figure 35) was chosen on the grassland as being representative of each zone.

A 10 m x 10 m plot was set up at each of the sites A to G, (Figure 36)and a 5 m x 5 m plot was set up at site H (due to the small size of the grassland population) and within each were made selected measures and counts. These included,

(a) The detection of pattern in the spatial arrangement of individual tufts, i.e. tuft dispersion.

(b) Estimates of percentage cover.

(c) The establishment of proportions of habit types.

(d) Measurements of vegetative and inflorescence characteristics.

(e) Counts of characteristics associated with reproductive capacity.

(f) Density counts.

(g) Estimates of biomass.

A special grassland site, I, was chosen to study the effect of regular sand application to plants of pingao (Section 6.4.4). As many of the above measures and counts as possible were recorded for I_s (subsite on which sand was applied) and I_{ns} (subsite control) but because of the

Figure 35. Site H on the grassland

Figure 36. An example of a 10 m x 10 m plot.
This is set up at site F on the reardunes

small size of these subsites, tuft pattern detection and percentage cover estimates could not be attempted.

6.2.2 Tuft Dispersion

An investigation was conducted within the plots at sites A to H in April 1982 to detect whether pingao tufts were randomly dispersed or whether some pattern to their spatial arrangement existed (Kershaw, 1973).

A 60 cm diameter circular wire quadrat was randomly thrown 50 times within each plot. The number of tufts within the quadrat were recorded at each throw. A table was constructed to show the frequency of occurrence, (f), of tuft numbers, (a), over the 50 throws. The mean and variance of $a \times f$ were found for each plot, and the variance: mean ratio (the coefficient of dispersion) was used as an index of contagion. When the variance and mean are equal the tufts are randomly dispersed. For values significantly >1 the tufts were assumed to be grouped, (contagiously dispersed), when significantly <1 they were assumed to be uniformly spaced, (regularly dispersed).

Results

The frequency of tuft occurrence within each thrown quadrat at each site A to H is tabulated in Appendix III, Table 27. The co-fficient of Dispersion and associated t test are presented with the tuft dispersion of the eight sites in Table 7.

Only site A tufts were randomly dispersed. Tufts at all other sites exhibited some pattern to their dispersion. Such patterns were highly significant ($p < 0.001$). Tufts at

Table 7 Detection of Non-Randomness

Site	Coefficient of Dispersion[1]	*t*	Tuft Dispersion
A	1.09	0.45 n.s.	random
B	0.22	-3.81 ***	regular
C	4.45	17.06 ***	contagious
D	3.26	11.19 ***	contagious
E	7.85	33.89 ***	contagious
F	8.48	37.02 ***	contagious
G	9.40	41.60 ***	contagious
H	7.28	31.08 ***	contagious

[1] Variance:Mean ratio

site B were regularly dispersed, each being approximately equidistant from its neighbours. The tuft dispersion at sites C to H was contagious, i.e. the tufts were arranged in discrete groups.

6.2.3 Percentage Cover

The percentage cover of the plots at sites A to H was estimated in March 1982. Due to problems of windiness and plant height the point frame method of estimating percentage cover proved inadequate. Also the non-random arrangement of tufts at most sites coupled with the regular spacings between frame points gave biased results.

Another technique was devised which involved the use of an eye-piece with a fine point marked at its centre. This was worn on a spectacle frame, enabling it to be kept in a fixed position in front of one eye. The lens was viewed through at 500 random spots within each plot and the object intercepting the point on the lens was recorded. Each view was of as vertical an aspect as possible.

Records were placed into one of five categories:

(a) Live pingao - any part of a tuft that was alive.

(b) Dead pingao - any attached part of a living tuft that was dead.

(c) Pingao litter - all dead tufts and unattached dead portions of pingao.

(d) Sand.

(e) Other - any other object intercepted, including other plant species (dead or alive) and rabbit/hare faecies.

able 8 Comparison of Percentage Cover between Sites A-D and E-H

	A	B	C	D	$\bar{x}_{A-D}$ (95% confidence)	E	F	G	H	$\bar{x}_{E-H}$ (95% confidence)	t
ive pingao	36.2 (37.0)	41.2 (39.9)	20.8 (27.1)	22.4 (28.3)	30.2 ± 16.1 (33.1 ± 10.1)	11.8 (20.1)	9.0 (17.5)	13.8 (21.8)	11.6 (19.9)	11.6 ± 3.1 (19.8 ± 2.8)	4.03**
ead pingao	33.4 (35.3)	40.6 (39.6)	39.6 (39.0)	36.0 (36.9)	37.4 ± 5.3 (37.7 ± 3.1)	26.8 (31.2)	26.4 (30.9)	37.4 (37.7)	42.0 (40.4)	33.2 ± 12.4 (35.1 ± 7.6)	1.03 n.s.
'ingao litter	2.2 (8.5)	1.2 (6.3)	3.8 (11.2)	4.0 (11.5)	2.8 ± 2.0 (9.4 ± 3.9)	16.0 (23.6)	12.8 (21.0)	7.8 (16.2)	11.6 (19.9)	12.1 ± 5.4 (20.2 ± 4.9)	-5.50**
;and	23.8 (29.2)	14.4 (22.3)	32.8 (34.9)	31.0 (33.8)	25.5 ± 13.3 (30.1 ± 9.1)	27.8 (31.8)	45.2 (42.3)	30.8 (33.7)	24.8 (29.9)	32.2 ± 14.4 (34.4 ± 8.7)	-1.08 n.s.
)ther [1]	4.4 (12.1)	2.6 (9.3)	3.0 (10.0)	6.6 (14.9)	4.2 ± 2.9 (11.6 ± 4.0)	17.6 (24.8)	6.6 (14.9)	10.2 (18.6)	10.0 (18.4)	11.1 ± 7.4 (19.8 ± 6.6)	-3.15*

(x) = Arcsin $\sqrt{\%}$ from which t was calculated

[1] Foredunes only: *Calystegia soldanella*
Festuca littoralis

Reardunes only: *Gnaphalium luteo-album*
Zoysia minima
Muehlenbeckia complexa
Carmichaelia appressa
Triquetrella papillata
Lichen sp.
Rabbit and/or Hare faecies

Grassland (Site H) only: *Raoulia australis*
Acaena agnipila

All sites: *Hypochoeris radicata*
Lagurus ovatus
Rumex acetosella

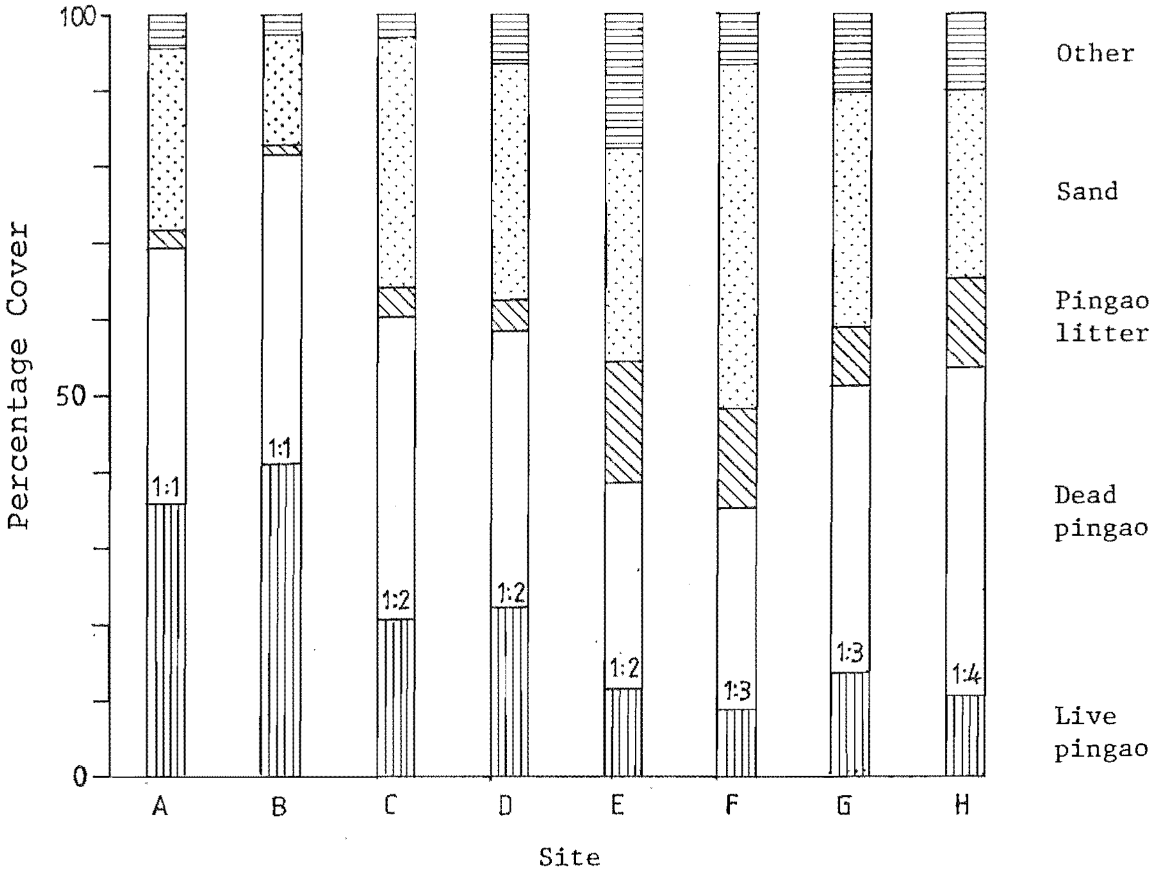


Figure 37. Percentage cover and approximate ratio of live pingao: dead pingao, for sites A to H

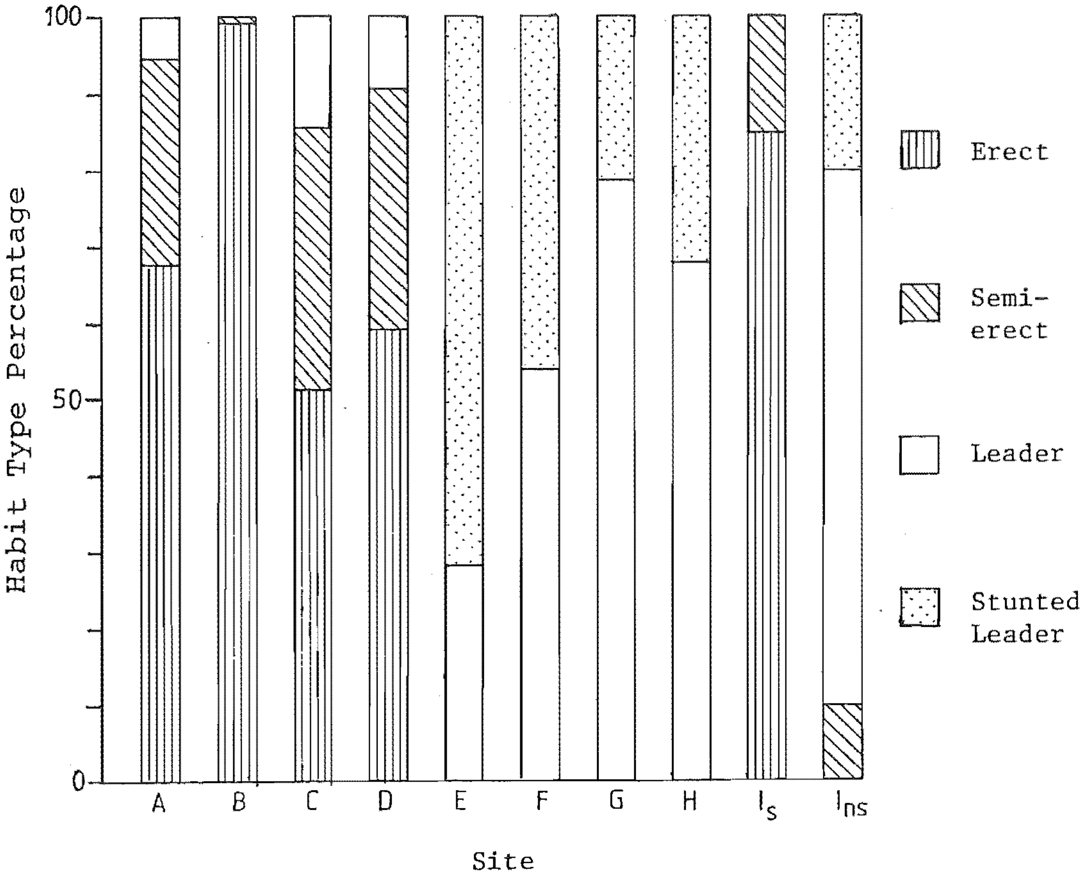


Figure 38. Percentage habit types of pingao for

t tests were made between the means of transformed percentages of the foredune and reardune sites, and approximate ratios were calculated of live pingao:dead pingao.

Results

Percentage cover results are shown in Table 8 and Figure 37. Between the foredune sites (A to D) and the reardune-grassland sites (E to H) the mean percentage covers of 'sand' and 'dead pingao' do not significantly differ. On the other hand the mean percentage covers of 'live pingao', 'pingao litter' and 'other' are significantly different between foredune and reardune-grassland sites, with the former being covered by more than twice as much 'live pingao', more than four times less 'pingao litter' and more than two times less 'other' objects, than the latter. Sites B and F are the two extremes.

The live pingao:dead pingao ratios for the foredune sites are equal to or lower than the ratios for the reardune sites which indicate that the reardune plants are made up of more dead material than plants of the foredunes.

6.2.4 Habit

The percentage of the different habit types of pingao tufts were estimated for each site A to I in March 1982. For convenience, there were four habits recognized, although habit type is a continuum ranging from the erect through to stunted leader form.

Descriptions of the four habits are:

(a) Erect - the tuft rhizome is perpendicular to the sand surface, (Figures 2 and 3).

(b) Semi-erect - the tuft rhizome is intermediate between the erect and horizontal position.

(c) Leader - the tuft rhizome runs horizontally along the sand surface, (Figures 2 and 4).

(d) Stunted Leader - the tuft rhizome is horizontal but it has extremely short internodes giving the appearance of a stunted erect tuft, (Figure 5).

Every live tuft in each of the 10 m x 10 m plots had its habit noted as did the tufts at subsites I_s and I_{ns}. Tufts that had developed into inflorescences were not counted. Habit indices for each site were calculated by summing the habit percentages after multiplying each habit by a weighting (erect = 4, semi-erect = 3, leader = 2, stunted leader = 1) and dividing the sum by 100. This index gives the average habit type for each site.

Results

It is clear from Table 9, and Figure 38 that the habit types and habit indices for the foredune sites (A - D) are similar to each other and the reardune-grassland sites (E - H) are similar to each other. But between the two groups there is a distinct difference.

The majority of tufts of the foredune sites were erect and many were semi-erect. Very few showed leader habit and no tufts were stunted leaders. The converse was apparent for tufts of the reardune-grassland sites. No tufts exhibited the erect or semi-erect habit, all were

Table 9 % Habit Types and Habit Index of Sites A-I

Habit	SITES									
	A	B	C	D	E	F	G	H	I_s	I_{ns}
Erect	67.8	99.3	51.4	59.2					85.0	
Semi-erect	26.8	0.7	34.4	31.5					15.0	10.0
Leader	5.4		14.2	9.3	28.2	54.0	78.9	68.0		70.0
Stunted Leader					71.8	46.0	21.1	32.0		20.0
Habit Index *	3.62	3.99	3.37	3.50	1.28	1.54	1.79	1.68	3.85	1.90

* Erect = 4
Semi-erect = 3
Leader = 2
Stunted Leader = 1

leaders and many of them were stunted. Extremes in habit type were apparent between sites B and E, the former with tufts that were 99.3% erect and the latter with 71.8% of its tufts stunted-leaders.

The habit indices of all the foredune sites fell between 3.37 and 3.99 meaning that their average habit types were intermediate of the erect and semi-erect forms. The habit indices of the four reardune-grassland sites were between 1.28 and 1.79 meaning that their average habit types were intermediate of leader and stunted leader forms.

6.2.5 Quantitative Measurements

6.2.5.1 Vegetative and Inflorescence Measurements

Within each plot, at sites A to I, the lamina length (cm) and width (mm) of 50 leaves of pingao were measured. Inflorescence length (cm) and width (mm), length of the lowest bract (cm) and bract number were also measured for 50 mature inflorescences. Length was taken to be the distance from the node of the leaf that subtends the culm to the apical spikelets. The width was taken just below the lowest bract. All measurements were made in March 1982.

6.2.5.2 Reproductive Capacity

Ten inflorescences were collected from each plot at sites A to I in March 1982. Twenty intact spikelets were randomly chosen from each inflorescence and dissected. The number of flowers and the number of fruit were counted for each spikelet. The total number of spikelets on each inflorescence was found by counting intact spikelets as well as the rhachillae of spikelets that had already fallen.

From these counts, calculations were made of the percentage of flowers that set fruit, flowers per inflorescence and fruit per inflorescence. Fruit produced per square metre at each site was found by multiplying fruit per inflorescence counts with counts of inflorescences per square metre, (6.2.5.3). Means of all these counts were calculated for each plot.

6.2.5.3 Density Counts

The total number of live tufts within each plot, for sites A to I, was counted in early November 1981 and from this the frequency of live tufts per square metre was calculated. At the same time the total number of inflorescences was counted for all plots by marking the inflorescence tips with oil-based paint. These were called 'early inflorescences'. Their frequency per square metre was calculated. In March 1982 all inflorescences that had arisen since the November count (identified by being unpainted) were counted. These were called 'late inflorescences' and their frequency per square metre was calculated.

From these counts were found the live tuft:inflorescence ratio and the early:late inflorescence ratio. Means were found for all counts and calculations.

6.2.5.4 Results

Means of the measurements and counts of pingao characteristics (1 to 17), at sites A to I, are presented in Table 10). Multivariate analysis and discriminant analysis (BMD05M) was attempted on this data but both were fraught with various problems which led to their abandonment.

Table 10. Means of the Characteristics of *Desmoschoenus* at Sites A to I.

	Characteristic	A	B	C	D	E	F	G	H	I_s	I_{ns}
1	Lamina Length (cm)	56.7	65.7	47.5	57.7	30.7	41.4	37.5	32.4	57.2	38.6
2	Lamina Width (mm)	4.2	4.1	3.6	4.4	2.7	2.8	3.0	2.7	3.7	3.0
3	Inflorescence Length (cm)	53.6	59.6	37.6	43.5	37.8	35.2	45.3	41.3	50.4	38.5
4	Inflorescence Width (mm)	4.7	5.5	3.5	4.6	3.2	2.3	3.9	3.4	4.4	3.9
5	Lowest Bract Length (cm)	42.8	50.0	38.8	36.2	26.3	23.3	36.7	34.0	44.9	28.2
6	Bracts per Inflorescence	14.9	13.7	12.9	13.8	9.6	9.9	11.8	11.8	13.2	12.1
7	Spikelets per Inflorescence	169.3	244.6	200.2	146.0	66.4	91.0	102.3	68.8	152.0	71.0
8	Flowers per Spikelet	10.56	8.49	6.81	7.83	7.96	5.62	7.38	8.21	8.75	7.31
9	Fruit per Spikelet	2.33	2.32	1.26	1.64	0.87	0.86	0.52	0.33	0.96	0.30
10	% Flowers that set Fruit	22.1	27.3	18.5	20.9	10.9	15.3	7.0	4.0	11.0	4.1
11	Fruit per Inflorescence	394.5	567.5	252.3	239.4	57.8	78.3	53.2	22.7	145.9	21.3
12	Fruit produced m^{-2}	6350	10776	4417	2399	73	90	79	40	1459	43
13	Live Tufts m^{-2}	27.20	27.76	32.20	31.31	20.72	16.40	19.13	19.28	27.50	23.00
14	Early Inflorescences m^{-2}	15.30	18.38	16.63	9.62	0.87	0.34	1.09	1.04	9.50	1.25
15	Late Inflorescences m^{-2}	0.80	0.61	0.88	0.40	0.40	0.82	0.39	0.72	0.50	0.75
16	Live Tuft: Inflorescence Ratio	1.69	1.46	1.84	3.12	16.31	14.14	12.93	11.48	2.75	11.5
17	Early:Late Inflorescence Ratio	19.13	30.13	18.90	24.05	2.18	0.41	2.79	1.44	19.00	1.67

Nevertheless, trends can still be seen from the data as it stands.

The means of the characteristics for the foredune sites and subsite I_s were very similar to each other but quite different from the means of the reardune-grassland sites and subsite I_{ns}. Means of the characteristics for the reardune-grassland sites and subsite I_{ns} were also similar to each other.

Compared to the pingao populations of sites E, F, G, H, and I_{ns}, the pingao populations of sites A, B, C, D, and I_s seem to have:

(a) longer and wider lamina;

(b) longer and wider inflorescences;

(c) longer bracts and a greater number of bracts per inflorescence

(d) a larger number of spikelets per inflorescence;

(e) a larger number of flowers and fruit per spikelet;

(f) a higher percentage of flowers that set fruit;

(g) more fruit per inflorescence and per square metre;

(h) more live tufts and more inflorescences per square metre;

(i) a greater proportion of tufts that produce inflorescences; and

(j) most of their inflorescences being produced early in the season.

t tests were performed between the means of characteristics 1 to 9 (Tables 11 and 12), to determine whether there were significant differences between:

(a) the foredune sites and reardune-grassland sites;

Table 11. Means of the Characteristics of *Desmoschoenus* at Fordune Sites (A-D), Reardune-Grassland Sites (E-H), and Subsites I_s and I_{ns}.

95% confidence

	Characteristic	Foredune (A-D)	Reardune/ Grassland (E-H)	SITES	
				I_s	I_{ns}
1	Lamina Length (cm)	56.7±2.1	34.7±1.7	57.2±1.6	38.6±1.2
2	Lamina Width (mm)	4.1±0.2	2.8±0.2	3.7±0.1	3.0±0.2
3	Inflorescence Length (cm)	48.6±4.4	36.0±3.5	50.4±1.1	38.5±1.9
4	Inflorescence Width (mm)	4.6±0.3	3.2±0.2	4.4±0.2	3.9±0.2
5	Lowest Bract Length (cm)	39.8±1.7	30.2±1.9	44.9±1.7	28.2±1.0
6	Bracts per Inflorescence	13.5±0.5	11.7±0.4	13.2±0.5	12.1±0.5
7	Spikelets per Inflorescence	180.3±20.6	84.1±14.9	152.0±14.3	71.0±12.4
8	Flowers per Spikelet	8.51±0.20	7.27±0.20	8.75±0.09	7.35±0.09
9	Fruit per Spikelet	1.81±0.09	0.65±0.08	0.96±0.06	0.30±0.05

Table 12. Comparison of the Characteristic Means of *Desmoschoenus* between Foredune Sites (A-D), Reardune-Grassland Sites (E-H), Subsite I_s and Subsite I_{ns}.

95% confidence

	Characteristic	*t* and *t'* scores			
		A-D vs. E-H	I_s vs. I_{ns}	A-D vs. I_s	E-H vs. I_{ns}
1	Lamina Length (cm)	31.66***'	18.07***'	-0.51n.s.'	-5.16***'
2	Lamina Width (mm)	20.69***'	6.93***'	5.06***'	-2.25*
3	Inflorescence Length (cm)	8.78***'	10.53***'	-1.42n.s.'	-1.9n.s.'
4	Inflorescence Width (mm)	16.40***'	3.82***'	-6.00***'	-5.82***
5	Lowest Bract Length (cm)	14.74***'	16.71***'	-2.25*	2.80**'
6	Bracts per Inflorescence	11.13***'	3.04**	1.37n.s.	-1.41n.s.
7	Spikelets per Inflorescence	10.63***'	6.02***'	1.82n.s.	1.14n.s.
8	Flowers per Spikelet	9.92***'	13.03***'	-2.04*'	-0.34n.s.'
9	Fruit per Spikelet	21.59***'	9.50***'	12.13***'	6.61***'

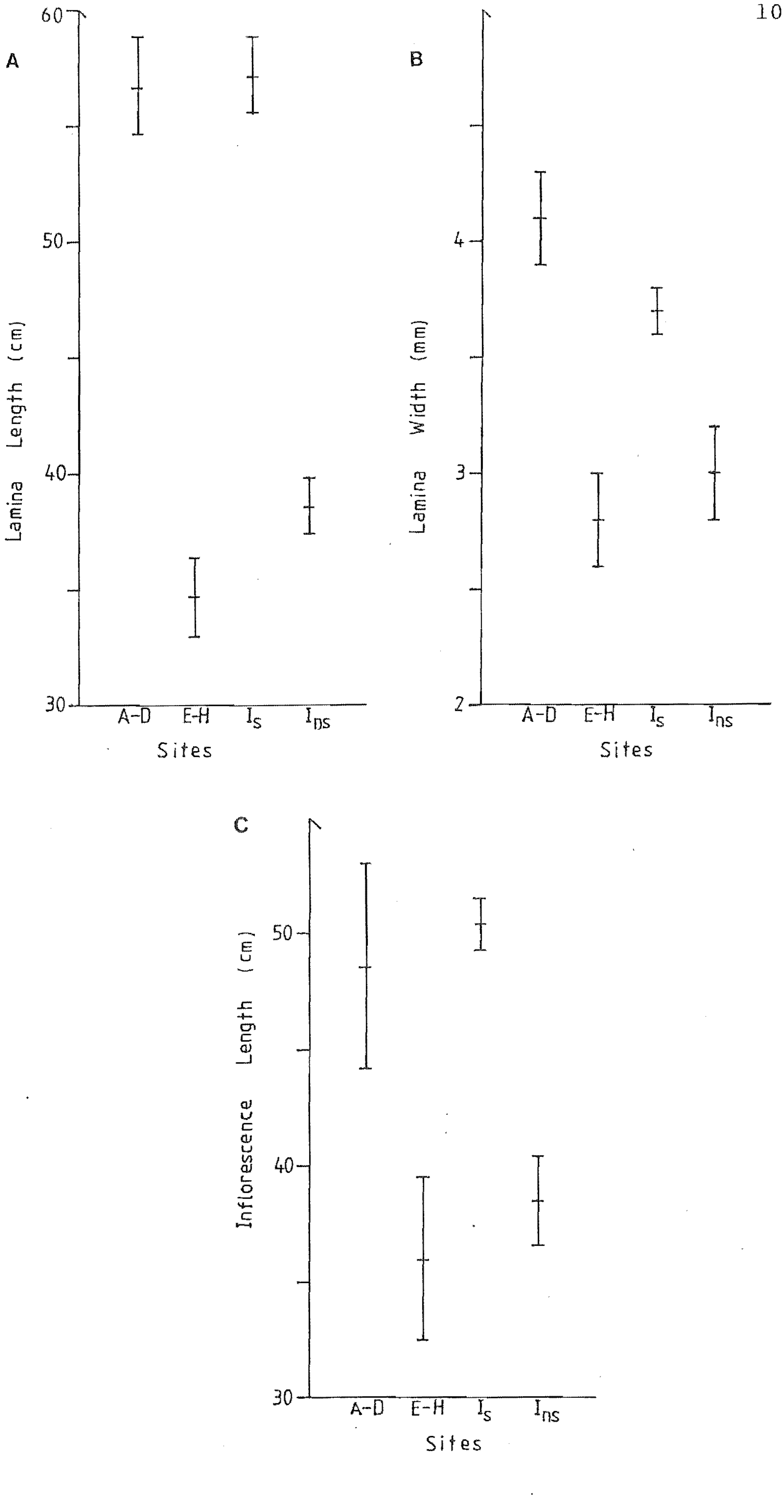


Figure 39. Lamina length, (A), and width, (B), and inflorescence length, (L), of *Desmoschoenus* at sites A-D, E-H, I and I

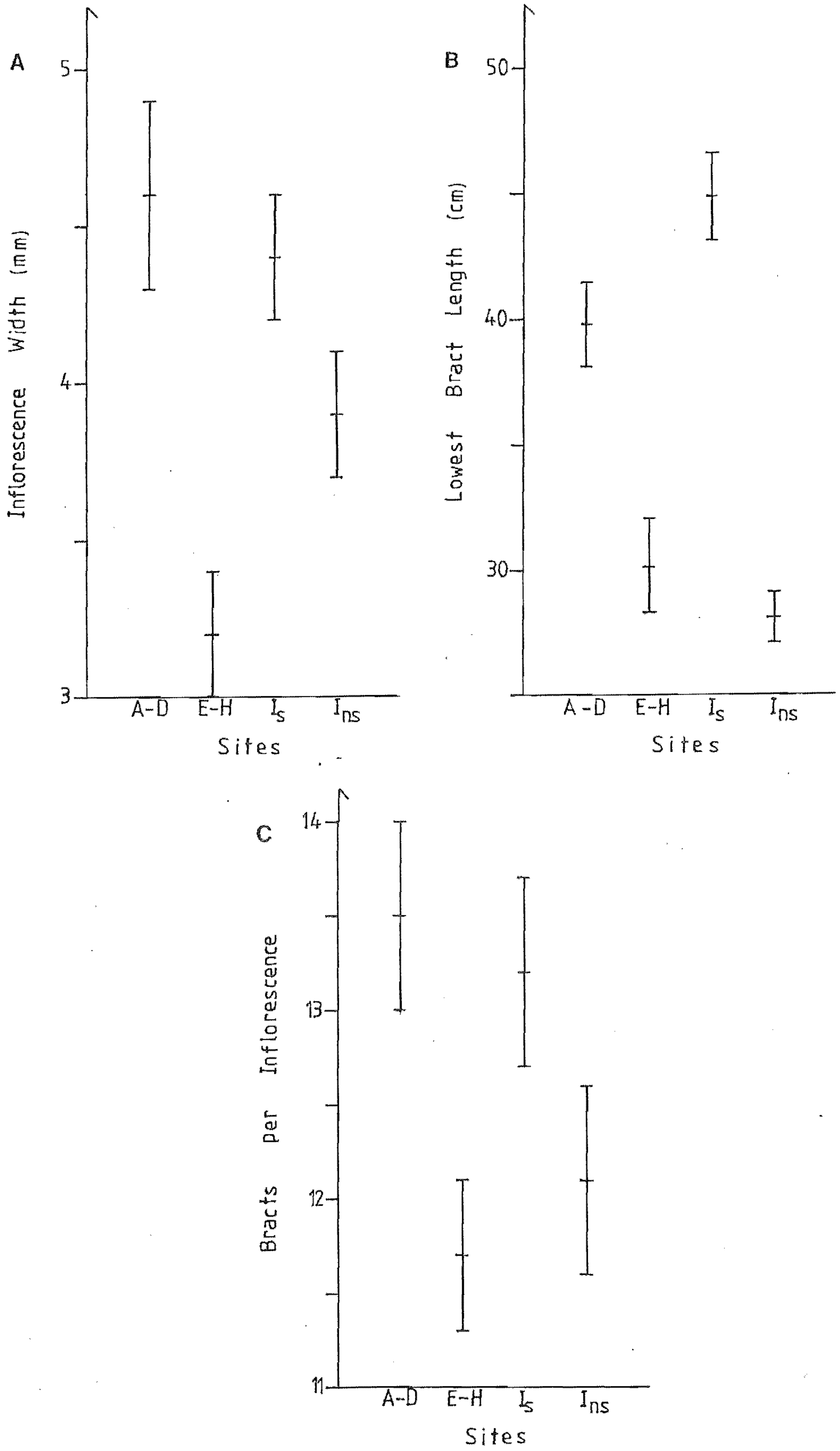


Figure 40. Inflorescence width, (A), lowest bract length, (B), and bracts per inflorescence, (C), of *Desmoschoenus* at sites A-D, E-H, I_s and I_{ns}.

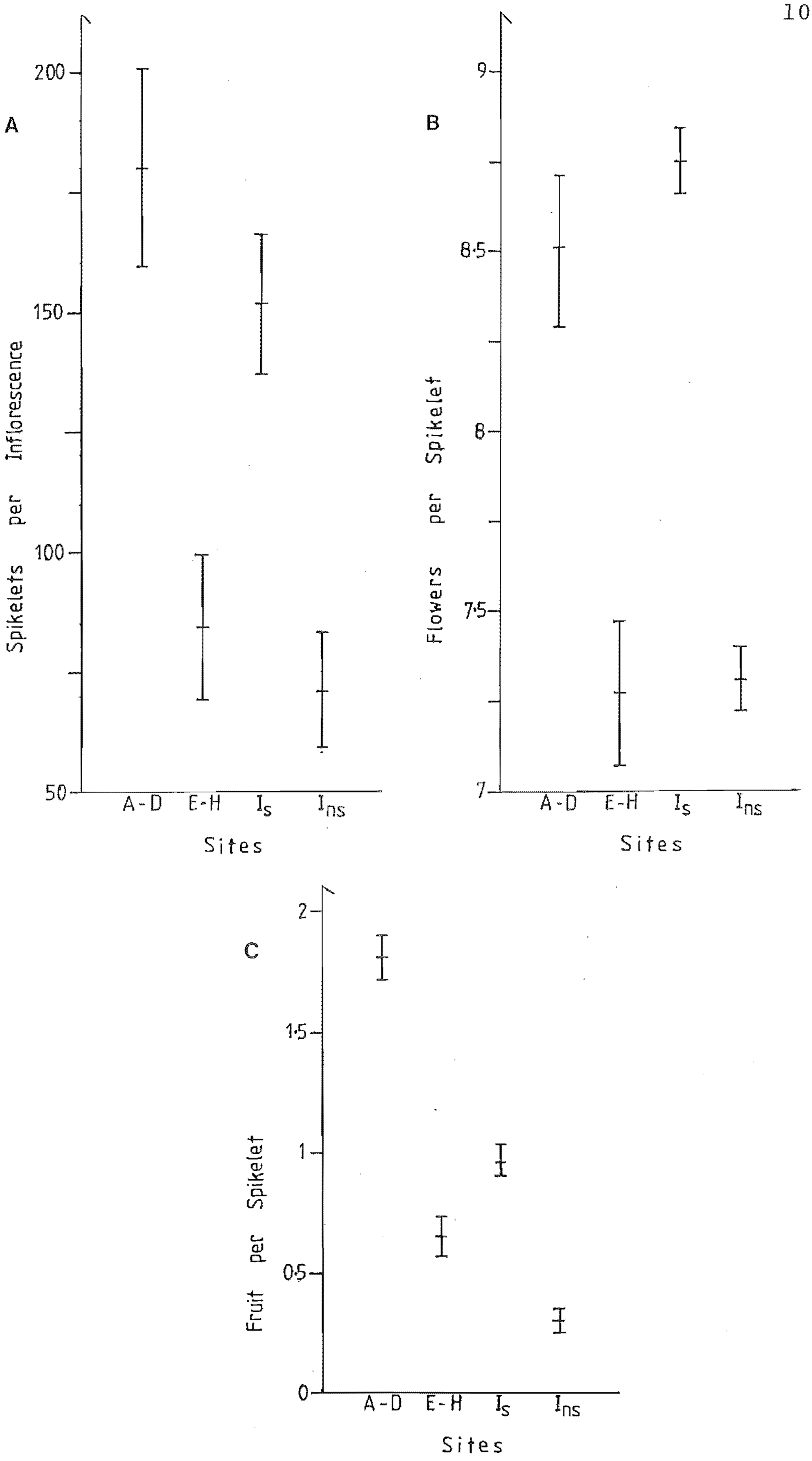


Figure 41. Spikelets per inflorescence, (A), flowers per spikelet, (B), and fruit per spikelet, (C), of *Desmoschoenus* at sites A-D, E-H, I_s and I_{ns}.

(b) subsites I_s and I_{ns};

(c) the foredune sites and subsite I_s; and

(d) the reardune-grassland sites and subsite I_{ns}.

Figures 39, 40 and 41 are graphs of these characteristics for sites A-D, E-H, I_s and I_{ns}.

The graphs and *t* tests show that highly significant differences existed between the means of all characteristics for the foredune sites and reardune-grassland sites, as well as between subsites I_s and I_{ns}. The comparison between the foredune sites and subsite I_s revealed that the means of four out of nine characteristics were not significantly different (lamina length, inflorescence length, bracts per inflorescence, spikelets per inflorescence). Also, the comparison between the foredune-grassland sites and subsite I_{ns} revealed that four out of nine characteristics were not significantly different (inflorescence length, bracts per inflorescence, spikelets per inflorescence, flowers per spikelet).

From these results it seems that before sand was deposited on the plants of I_s (Section 6.4.4) they resembled plants of the reardunes and grassland but subsequent to regular deposition such plants more resembled foredune plants.

6.2.6 Estimate of Biomass

Thirty tufts were randomly chosen and harvested from within the plots at each of the sites A to H, in April, 1982. Due to the small size of site I only twenty tufts were randomly chosen and harvested, ten from I_s and ten from I_{ns}. Any inflorescence that was randomly chosen was included in the samples. The habit of each tuft was noted.

The tufts were dissected and all living matter separated from dead matter. The live matter was oven dried at 105°C for two days and then weighed to give an estimate of tuft biomass (the total amount of living organic matter above ground).

The mean and confidence limit of tuft biomass were calculated for each site, by multiplying the tuft biomass means by the number of live tufts per metre square (Section 6.2.5.3). The biomass per square metre was calculated for each site. The mean biomass was also found for tufts of different habits.

An analysis of variance was done on:

(a) tuft biomass of foredune sites A to D, and reardune/grassland sites E to H; and

(b) tuft biomass among habit types

and *t* tests (or *t* test approximations) were computed for tuft biomass between sites A-D, E-H, I_s and I_{ns}.

Results

Mean tuft biomass and mean tuft biomass per square metre, for sites A to I are given in Table 13.

All the foredune sites as well as subsite I_s have more biomass per tuft than that of the reardune-grassland sites and subsite I_{ns}. This difference is statistically significant with 95% confidence, except for site G whose tufts have a biomass similar to tufts of the foredune sites D and A, I_s, and the grassland site H. *t* tests for tuft biomass between A-D, E-H, I_s and I_{ns} (Appendix III, Table 30) show that they are all significantly different from one another except for sites A-D and I_s, and sites E-H and I_{ns}.

Table 13 Mean Biomass (g) and Biomass.m^{-2} of Tufts at Sites A to I①

Site	Mean Tuft Biomass (g)	Significant Difference[2]	Mean Tuft Biomass.m^{-2}*
B	9.21 ± 1.47	*a*	255.7
C	7.63 ± 1.16	*a b*	245.7
A	6.61 ± 1.12	*b c*	179.8
I_s	6.47 ± 1.41	*a b c*	177.9
D	6.18 ± 1.51	*b c*	193.5
G	5.13 ± 1.01	*c d*	98.1
H	3.45 ± 0.78	*d e*	83.8
E	3.16 ± 0.89	*e*	65.5
I_{ns}	2.95 ± 0.90	*e*	67.8
F	2.73 ± 0.54	*e*	44.8

Table 14 Mean Biomass (g) of Tufts of Different Habits①

Habit	Mean Tuft Biomass	Significant Difference②
Erect	7.72 ± 0.78	*f*
Semi-erect	5.82 ± 1.28	*f g*
Leader	4.53 ± 0.54	*g*
Stunted Leader	1.85 ± 0.53	*h*

① N (tufts) = 260

95% confidence

② Habits or sites that have the same italics are not significantly different from one another.

* Tufts harvested March 1982.

An analysis of variance of tuft biomass between foredune sites and reardune-grassland sites (Appendix III, Table 28) reveal that although there was a significant amount of variation of tuft biomass among sites A, B, C and D and E, F, G and H, by far the most variation occurred between the two groups of sites A, B, C, D and E, F, G, H.)

The mean tuft biomass per square metre was much higher for the foredune sites and subsite I_s than for the reardune-grassland sites and subsite I_{ns}. Taking the extremes, the biomass per square metre is nearly six times greater at site B than it is at site F.

The mean biomass of tufts in relation to the habit they exhibit is given in Table 14 . Erect tufts, leader tufts and stunted-leader tufts all have a significantly different mean biomass. The mean biomass of an erect tuft is over four times that of a stunted-leader. Tufts with semi-erect habits have a mean biomass which is not significantly different from the mean biomass of erect tufts and leader tufts.

An analysis of variance of tuft biomass with relation to habit type (Appendix III, Table 29) reveals that most of the variation in biomass occurred among the groups rather than within the groups.

6.3 GROWTH ANALYSIS

6.3.1 Introduction

Aspects of the growth of *Desmoschoenus* are investigated in this section. Selected plants of *Desmoschoenus* (a plant being a group of tufts that are connected to each other) were monitored at sites A, C, E, G and H for one year. Monthly records were made of rhizome growth, new tuft production, inflorescence growth, leaf production and lamina die-back. Graphic representations of tufts are illustrated to highlight the dynamics of leaf production and die-back rate over a one year period.

6.3.2 Methods and Materials

A total of 19 plants were monitored, six at site A, three at sites B, C and E, and four at site D. Plants were labelled AA, AB, AC, AD, AE, AF, BA, BB, BC, CA, CB, CC, etc. All plants varied considerably with respect to tuft number which ranged from one (AD) to 25 (HD). A total of 190 tufts were monitored, 68 on the foredune sites, 76 on the rear-dune sites and 46 on the grassland site. Tufts were labelled from oldest to most recently produced (e.g. AA1, AA2,...AA23, i.e. plant AA had 23 tufts).

Counts were taken at the end of each month from December 1980 to January 1982, of the new leaves that were produced from each tuft. For this purpose the tips of all new leaves were painted with oil paints in a colour that distinguished the month they were produced from other months, i.e. only leaves produced in February had their tips painted red, March leaves were yellow, April leaves - black etc. From these results the average number of leaves produced per tuft at each site for each month was found. All new tufts that arose from the monitored tufts were labelled, (e.g. AC1a, AC1b, i.e. new tufts a and b arose from tuft 1 of plant AC during monitoring). New tufts were also monitored for leaf production. An example of leaf production counts is given in Appendix III, Table 31.

Monthly culm-peduncle measurements were taken of all new inflorescences. Rhizome growth was measured for a one year period (April 1981 to March 1982) of the terminal tuft of each leader plant. This was done by placing a stake at the rhizome tip of each terminal tuft and measuring the increase in distance between tip and stake each month.

At least two tufts were selected from each monitored plant (46 tufts in total). Their laminae were painted with oil paints as a means of recording die-back. Such a record was made as follows. The interface of the dead part and living part of every pingao lamina is usually quite distinct, being an obvious orange band separating the tawny dead portion towards the tip from the green-orange portion towards the sheath. The interface of every lamina making up these 46 tufts was painted at the end of every month, at the same time as the leaf tips of new leaves, and with the same colour. Thus the monthly positions of the interface as it travelled from leaf tip to sheath were imprinted on the lamina.

After a year of such recording the 46 tufts were removed from their plants, at the beginning of February 1982, and dissected leaf by leaf. The distance from lamina base to each marking per leaf was measured. Because of the persistance of inclement weather at the end of July and the beginning of August, painting the selected tufts could not be attempted for July. Due to the differences in the permanence of some of the oil paints combined with subjection to harsh environmental conditions between painting and harvesting, some information was lost, especially from December to February when monitoring began. Retouching was attempted on a few occasions especially during the winter months when many of the markings were becoming faint. Despite the losses, much information was retained. An example of die-back measurements appears in Appendix III, Table 35. From these measurements the average lamina die-back per month for each site was found.

A graphic representation was made of each selected tuft to put into a visual form the dynamics of leaf production and die-back rates over a one year period. From information gathered from the graphs, viz. leaf longevity, it was possible to estimate the above-ground biomass produced by pingao per metre per year, at each site.

6.3.3 Results and Discussion

From 173 of the monitored tufts were produced 247 new tufts over the period of monitoring (Figure 42, and Appendix III, Table 32). From monthly counts it was found that definite seasonal differences in tuft production occurred. Very few new tufts were produced from March to August with none in May to July. The onset of spring resulted in an increase with peak tuft production occurring in November. There is a rapid decline throughout the summer and a more gradual decline throughout the autumn. There appear to be

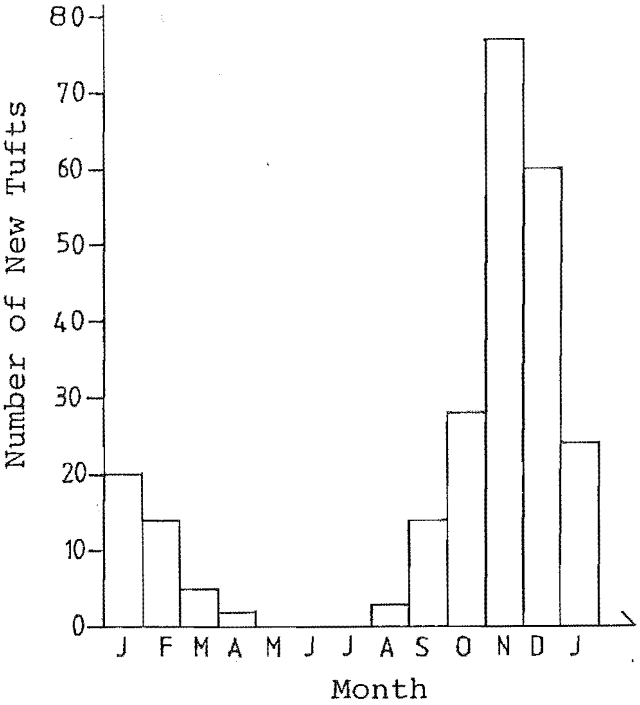


Figure 42

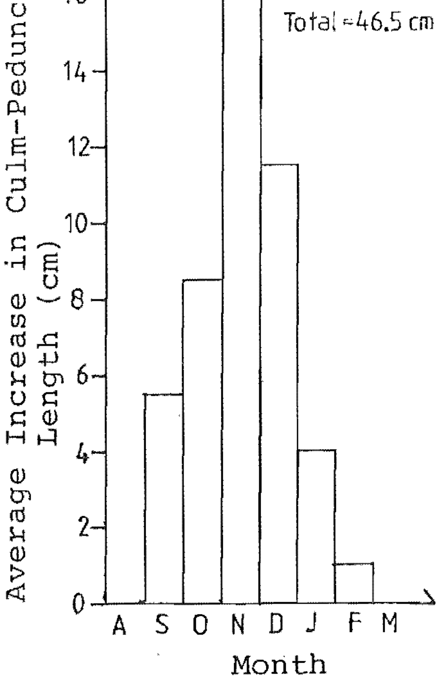


Figure 43

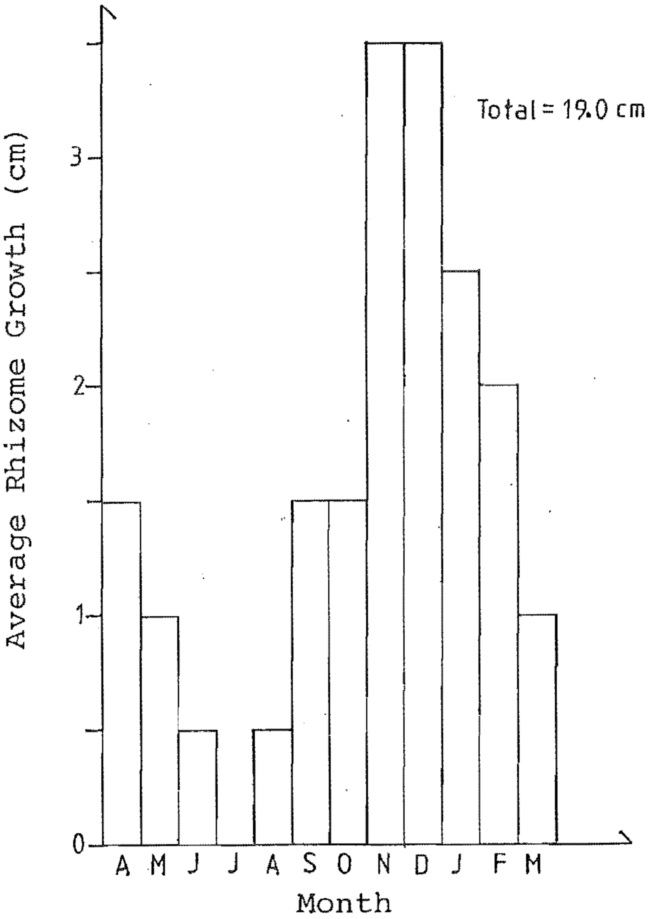


Figure 44

Figure 42. New tufts arising from monitored tufts, January 1981 to January 1982, N = 173.

Figure 43. Average increase in the length of developing culm-peduncles, April 1981 to March 1982, N = 12.

Figure 44. Average rhizome growth of monitored plants, April 1981 to March 1982, N = 13.

no significant differences in the numbers of new tufts produced among the five sites.

Of the 190 monitored tufts, only 12 produced inflorescences over the period of monitoring. Nine of the 12 inflorescences were produced from tufts of the two foredune sites. The average increase in culm-peduncle lengths is presented in Figure 43, and Appendix III Table 33. The culm and peduncle which support the rest of the inflorescence began to grow in September and had an average growth of 5.5 cm over this month. The rate of growth increased from September to November. Over November the culm-peduncle grew its most, (16.0 cm). Growth rate decreased over summer and growth ceased altogether by March. The mature average culm-peduncle length measured 46.5 cm.

A similar trend can also be seen for the average rhizome growth of pingao over a year, Figure 44, Appendix III Table 34. There was a decrease in rate of rhizome growth from April to July. June, July and August were months over which there was little or no rhizome growth. There was an increase in growth rate over the spring months with a peak of 3.5 cm per month over November and December. The rate decreased from December to March after which time monitoring was stopped. The growth of an average rhizome over a one year period was 19.0 cm although as much growth as 51 cm was recorded, (EC14). Differences in rhizome growth were found to exist among plants of the five sites. Rhizomes of the foredune plants (not including those that grew due to inflorescence development) had an average annual growth greater than that of rhizomes of the reardune-grassland zones.

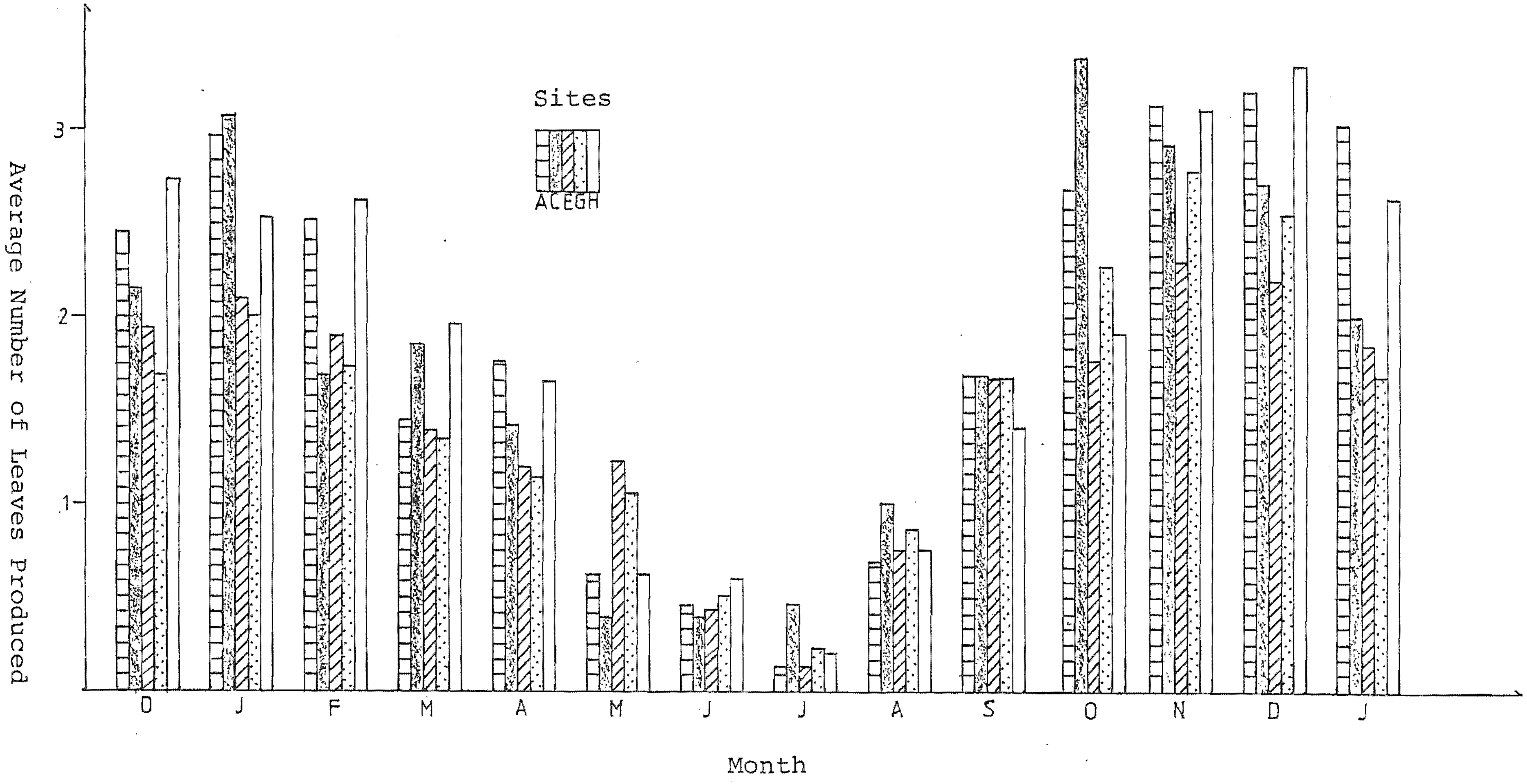


Figure 45. Number of leaves produced per average tuft per month at sites A, C, E, G and H, (December 1980 to January 1982).

Table 15 Number of Leaves Produced per Average Tuft per Month at Sites A, C, E, G and H. (December 1980 to January 1982)

Site	Number of Tufts Counted	MONTH														Leaves Produced per Average Tuft from Jan - Dec. 1981
		D	J	F	M	A	M	J	J	A	S	O	N	D	J	
A	29	2.45	2.97	2.52	1.45	1.76	0.62	0.45	0.14	0.69	1.69	2.69	3.14	3.21	3.03	21.33
C	13	2.15	3.08	1.69	1.85	1.39	0.39	0.39	0.46	1.00	1.69	3.39	2.92	2.77	2.00	21.02
E	25	1.95	2.10	1.91	1.40	1.20	1.23	0.43	0.13	0.75	1.68	1.78	2.30	2.20	1.84	17.11
G	30	1.68	2.00	1.73	1.36	1.14	1.09	0.50	0.23	0.86	1.68	2.27	2.77	2.55	1.68	18.18
H	38	2.74	2.95	9.63	1.97	1.66	0.61	0.60	0.11	0.74	1.42	1.84	3.11	3.34	2.63	20.98

Note: Leaf counts were not included of tufts that arose during monitoring, tufts that developed into inflorescences, or tufts that died during monitoring.

The range of rhizome growth was greatest for the reardune zone, with the terminal tufts EC14 and GC9 having rhizomes that grew far longer than other tufts of the same zone.

The results of the leaf production counts are presented in Figure 45 and Table 15. As a general trend it can be seen that leaf production for each site also varied seasonally. The highest rate occurred during the late spring and early summer months, the peak being January 1981 and November-December 1982. From late summer to July the rate of leaf production declined markedly but increased again from July back to late spring and early summer. This seasonal trend closely follows the seasonal changes in average temperature (Figure 26) which seems to be the dominant factor controlling leaf production.

The variation among sites was greatest over summer and least over winter and early spring. During summer leaf production at sites E and G were slightly lower than that of sites A, C and H, but overall the average number of leaves produced at each site per month was similar. This is best illustrated in Table 15 which gives the number of leaves produced per average tuft in one year, (January-December 1981), for the five sites. Tufts at sites A, C and H have a yearly production of 21.33, 21.02 and 20.98 leaves respectively, whereas tufts at sites E and G have a slightly lower yearly production of 17.11 and 18.18 leaves respectively.

The results of average lamina die-back are presented in Figure 46 and Table 16. There was an increase in die-back from February to April and a decrease from April to July and August. It gradually rose again from October to January. Compared to laminae of the foredune sites, laminae of the

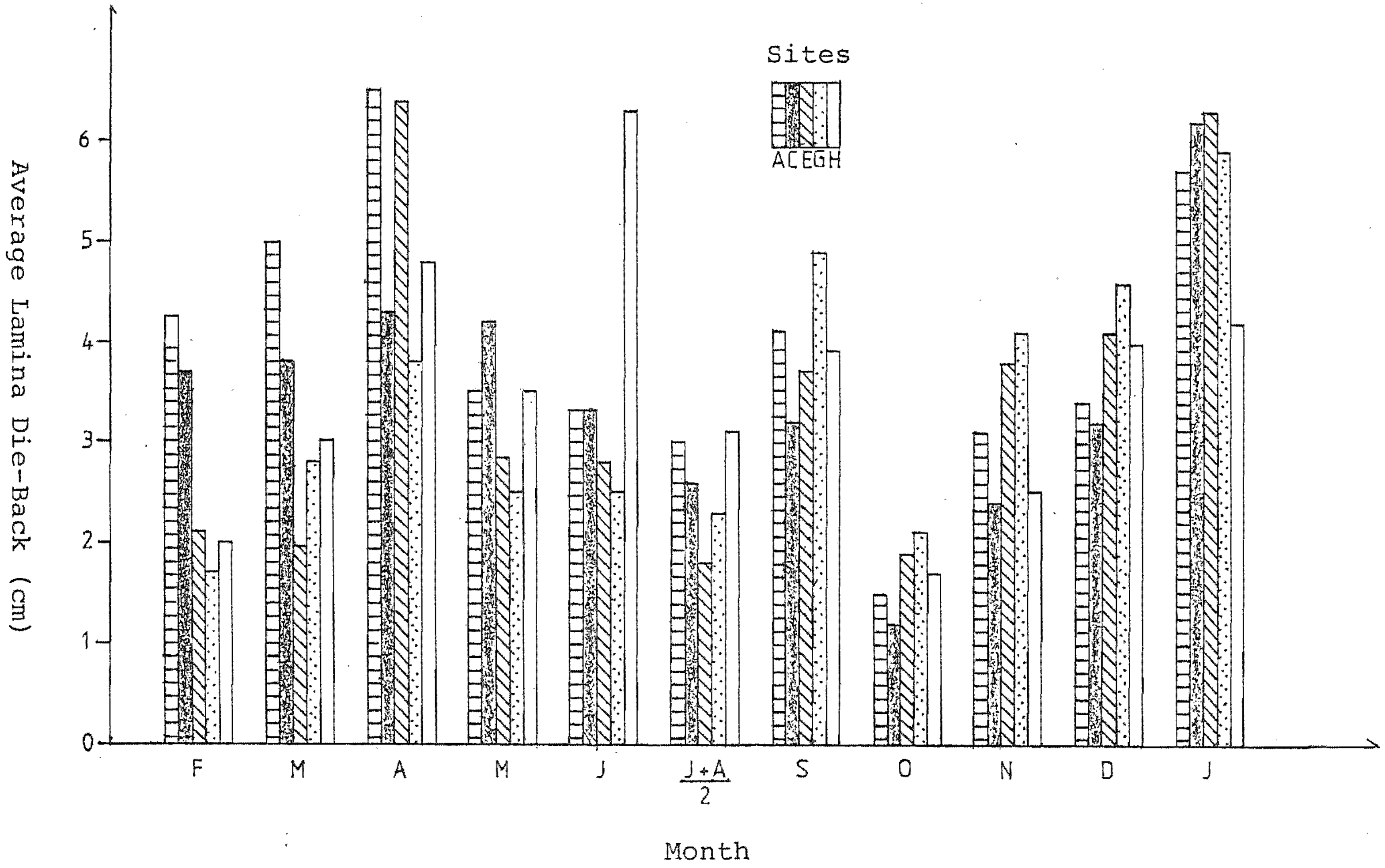


Figure 46 . Average lamina die-back (cm) per month at sites A, C, E, G and H, (February 1981 to January 1982).

Table 16 Average Lamina Die-Back (cm) per Month at Sites A, C, E, G and H. (February 1981 to January 1982)

Site	Number of Tufts Monitored	MONTH											Average Lamina Die-Back (cm) (Feb 81-Jan 81)
		F	M	A	M	J	J&A	S	O	N	D	J	
A	13	4.3	5.0	6.5	3.5	3.3	6.0	4.1	1.5	3.1	3.4	5.7	46.4
C	6	3.7	3.8	4.3	4.2	3.3	5.2	3.2	1.2	2.4	3.2	6.2	40.7
E	10	2.1	1.9	6.4	2.8	3.5	3.5	3.7	1.9	3.8	4.1	6.3	39.3
G	6	1.7	2.8	3.8	2.5	4.6	4.6	4.9	2.1	4.1	4.6	5.9	39.5
H	11	2.0	3.0	4.8	3.5	6.3	6.2	3.9	1.7	2.5	4.0	4.2	42.1

reardunes seem to have higher die-back rates during autumn and winter, but slightly low die-back rates in the spring and summer.

It is unknown why site H should have such a high June die-back. The increase in die-back for all sites in September is most likely to be due to the drying out of the laminae. After being continually wet over the winter months the orange line delineating the live and dead portions of the laminae became very diffuse (up to 2 cm long) as die-back was occurring over a wider area than it usually did. Consequently, when the leaves dried out with warmer temperatures in September, much of the slow winter die-back was included in the September results.

As can be seen in Table 16 the average yearly lamina die-back is very similar among the five sites; sites A, C and H have the most annual die-back of 46.4, 40.7 and 42.1 cm respectively and the reardune sites E and G with annual die-backs of 39.3 and 39.5 cm respectively. The amount of die-back of an average leaf seems to be related to its length; the longer the leaf the higher the rate of die-back.

Examples of the graphs of the tufts monitored for die-back are illustrated in Figures 47 to 59. The laminae are arranged consecutively down each page, the oldest first and the youngest nearest the apex; the lamina bases to the right and the tips to the left. The month in which each leaf was produced is labelled at each leaf tip. Markings along the length of each lamina represent points of monthly die-back. Lines join corresponding months among the laminae. The portions of laminae to the left of the line demarcating the January die-back are the living parts of the tuft at the

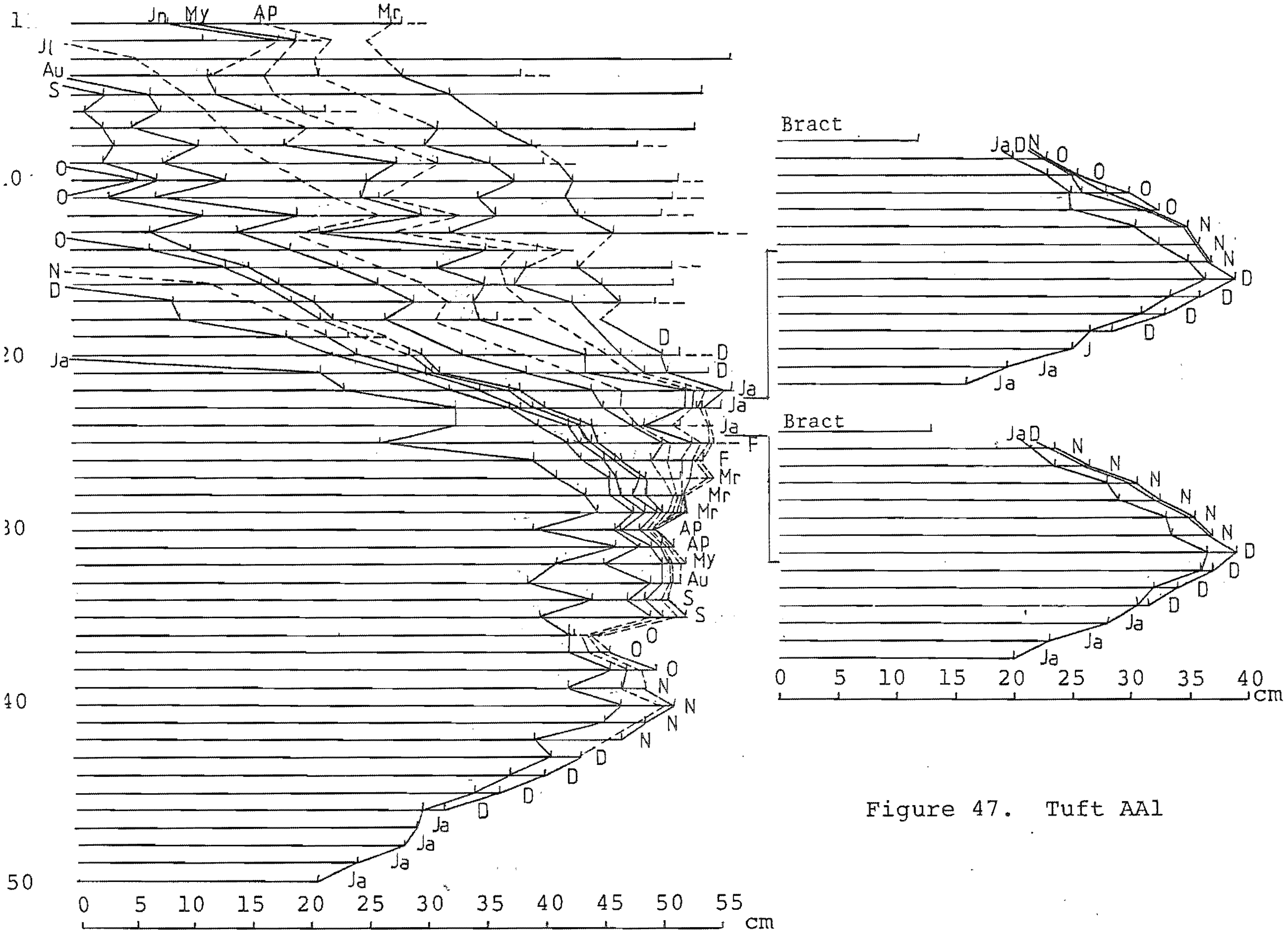


Figure 47. Tuft AA1

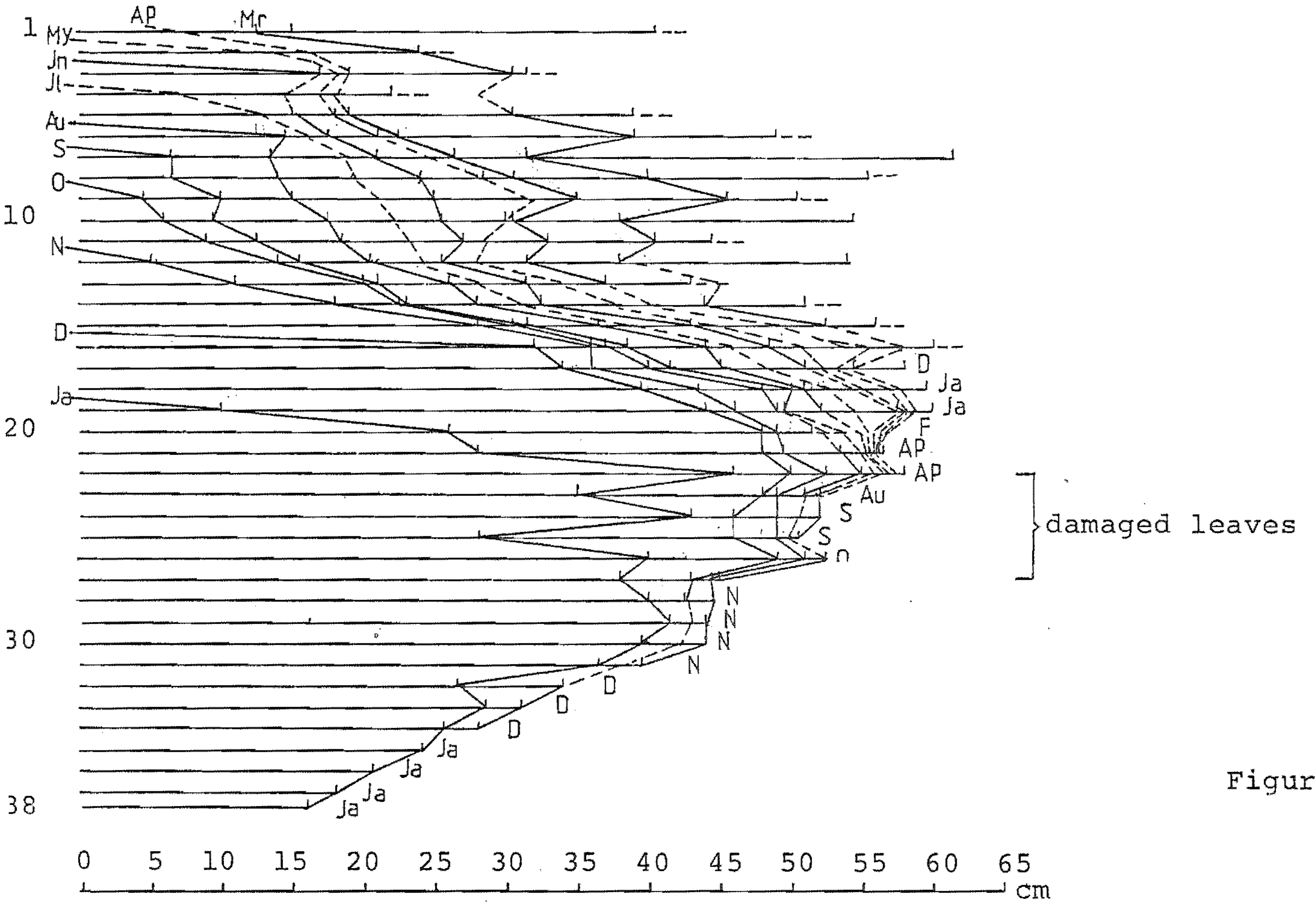


Figure 48. Tuft AA6

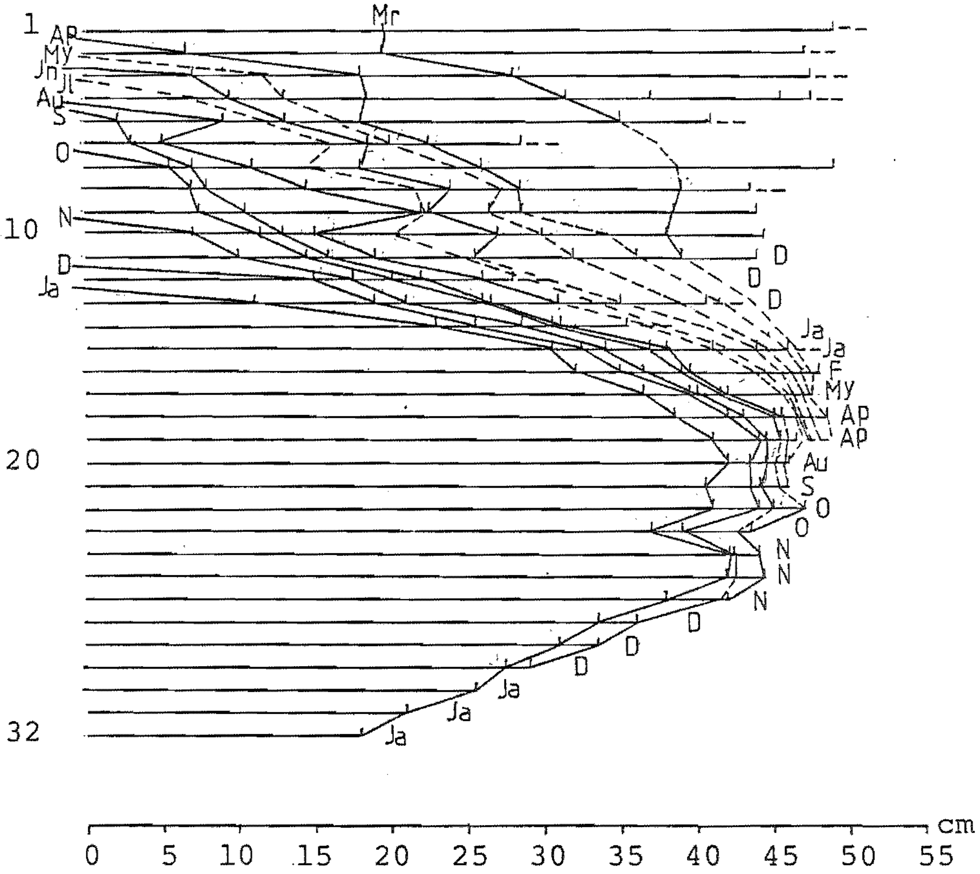


Figure 49. Tuft AA18

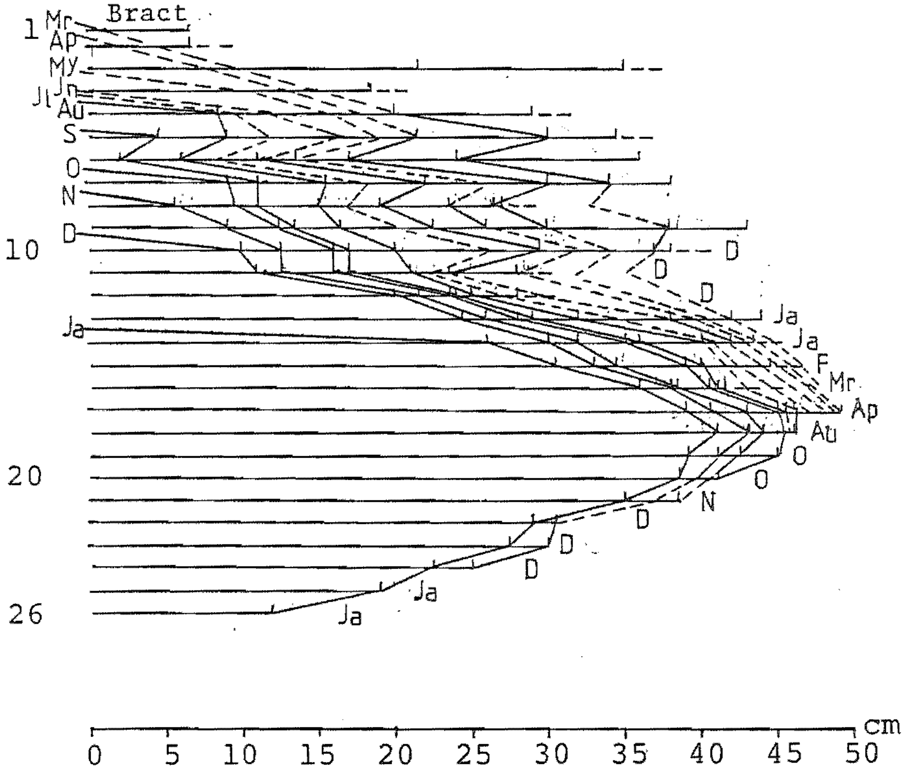


Figure 50. Tuft AA21

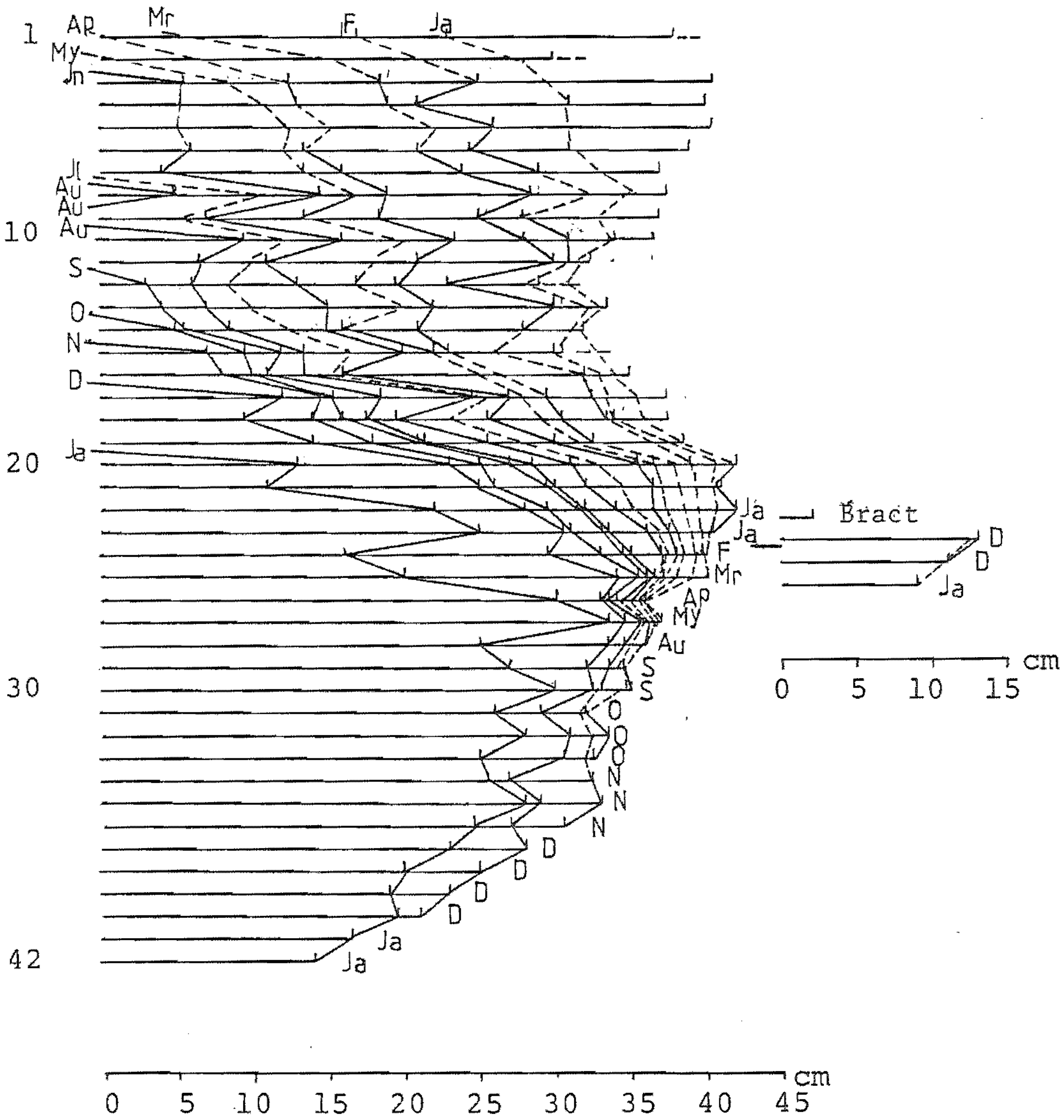


Figure 51. Tuft CB1

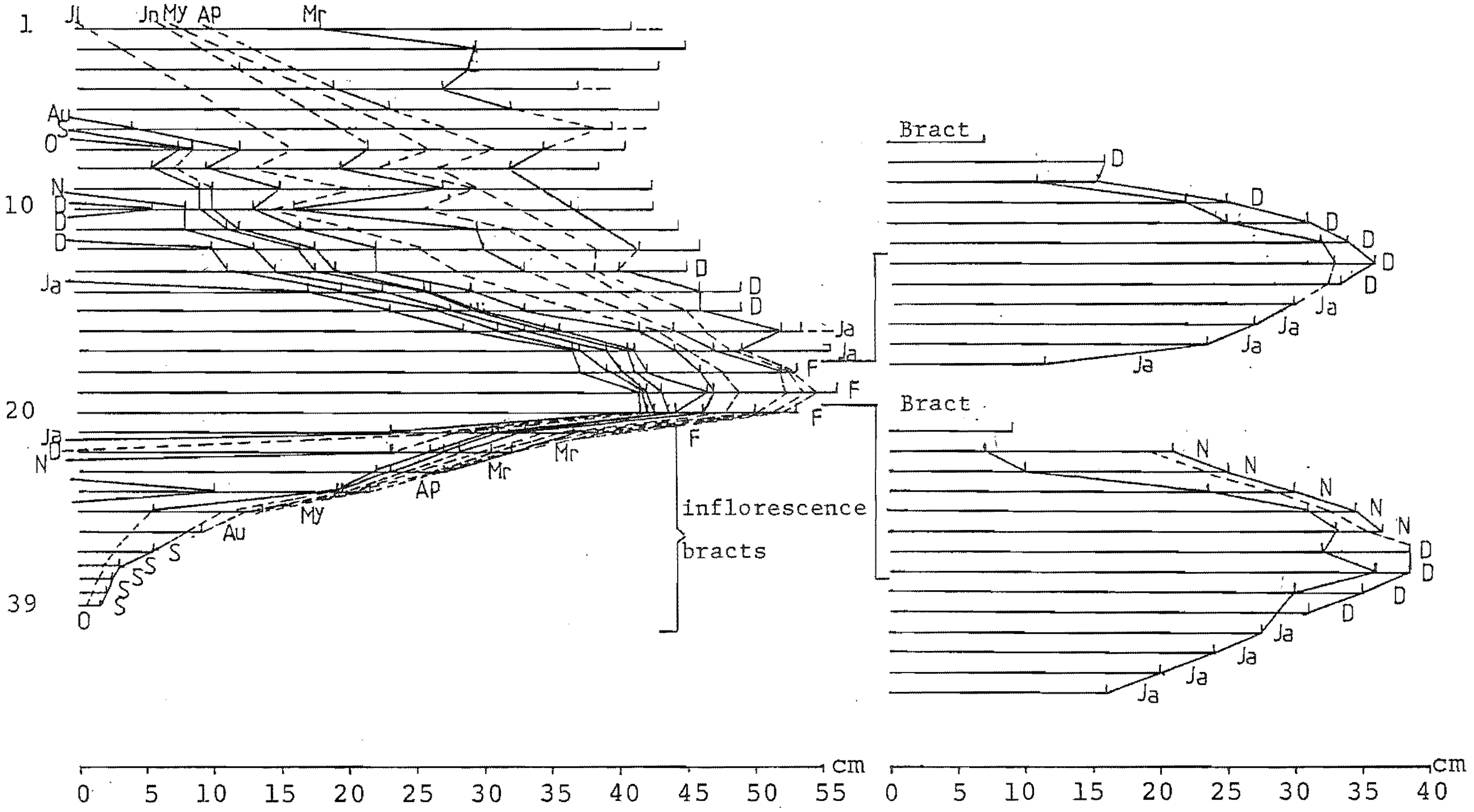


Figure 52. Tuft CC1

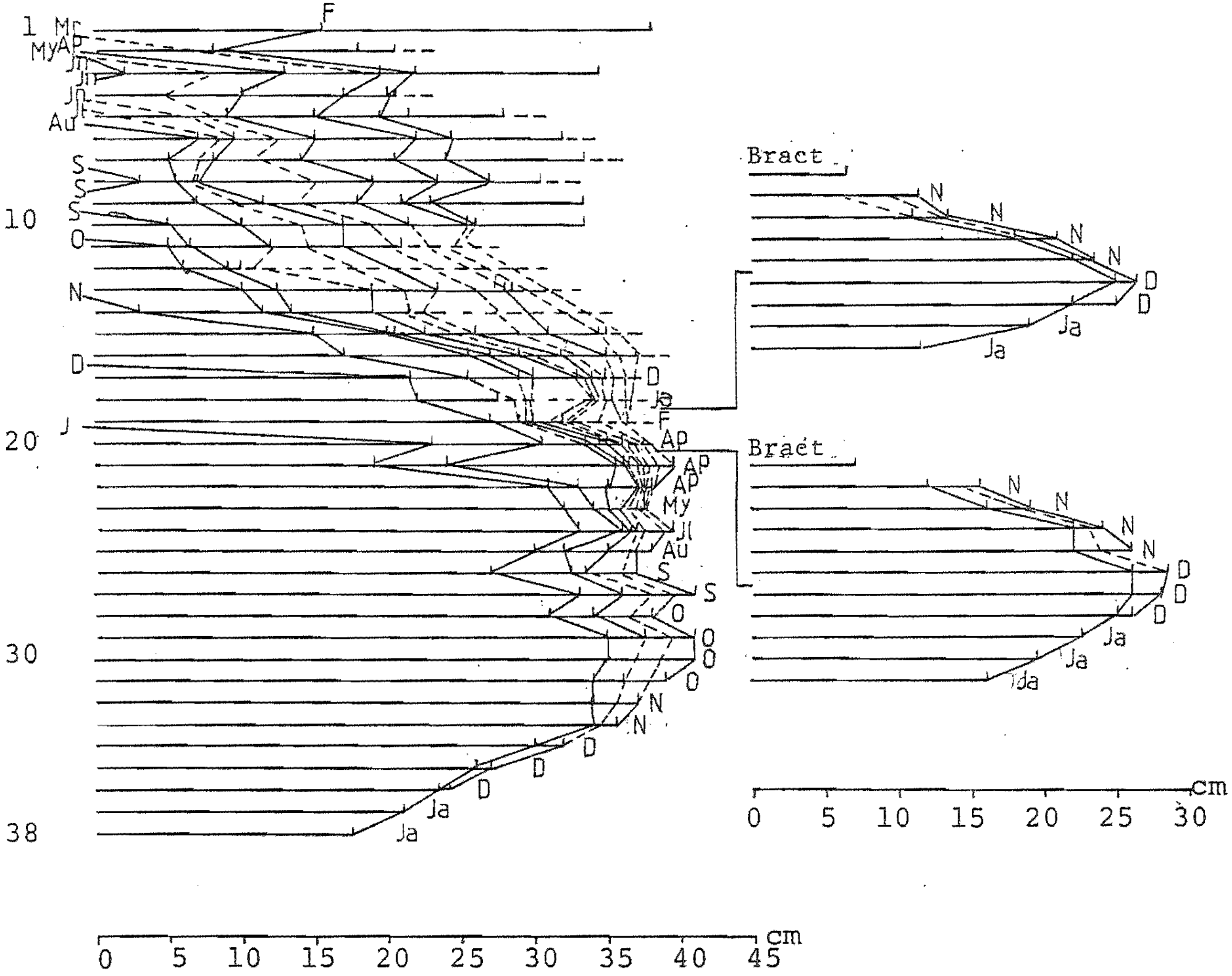


Figure 53. Tuft EA4

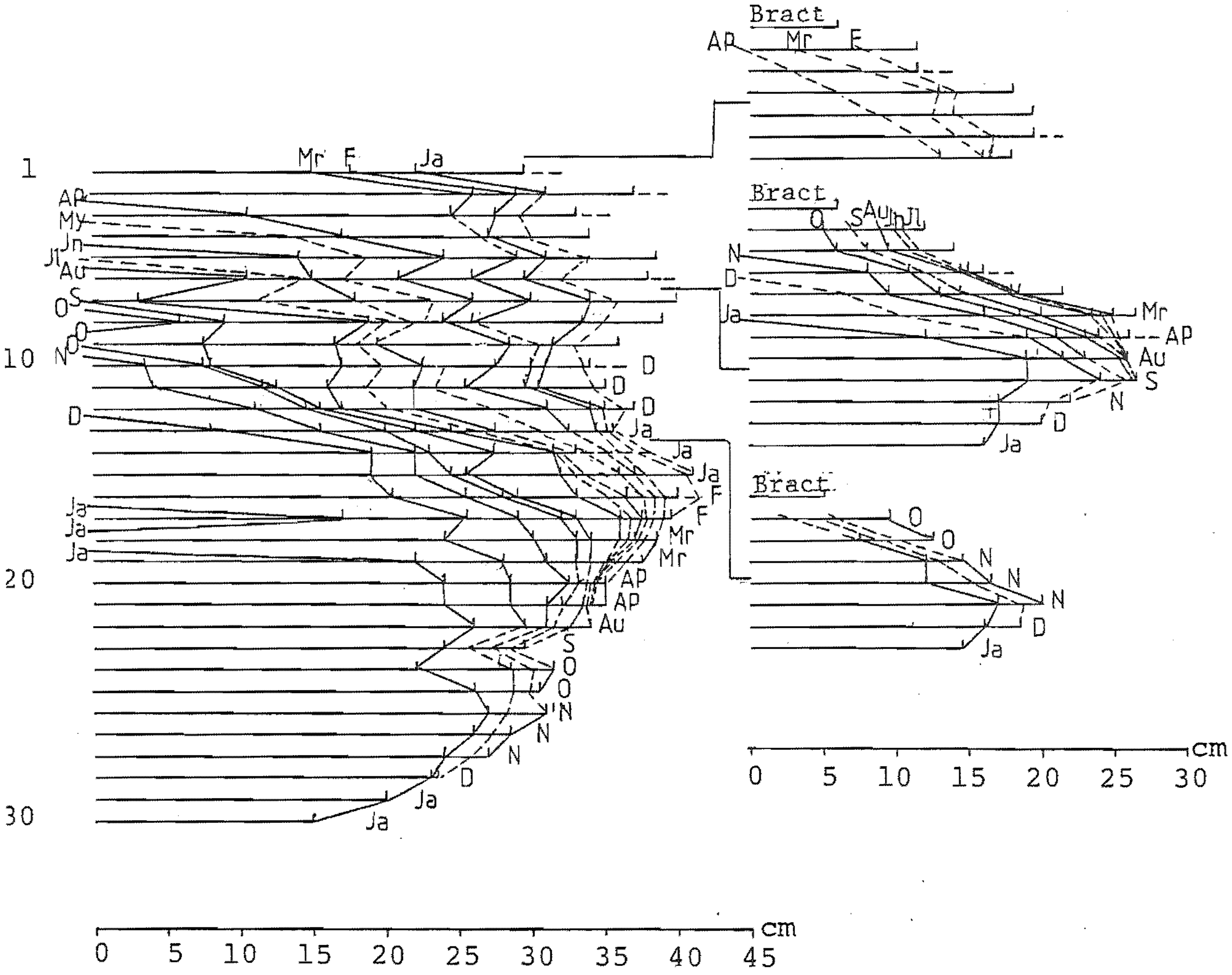


Figure 54. Tuft EB3

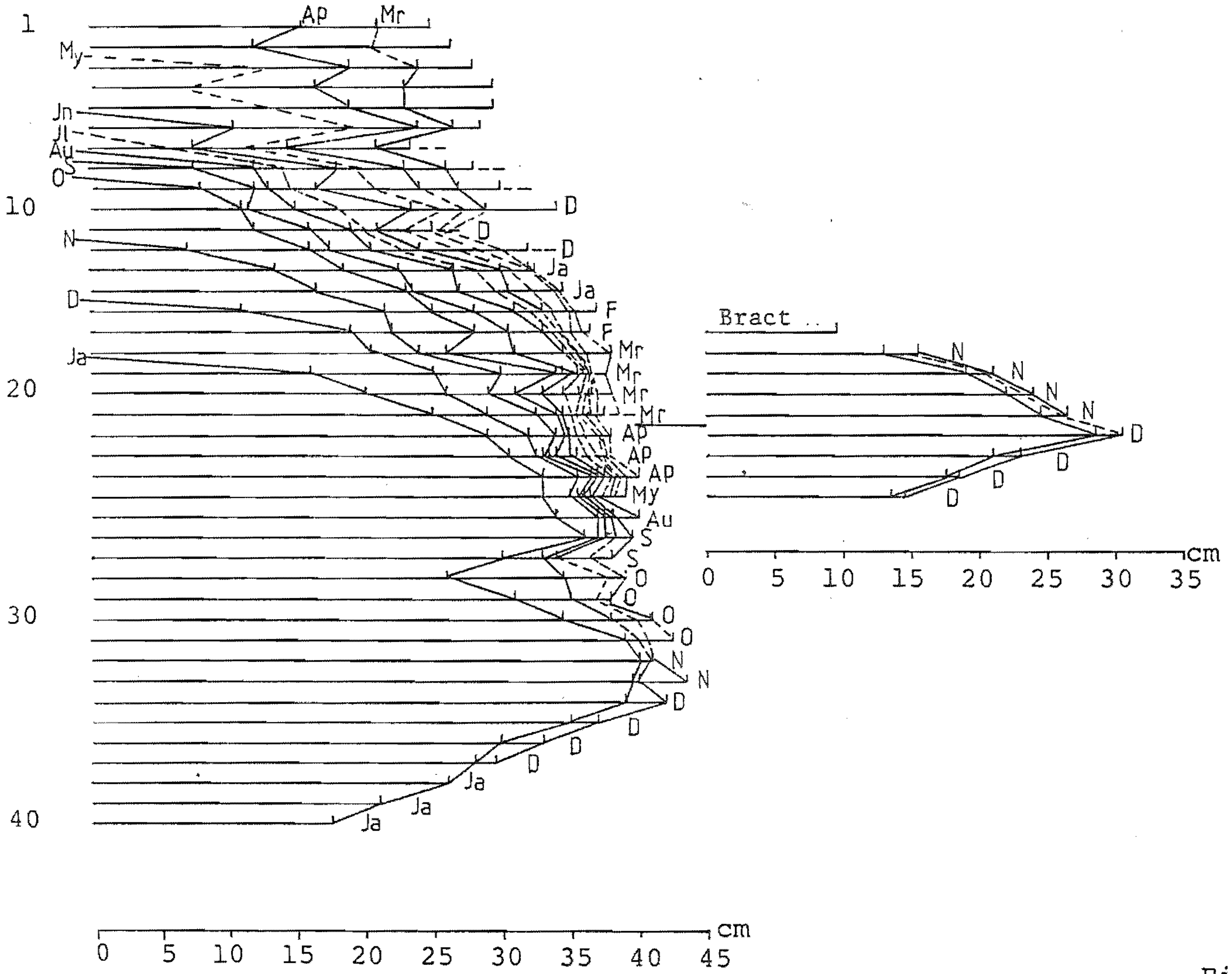


Figure 55. Tuft EC4

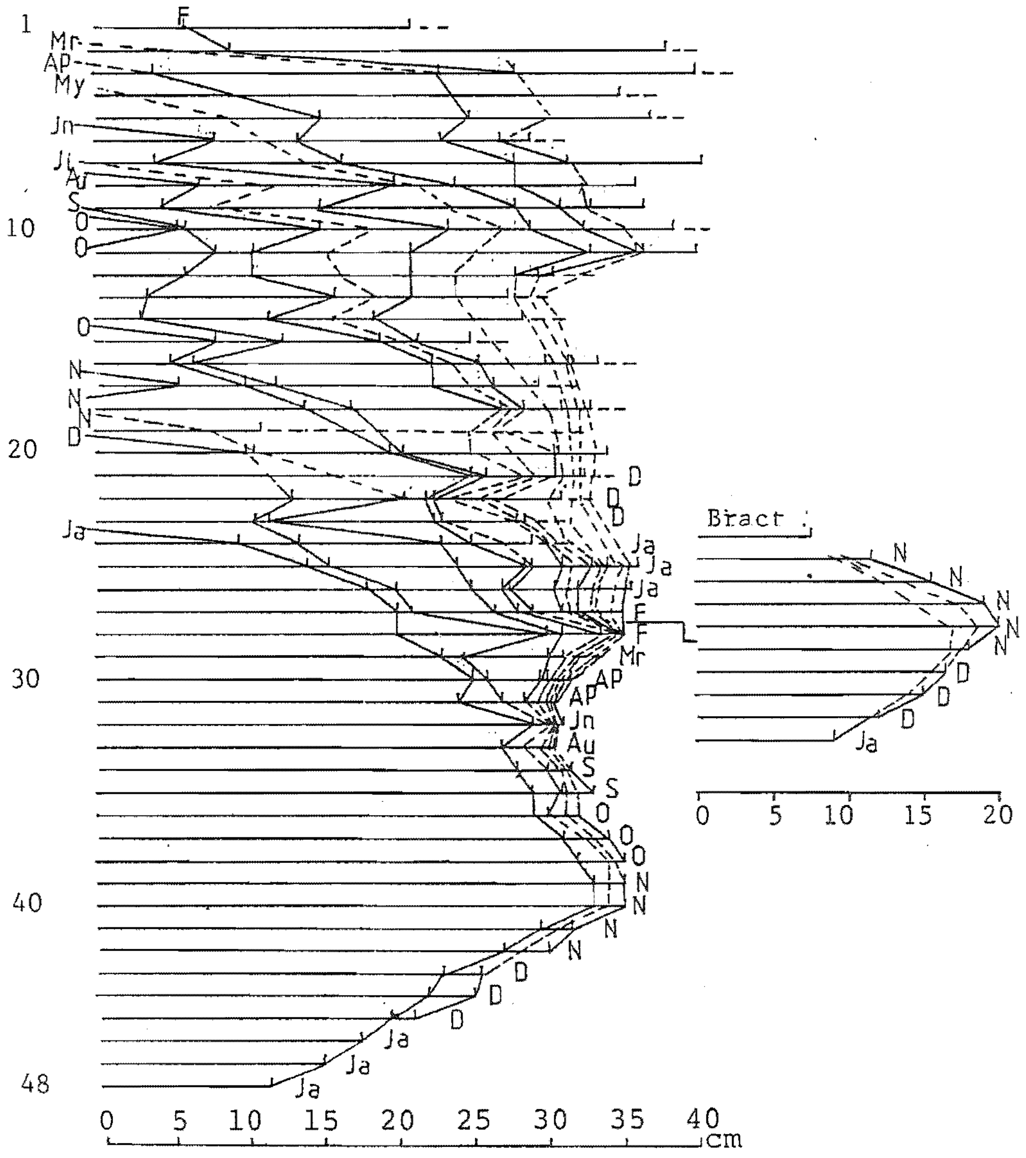


Figure 56. Tuft GA3

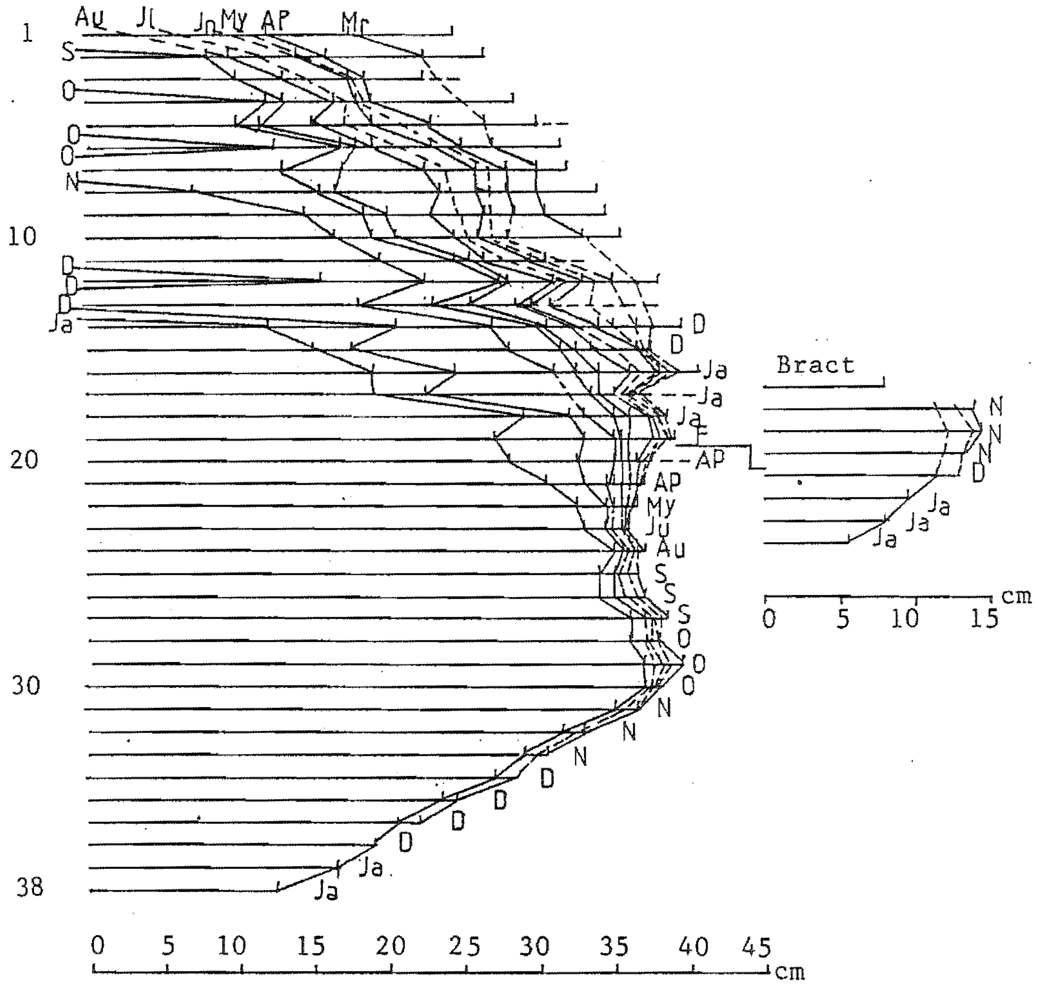


Figure 57. Tuft GB16

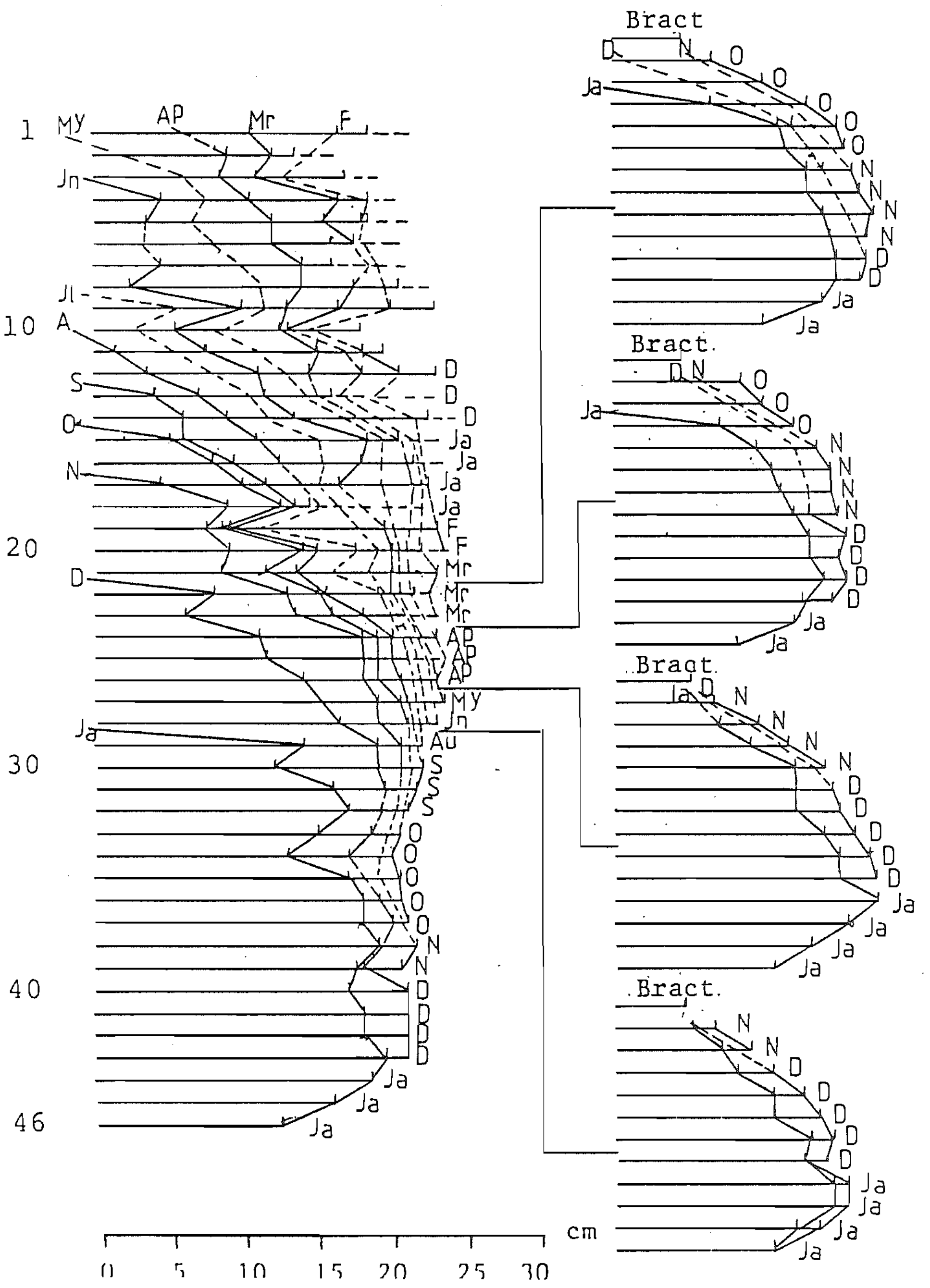


Figure 58. Tuft HA4

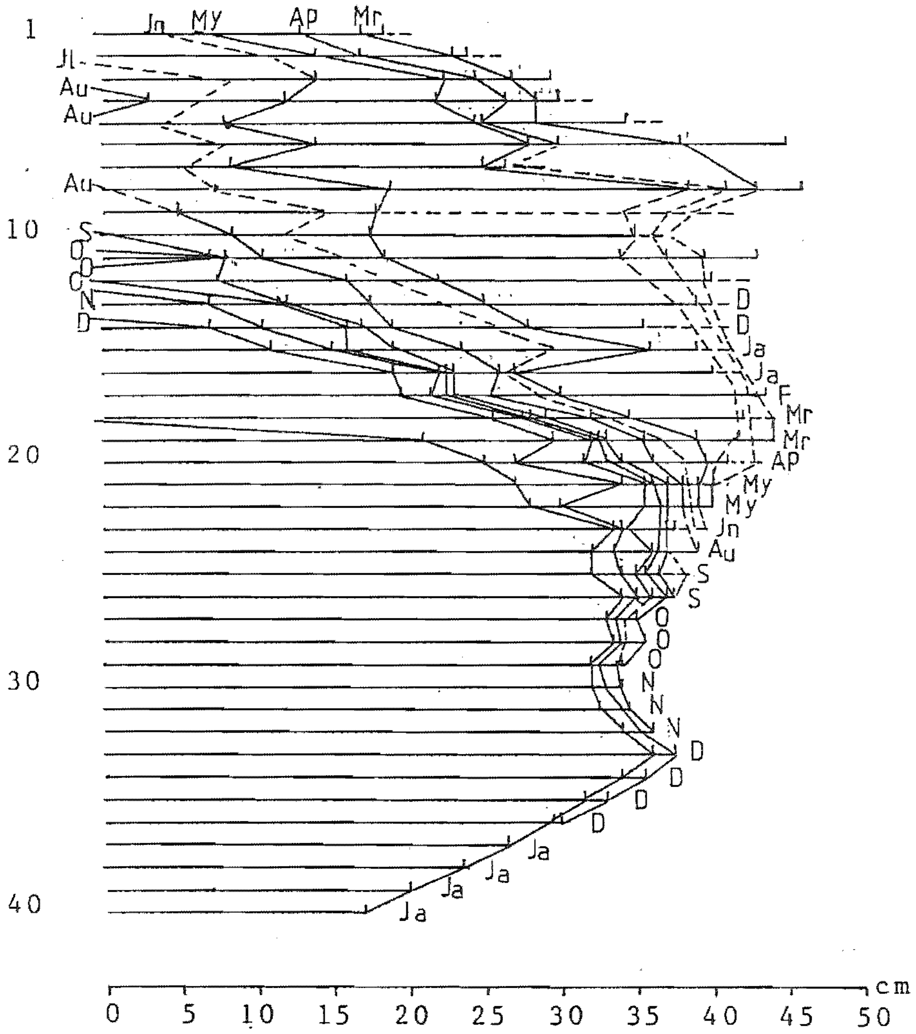


Figure 59. Tuft HD16

time of harvest. New tufts are also graphed showing their positions along the parent tuft. Lamina which are broken are shown by dashed lines.

It is apparent that there are obvious seasonal changes of die-back rates for all tufts. Although no pattern of die-back is exactly replicated among any of the tufts, definite trends common to most tufts can be seen. Die-back was slowest in spring especially October. Periods of most die-back were over the autumn and summer months especially April and January.

Of consecutive leaves the older one does not necessarily die first. Because of this a wave effect is produced whereby the month lines that connect each lamina do not travel through them in a straight line but follow a zig-zag path. This is due to the orientation of each leaf on the tuft. Leaves with a north-facing aspect die back slightly ahead of their consecutive older south-facing leaves. The greater amount of exposure to the sun of the north-facing leaves is probably the cause of the non-sequential die-backs.

The rate of die-back of an individual lamina as well as being seasonally determined is controlled by a process inherent in the leaf itself. While the leaf develops, die-back is very minimal. Only as it reaches maturity does its die-back rate increase. Die-back is fastest along the basal 10 cm of lamina. Conversely, the rate of growth of developing laminae seems to be constant until they near maturity at which time it decreases. Lamina length is not constant from leaf to leaf. This may also be seasonally determined but this is difficult to establish due to the breakage and loss of lamina parts of the older dead leaves.

Tuft graphs of AA1, AA6, AA17 and AA21 (Figures 47 to 50) illustrate the differences among tufts along a single rhizome. Apart from the large amount of die-back in January for tuft AA6 trends are seen to be more similar among these tufts than among tufts from other plants. Only in detail are there differences.

An example of inflorescence development is illustrated for tuft CC1, (Figure 51). New leaf emergence ceased in September. Growth of developing leaves also ceased which included all leaves up to those produced the previous March. These stunted leaves became the inflorescence bracts upon culm-peduncle growth. They were still subject to the same patterns of die-back as the older leaves but because they were smaller in length they died at the same time as leaves that were much older.

Most new tufts arose at the beginning of spring, from the axils of leaves produced six to nine months earlier (usually in January to March). Later in the growing season some tufts gave rise to new tufts from leaves produced only two months previous. New tufts are usually produced in pairs on opposite sides of the parent rhizome, one a few weeks before the other. The younger tuft is nearly always produced two leaves closer to the apex than the older tuft. The only instance of a younger tuft developing behind an older tuft was after the parent tuft had infloresced, (Tuft CC1) (Figure 51).

All new tufts began with one or two bracts which are merely sheaths with little or no lamina development. All prospective leaves arose out of them, the first ones usually as a group of four to six. They reached maturity at lengths much smaller than those of mature leaves of the parent tuft. Subsequent leaves mature at progressively longer lengths, presumably until a length comparable to that of the mature leaves of the parent is reached.

For each monitored tuft leaf longevity was found from their graphs. These results are given in Table 17. For the five sites average leaf longevity was very similar. Leaves at sites A, C, E, G and H had an average longevity of 12.0, 11.9, 12.0, 11.8 and 11.3 months respectively.

It can be concluded that an average leaf of pingao was living for about one year at these sites and presumably at all sites. With this established, the above ground biomass produced per unit area per year can be found for each site as the living portions of a tuft is its total biomass production for one year. Because recycling of assimilates may be occurring, any calculation of biomass per unit area per year can only be regarded as an estimate.

Dry weight calculations have already been done in Section 6.2.6, Table 13, which provided an above ground biomass $.m^{-2}$ estimate. These results were used to estimate the above ground biomass $.m^{-2}.yr^{-1}$ of pingao at each site. These results are shown in Figure 60. Because of their greater density and larger biomass pingao tufts of the foredune sites A to D and subsite I_s produced more biomass $.m^{-2}.yr^{-1}$ than the pingao of the reardune-grassland sites E to H, and subsite I_{ns}. Site B had the highest biomass. $m^{-2}.yr^{-1}$ estimate of 255.7 $g.m^{-2}.yr^{-1}$ and site F had the lowest estimate of 44.8 $g.m^{-2}.yr^{-1}$. Relative to other plant ecosystems these values are very low and are comparable

Table 17. Average Leaf Longevity of Tufts at Sites A,C,E,G & H.

Tuft	Average Leaf Longevity (Months)	
AA1	11	
AA6	12	
AA18	13	
AA21	13	
AB1	13	
AB4	12	$\bar{x}$ Site A
AC1	12	= 12.0
AD1	12	
AE1	12	
AE2	12	
AE4	11	
AF1	12	
AF3	11	
CA1	11	
CB1	13	
CB3	12	$\bar{x}$ Site C
CC1	13	= 11.9
CC2	12	
CC4	10.5	
EA1	Tuft died	
EA2	12	
EA4	12	
EB3	12	
EB5	13	$\bar{x}$ Site E
EB11	14	= 12.0
EC1	Tuft died	
EC4	11	
EC10	10	
GA1	Tuft died	
GA3	12	
GB1	13	
GB16	12	$\bar{x}$ Site G
G61	11	= 11.8
GC6	11	
HA1	9	
HA4	10	
HB1	12	
HB5	10.5	$\bar{x}$ Site H
HC1	12	= 11.3
HC9	12	
HC17	12	
HD1	12	
HD9	13	
HD16	11	
HD23	11	

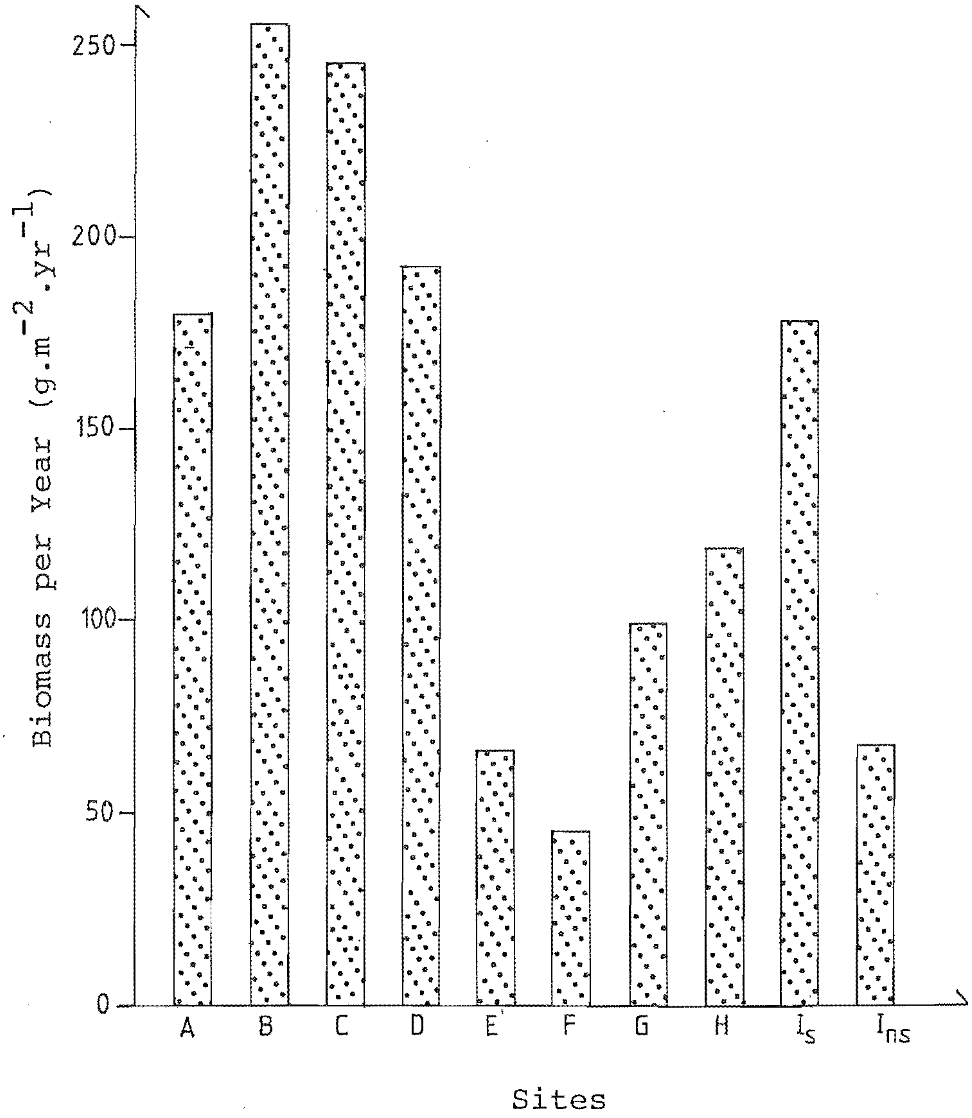


Figure 60. Estimate of biomass produced per square metre per year at sites A to I.

to the above ground biomass estimate of 200-300 $g.m^{-2}.yr^{-1}$ for cushion-fellfield communities (Williams 1974, Meurk 1978).

6.4 ENVIRONMENTAL FACTORS

6.4.1 Introduction

An investigation of selected environmental factors was undertaken to try and account for any differences in the quantitative and growth analyses of *Desmoschoenus* between the foredune and reardune-grassland sites. These factors included:

(a) soil water content
(b) salt content
(c) sand movement
(d) burial by sand
(e) interactions with other plants
(f) interactions with animals
(g) storm surges and high tides

6.4.2 Soil Water Content

Gypsum blocks (Model 5200) were used to investigate changes in soil water content of the dune system over a one year period, and to determine the availability of water to *Desmoschoenus* around the zone of root initiation.

The blocks are comprised of two electrodes embedded adjacent to each other in a plaster of paris matrix. A two metre long, plastic-coated wire leads from each electrode to a terminal. Upon burial the block's porosity enables rapid moisture equilibrium with the surrounding soil. The amount of moisture held in the soil determines the resistance to the passage of an electric current between the two electrodes, which is measured by the terminals' connection to a resistance metre.

Two gypsum blocks were buried at each of the sites A, C, E, G, H, J, K and L, one at 30 cm depth and the other at 90 cm depth. Care was taken to ensure that the whole of each block surface was in contact with the substrate surrounding it.

The blocks' terminals were positioned just above the substrate surface. Resistance was measured at 12 noon at the beginning of each month from January to December 1981, after which time the blocks were unearthed and washed. They were repositioned under all monitored plants (except AA, AD, AE, HA and HD due to the limited supply of blocks) adjacent the section of rhizome where root initiation was occurring (Figure 61). Two blocks were also positioned at site I. One under a plant on which sand was being regularly deposited (I_sA) and the other under a nearby control ($I_{ns}H$), (refer to Section 6.4.4). Resistance measurements were taken at 12 noon on seven occasions over a five week period during late summer 1982, when water stress was most likely to be occurring.

All resistance readings were converted to both percentage water content and water potential (bars), from a calibration curve established from Hanford sand by Soil Moisture Equipment Corporation.

Results

The calibration curve for sand (Figure 62) shows that at low water potentials the sand's water holding capacity is an amount of water equal to 44% of its dry weight. The water potential at field capacity is taken to be between -0.1 and -0.3 bars (7-11% water content), and the permanent wilting point is taken to be greater than -15 Kbars (a water content

Figure 61. A gypsum block being buried adjacent to the rooting zone of pingao

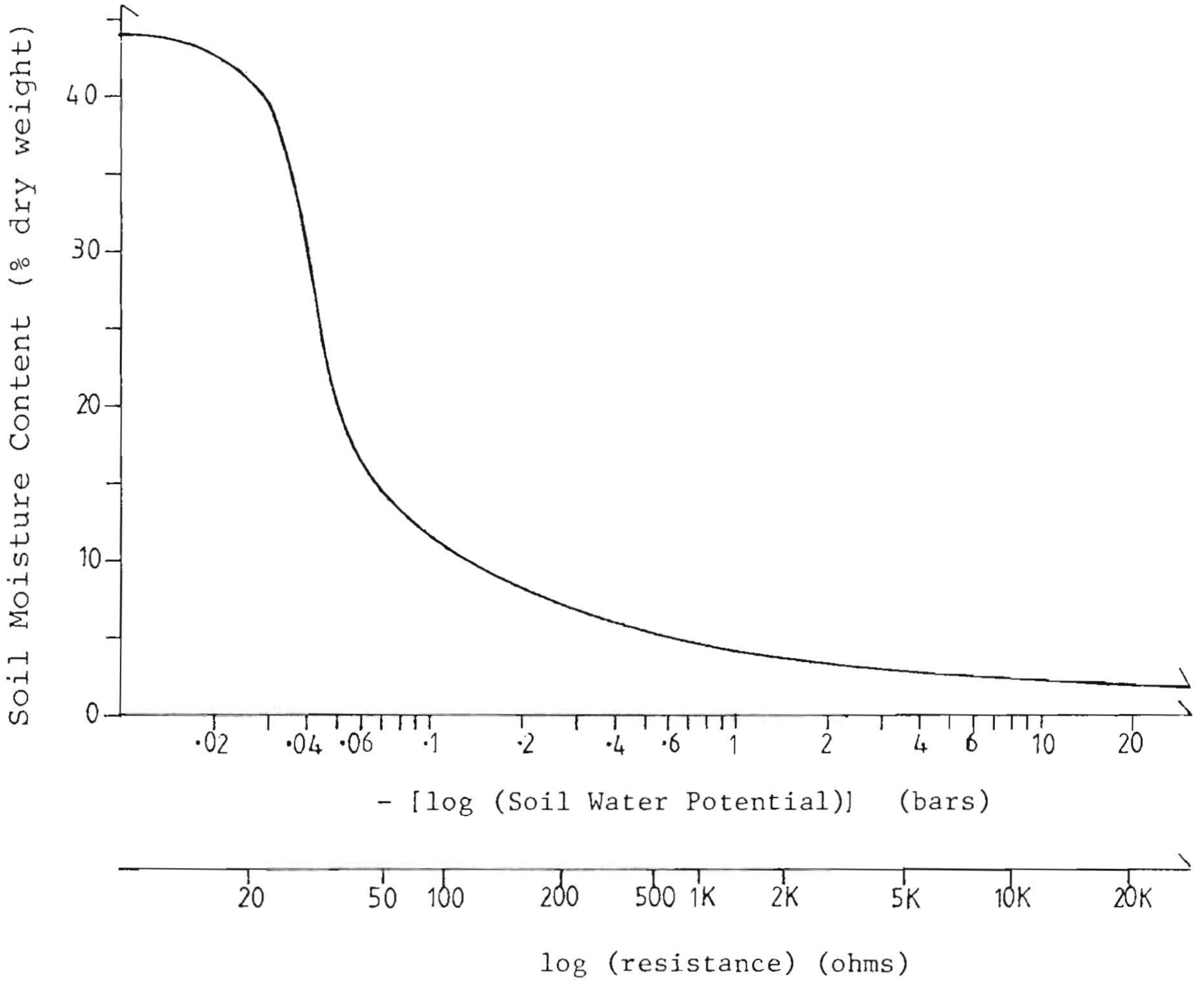


Figure 62. Soil moisture content calibration curve for Hanford sand (after Soil Moisture Equipment Corporation)

of 2% or less) (Etherington, 1975). Soil moisture stress is usually first apparent in plants that are found in soils with a water potential of -4 to -6 bars, (*ibid.*).

The range of the resistance metre was from 500 to 20,000 ohms (-0.57 to -20 bars). Measurements below 500 ohms indicated a soil that was very close to field capacity, whereas a soil measuring a resistance of greater than 20,000 ohms indicated that it was above permanent wilting point. Figure 62 also shows that resistance (ohms) and water potential (bars) have an approximate linear relationship and that water potentials have been approximated, however, they are still accurate enough for the purposes of the experiments.

The results of the water content of the dune and grassland sites throughout the year are presented in Table 18. All the measured foredune and reardune dune sites had soil water contents at, or close to, field capacity at both 30 cm and 90 cm depth. This suggests that water is not a limiting factor for pingao on the foredunes and reardunes where their functional roots reach a depth of 30 cm or more.

On the other hand, the water content of the soil under grassland (site J) and the remnant dune soils (sites K and L) varied considerably between field capacity and wilting point at both depths. These soils were close to field capacity at every measurement from June to October and for many measurements throughout the rest of the year. Summer and autumn measurements gave the largest range (-0.57 to -20 bars) indicating that at times of high water

Table 18 Water Potential (bars) of Dune and Grassland Substrates at 30cm & 90cm Depth. (1981)

Sites	MONTH															
	Jan		Feb		Mar		Apr		May		Jun-Oct		Nov		Dec	
	30	90	30	90	30	90	30	90	30	90	30	90	30	90	30	90
ACEG & H	a*	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
J	a	a	-1.3	-5.9	b*	b	a	b	a	a	a	a	-1.6	a	b	-15
K	a	a	a	a	a	a	a	-12	-0.67	a	a	a	a	a	-4.5	a
L	-1.9	a	-0.78	b	a	a	a	a	a	a	a	a	-0.75	a	b	-0.80

Table 19 Water Potential (bars) of Sand Adjacent Rooting Zone of Pingao Rhizome

Day	PLANT																Weather
(1982)	AB	AC	AF	CA	CB	CC	EA	EB	EC	GA	GB	GC	HB	HC	I_sA	$I_{ns}H$	
6/2	a*	a	a	a	a	a	-0.95	a	a	-0.60	-0.60	a	-4.0	b*	b	b	Light rain on 5/2
21/2	a	a	a	-8.0	b	b	b	b	a	b	b	a	b	b	a	b	No rain. Dry
25/2	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	Very heavy rain on 23/
3/3	a	a	a	a	a	a	b	b	a	b	b	a	-2.0	-15	a	b	Dry
7/3	a	a	a		a	a	b	b	a	b	b	a	b	b	a	b	Dry
10/3	a	a	a	-0.70	-0.70	a	b	b	a	b	b	-1.1	b	a	a	b	Dry
11/3	-0.70	a	a	-1.7	b	a	b	b	a	b	b	-8.0	b	b	a	b	Dry

* a = > - 0.57 bars (= <500 ohms)

b = < -20 bars (= >20K ohms)

potential soil water was low enough to limit plant growth.

It is interesting to note that water content can vary considerably at different depths at the same time. This may be explained by the percolation of rain water through the soil profile over time.

Table 19 shows the water content, on several occasions, of sand adjacent to the zone along the rhizome at which monitored plants of pingao were rooting. For the sand around the rooting zones of the six monitored plants on the foredune (AB, AC, AF, CA, CB and CC), and the monitored plant of subsite I_s, water was very rarely limiting even during continuous dry weather. This was because the rooting zone was at a depth where the surrounding sand remained close to field capacity probably due to internal dew deposition (Section 4.4.2).

In most cases, (EC, GC and I_sA being the exceptions), the sand around the rooting zones of the monitored reardune and grassland plants including the monitored plant at subsite I_{ns} had very high water potentials (-20 bars) for most of the time, the only exceptions being after a rainfall which resulted in the water potential being low for a few days. Very little, or no water, was available for uptake by the new roots.

Unlike the pingao on the foredunes, the habits of reardune-grassland plants are such that many of them produce new roots very close to the surface into sand that is usually extremely dry and extremely variable in temperature. This is discussed further in Chapter VII. The typical dry summers experienced at the Spit suggests that the non-availability of water to new roots of plants of pingao on the reardunes-grassland is a common seasonal phenomenon.

The two monitored plants at site I gave extremes of water potential results. The sand surrounding the rooting zone of plant I_sA (which had been subject to regular deposits of sand), for most measurements, had a water potential of less than -0.57 bars indicating that the sand water content was at, or close to, field capacity. Conversely, the sand surrounding the rooting zone of plant $I_{ns}H$ (which had not been subject to sand deposits), for most measurements, had a water potential exceeding -20 bars indicating that where new roots were being produced water was extremely limiting.

6.4.3 Salt Content

The salt content of sand water, if in high enough concentrations, could be responsible for limiting the growth of *Desmoschoenus* and/or affecting the conductivity of the gypsum blocks.

Wraight (1957) and Burrows (1969) in their analyses of the Kaitorete Spit Kairaki sands both concluded that the amount of sodium present in sand water was negligible. Kearney (1904) states that sea beach sand contains a very small amount of salt. B.C. Aston (Soils of the Manawatu District, N.Z.J.Ag., 1920) found very low levels of chlorides in dune soils throughout New Zealand and remarked that rainfall was sufficient to maintain the chlorides at low levels.

Ewart and Baver (1950) have found that the performance of gypsum blocks was little affected by salt concentrations up to 0.2%, so that even in mildly saline regions (i.e. areas where plants except the more tolerant ones do not thrive well) salt concentrations present in the soil are not high enough to influence unduly the reliability of the gypsum block electrical resistance method.

Salt spray, which is the main contributor of salt to the Spit dune sands, as far as can be determined is not responsible for the zonation of pingao within the dune system. In such a circumstance unhealthy plants would be expected close to the strand line rather than on the reardunes. Conversely, the reardune plants, especially those on the north-facing slopes, would be more vigorous than they are.

On the leaves of plants along the strand line, however, are frequently found precipitated salt crystals. The vigour of these plants indicates that such salt deposition is not limiting to growth or survival.

6.4.4 Sand Movement

An attempt was made to find out how much sand movement occurred around plants of pingao at different sites over a one year period. Aluminium stakes, 2.5 mm thick, were etched along their lengths with 1 cm gradations. They were placed within selected tufts of all monitored plants (Figure 63) at sites A, C, E, G and H at the beginning of April 1981 to check sand accumulation and deflation.. Measurements were read with an accuracy of 0.5 cm and were taken at the beginning of each month from May 1981 to April 1982.

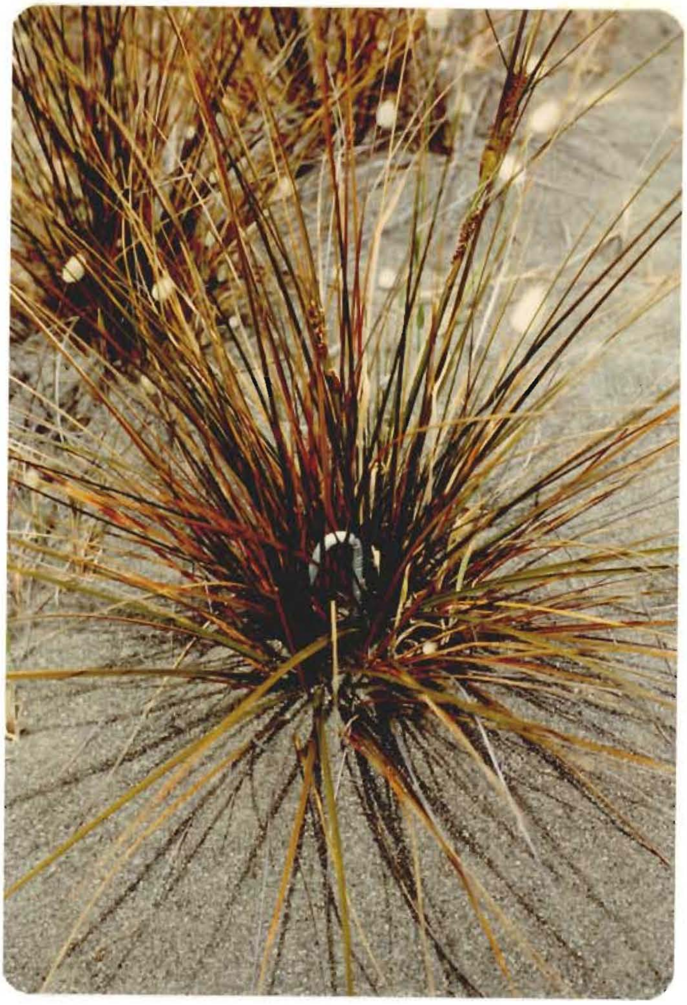


Figure 63.
Graduated stake positioned within a plant to monitor the amount of sand movement

Figure 64.
Transverse dune showing slowly eroding windward slope resulting in the undermining of pingao on the crest

The effect of regular sand deposition on *Demoschoenus* was investigated at site I which comprises an isolated 2 m x 1 m patch of pingao on the grassland, (Figure 28). Sand from the rear dunes was deposited on about half of the pingao tufts (subsite I_s). The undisturbed tufts served as controls (site I_{ns}). Sand was applied when necessary over the year to keep the tufts apices below the sand surface. No tufts were completely buried. It was ensured that much of the photosynthetically active portions of the laminae remained emergent. A stake monitored the amount of sand applied. The effects of regular sand accumulation have been presented in Sections 6.2.4, 6.2.5, 6.2.6 and in the final discussion, Chapter VII.

Patterns of sand movement associated with an eroding transverse dune were also investigated to gain an understanding of the dynamics of the dune system and how *Desmoschoenus* is affected. Nine stakes were positioned at selected points around the transverse dune near sites B and M, (Figures 21,28 & 64 and Table 2). Graduated stakes (1-7) monitored sand accumulation and deflation at various stations around the dune. Stakes 8 and 9 were positioned 100 cm to the lee (east) of the transverse dune crest and measurements were taken of the distance between the crest and stakes to monitor the rate of dune erosion. All stakes were positioned at the beginning of April and all measurements were taken at the beginning of each month for a year (May 1981 to April 1982).

Results

Table 20 shows the amounts of sand accumulating and being removed from monitored tufts of pingao plants over 12 months.

All sand movements were very small and mainly confined to plants of the foredune. This supports the opinion that the Kaitorete dunes are relatively stable, (Peace 1975). Net sand accumulation was apparent within all monitored foredune tufts and tufts EC12 and GC9 of the reardunes. All other monitored reardune-grassland tufts were not subject to any sand movement. It appeared that the substrate of such tufts was very stable.

The table also shows that a total of 14 cm of sand had been deposited on one of the tufts at subsite I_s. The other tufts of this subsite received identical treatments. The monitored tuft of the adjacent control subsite recorded no sand movement throughout the year, (Figure 65).

Sand movement associated with the transverse dune is presented in Table 21. From stakes 8 and 9 it is apparent that the whole dune retreated at a rate of about 45 cm over the year of monitoring. Sand that was eroded off the exposed windward face was being blown over the crest and deposited on the leeside along a strip of about 50 metres or less where it accumulated (stakes 2, 5, 6 and 7). The sand was also funnelled past stake 1, over the deflating crest (stake 4) and deposited on the crest's lee side (stake 3), (Figure 66).

Table 20 Sand Movement (cm) Around Pingao Tufts

	Tufts Staked	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Net Sand Accumulation (cm)	Total Sand Movement (cm)
					MONTH (1981 - 82)										
FOREDUNES	AA23		1.0	1.0							-1.0	1.5		2.5	4.5
	AB6		1.0								-1.0	0.5		0.5	2.5
	AC1			1.0		0.5					-0.5		0.5	1.5	2.5
	AE7				0.5	1.0						1.0	0.5	3.0	3.0
	AF6	1.0	0.5		0.5	1.0		0.5			-0.5	0.5		3.5	4.5
	CA6				1.0			0.5					0.5	2.0	2.0
	CB7					0.5						0.5	0.5	1.5	1.5
	CC7		0.5		0.5		1.0	-2.0		0.5	0.5		-0.5	1.5	5.5
REARDUNES AND GRASSLAND	EA4													0	0
	EB15													0	0
	EC12		0.5		0.5	0.5		0.5				-0.5		1.5	2.5
	GA7													0	0
	GB21													0	0
	GC9		0.5							0.5			0.5	1.5	1.5
	HA4													0	0
	HB6													0	0
	HC9													0	0
	HD25													0	0
*	I_sA1	4.0	3.0	1.0			2.0	1.0		1.0	1.0		1.0	14.0	14.0
	I_{ns}H8													0	0

* Sand Deposition Experiment Site
s = sand applied to tuft
ns = no sand applied to tuft; control.

Table 21 Sand Movement (cm) Associated with Transverse Dune

Stakes[1]	MONTH (1981 – 82)												Net Sand Accumulation (cm)	Total Sand Movement (cm)
	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar		
1[1]	0.5			0.5	-12.0	8.5		0.5	0.5	1.5	0.5		0.5	24.5
2		-1.0		0.5						0.5			0	2.0
3		1.0					1.5	0.5		3.0			6.0	6.0
4		-1.0			- 4.0	-3.0	-0.5	-1.0	1.0		-0.5	-0.5	-9.5	11.5
5		0.5			1.5	1.0				1.0		1.0	5.0	5.0
6		0.5			0.5		2.5	-1.0		0.5	0.5		3.5	5.5
7		1.0	0.5		1.0		2.0				1.0	0.5	6.0	6.0
8[2]	7	2	2		2		7	7	7		4	5	-	43.0
9[2]	8	1	2		2		6		14	7	6	4	-	50.0

[1] For stake positions refer to Fig.

[2] Monitors the rate of retreat of the eroding crest of the transverse dune.

Figure 65. Site I on the grassland with subsite I_s on the left and subsite I_{ns} on the right. Note the differences between tufts of the two subsites as a result of sand deposition on the tufts of I_s.

Figure 66. Leeside of the eroding transverse dune, looking north-west.

6.4.5 Burial by Sand

Burial of pingao tufts by sand was investigated on the foredunes at site N (Figure 28).

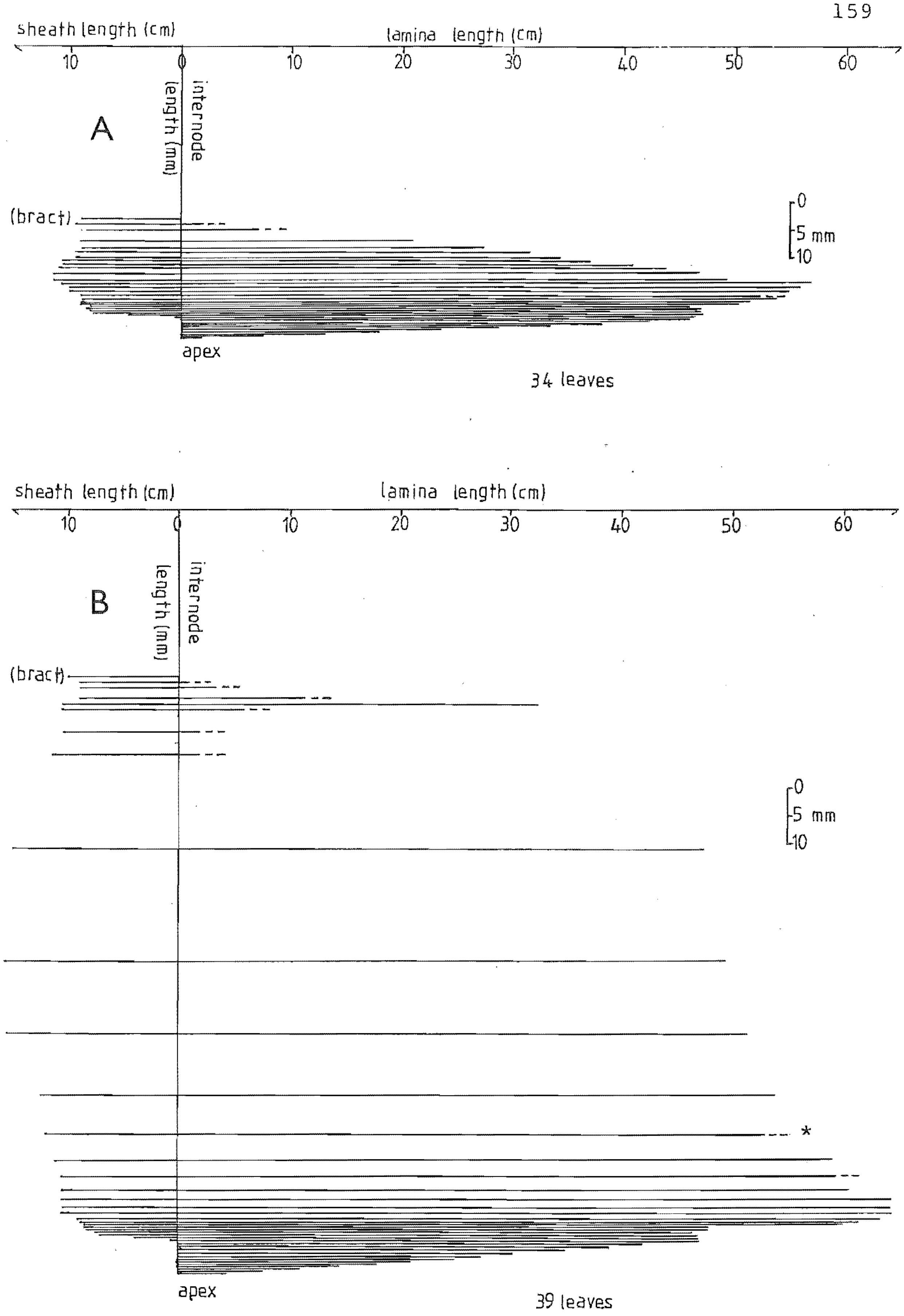
In July 1981 ten tufts were randomly chosen and the most recently emerged leaf of each was marked with tape. The tufts were then completely buried to a depth of about 10 cm with sand collected from the strand zone, and left for six months before being harvested in January 1982. Ten non-buried tufts adjacent to the buried tufts were also harvested. These served as controls.

All collected tufts were dissected. The lengths of each successive lamina, sheath and internode were measured.

Results

A representative of a buried tuft (39 leaves) and a control tuft (34 leaves) were graphed, (Figure 67). The vertical axis of each graph represents the tuft's rhizome which starts at the leaf bract and finishes at the apex. The horizontal lines to the right of the vertical axis represent successive laminae, and to the left, successive sheaths. Successive leaves delineate consecutive internodes.

From these diagrammatic representations it can be seen that the internodes of the buried tuft are markedly elongated compared to the control. From leaf bract to apex the control's rhizome length was 21 mm whereas the buried tuft's rhizome length was 106 mm. Such an elongation resulted in their emergence from burial (Figure 68). Once the tuft apex reached the sand surface internode elongation ceased.



--- broken laminae

* the most recently emerged leaf before burial

Figure 67 . Lengths of successive laminae, sheaths, and internodes of (A) a non-buried tuft (control), and (B) an adjacent buried tuft.

Figure 68. Buried tufts,just before harvesting, with new emergent growth

The asterisk marks the most recently emerged leaf before burial. From this it can be seen that it was the internodes of the leaves already produced before burial that were responsible for most of the elongation rather than the internodes of leaves that were produced later. For all samples measured it was apparent that most of the elongation was restricted to the internodes of the youngest five to ten leaves of the tuft when burial took place. Leaves older than this had finished developing and their internodes had elongated either very slightly or not at all. Adventitious roots were being initiated from many of such internodes and it seems that this precluded any elongation.

No tufts died as a result of burial. It seems that pingao is very well suited to unstable dune habitats and that complete burial by sand at least up to 10 cm (and probably deeper) poses no threat to its survival due to the ability of its rhizome to elongate.

6.4.6 Plant Interactions

6.4.6.1 Competition

On the Spit only a small number of species occupy the same habitat as pingao. This can also be said of other dune systems in New Zealand.

Most competition with pingao occurs on the rear dunes and the ancient dunes. On the former *Muehlenbeckia complexa* has been observed scrambling over pingao tufts, and a few dead tufts have been noted amongst a few of these shrubs. *Carmichaelia appressa* also completes with pingao on the rear dunes and ancient dunes. It produces a mat of densely interlacing decumbent branches which have been observed growing around pingao tufts and covering the surrounding bare sand. The tufts grow on top of this mat but are unable to send new roots through to the sand beneath, and so eventually die.

Pteridium esculentum (bracken) grows profusely amongst pingao over large areas of dunes east of the study area. Although occurring mostly on the reardunes it reaches the foredunes in some places. Bracken also occurs with remnant patches of pingao on some of the ancient dunes. Numerous dead pingao tufts amongst stands of bracken close to the remnants are evidence to suggest that bracken is expanding at the expense of pingao.

Ammophila arenaria (marram) has become established on the Spit after plantings by farmers in the past to prevent dune erosion. It has also been planted at the sand mining site east of the study area. Frequent small populations of self sown marram are dotted along the foredunes and strand zone throughout the length of the Spit, e.g. Figure 69.

Marram has a competitive advantage over pingao because of its habit and mode of growth. While pingao forms open, well-spaced tufts marram forms densely clumped swards of tillers, (Greigsmith *et al*, 1947). The rhizome of marram is also very small in diameter and leaves which arise from it are capable of being modified to small scales. This enables the rhizome of marram to travel underground for distances exceeding a metre before sending up tillers.

Dead and moribund tufts of pingao have been noticed amongst marram swards and rhizomes of marram have been discovered growing under pingao and surfacing between tufts

Figure 69. A sward of self-sown marram expanding at the expense of pingao

Figure 70. The arrow indicates a tiller of marram whose rhizome has travelled under pingao from the main sward on the right

some distance away from the parent sward, (Figure 70). It is thought that this is how marram spreads at the expense of pingao.

A moderate sized population of *Lupinus arboreus* (lupin) is growing behind the foredunes at the western end of the reserve. No pingao is found under it but it is not known whether pingao has been ousted or whether the lupin colonized bare sand. *Lagurus ovatus* (harestail) seed collects and germinates amongst tufts of pingao. Dense stands sometimes arise, which may compete with pingao for water but because it completes its growth before water becomes limiting in summer it is considered to be only a minor competitor.

6.4.6.2 Pathogens

A spot fungus localized to a small group of pingao tufts was noticed from August to December 1981, and was not observed since. Infection was mainly confined to live culms and bracts but the fungus also occurred occasionally on living leaves. No other pathogenous interaction has been observed, the lack of such being more likely due to unfavourable environmental and climatic conditions for growth of fungi rather than resistance of pingao to infection.

6.4.7 Animal Interactions

6.4.7.1 Predation

The harsh stiff leaves of pingao makes it generally unpalatable. Cattle have not been observed eating it. Sheep usually browse between pingao tufts such plants as *Hypochoeris radicata, Rumex acetosella* and *Calystegia soldanella,* and only eat pingao when no alternatives exist. A sheep accidentally entangled in cordage delimiting plot B browsed on the surrounding pingao until it was released, (Figure 71).

Figure 71. Pingao plant damaged by sheep browsing

Figure 72. Tufts of pingao browsed by hares or rabbits

Hares and possibly rabbits browse adult plants, especially when such plants are conspicuous, i.e. solitary tufts or plants on the strand line, (Figure 72). Very frequently leaves are cropped and left lying around the damaged tuft. The reason for this is unknown although it may be associated with track maintenance by rabbits. The control of hares and rabbits has meant that browsing is not severe, but if population checks are not maintained the increase in pingao damage would eventually lead to an increase in sand instability, (Cockayne 1906). The browsing of seedlings by hares and rabbits is discussed in Section 5.5.

The larvae of a pyralid moth has been found to eat shoot apicies and bases of young leaves of pingao. The chaetotaxy is suggestive of the subfamily *Crambinae* which includes many species of *Orocrambus* that are associated with cyperaceous plants, (J.S. Dugdale, Entomology Division, D.S.I.R., Auckland, pers.comm.). *Orocrambus abditus* is the only species of the genus to have been collected from Kaitorete Spit (Gasken, 1975), but the only sure method of identification was to rear the larvae to the north stage. This was unsuccessful.

Infestations of the larvae are infrequent, occur mainly on the foredunes, and are most common during the summer and early autumn months. Initially the larvae creates a small entry hole by eating its way into the growing tip through the outer laminae and sheaths. All the non-sclerified tissue is eaten including leaf primordia and the bases of developing and emergent leaves. As many as 10 to 20 leaves are killed per tuft, such leaves being conspicuous by their bright yellow coloration (unlike the colour of leaves that die naturally). The larvae either exit to infest another tuft after eating the apical tissue, or they pupate within the eaten-out apex.

As well as seed predation (Section 5.3) insects have also been seen to feed on pollen from dehiscent anthers. Such insects are most active during October and November and coincide with the appearance in abundance of eleven spotted ladybirds *(Coccinella* 11-*punctata)*.

6.4.7.2 Other interactions

Larvae of the sand scarab, *Pericoptus truncatus,* were frequently found under plants of pingao. Although they were most abundant under driftwood and on the foredunes they were also dug up from the reardunes. As the larvae feed on dead vegetation (Brown 1879, Dale 1956) it is presumed that as well as driftwood they utilize the dead subterranean organs of pingao as a food source.

When cattle were present in the study area their frequent wanderings across the dune system resulted in the trampling of pingao. The uprooting of plants and the dislocation of parts of rhizomes were also noticed, (Figure 73).

Minor modification to plants of pingao result from the fashioning of shelters among tufts by hares. Australasian harriers *(Circus approximans)* have also been observed amongst foredune tufts on a 40 cm high nest made from pingao leaves.

6.4.8 Storm Surges and High Tides

It is considered that sea surges caused by stormy conditions, as well as high spring tides are the main

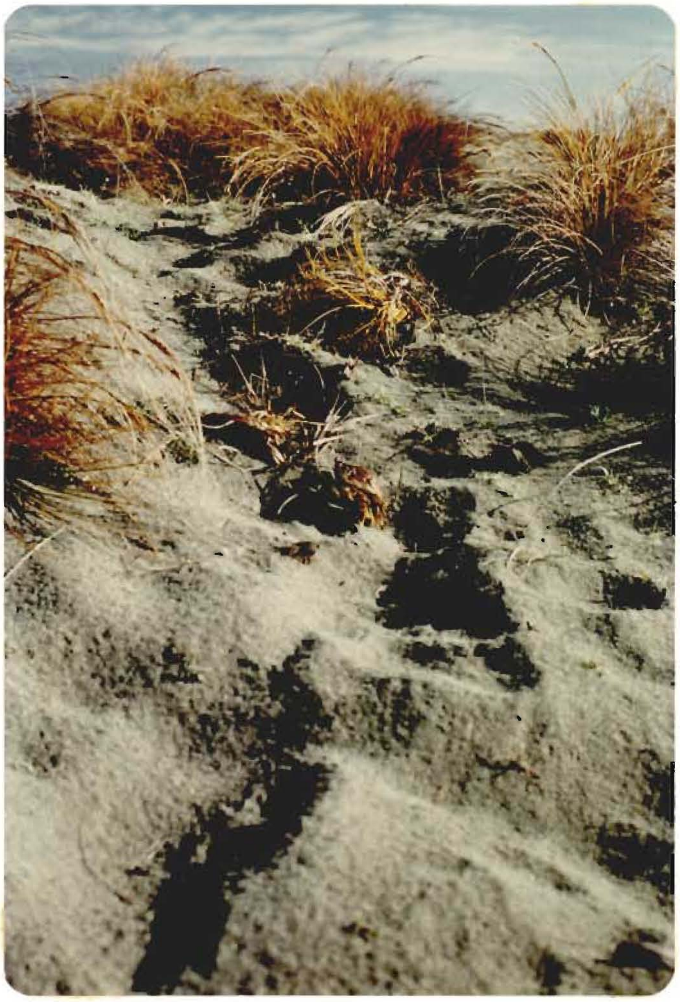


Figure 73. Pingao uprooted by the passage of cattle

factors in determining how close to the foreshore *Desmoschoenus* is able to grow. Major storms are very infrequent along the Canterbury coastline and there were no storms throughout the duration of fieldwork, but a field check in November 1982 revealed that during a storm from the previous winter the sea level encroached by as much as two metres onto the foredune population of pingao. Plants had been uprooted and tufts detached. Many intact plants were also dead (probably a result of the effects of saltwater). Seedlings that were establishing on the strand zone were either washed away or partially uprooted. None were found alive.

CHAPTER VII

FINAL DISCUSSION

The comparative analyses were successful in:

a. showing that differences existed between the pingao populations of the foredune and reardune-grassland zones, and

b. elucidating the environmental factors that may be responsible for these differences.

The foredune plants have been found to be more vigorous and robust than the reardune-grassland plants. They also have more tufts, more inflorescences and a greater biomass per square metre, a more regular tuft dispersion, and a greater percentage cover than reardune-grassland plants.

By the comparative analyses of the environmental factors between zones, it was found that during the driest months of the year water was still available for uptake around the rooting zones of plants that grew on the foredune, but very little water was available around the rooting zones of plants that grew on the reardune-grassland. The reason for this is that most foredune plants have an erect to semi-erect habit which means that their rooting zone is in the moist sand below the dry hot surface layer of sand. Conversely, the plants of the reardune-grassland zone have a leader habit whereby their rhizomes run along the sand surface so that their rooting zone lies along the dry surface layer of sand. New roots which grow into this layer die before reaching the moist layer below it.

The other environmental factor that differed between the zones was sand movement. There was a slight build-up of sand around foredune plants over a year of monitoring but there was no movement of sand around monitored plants of the reardune-grassland zone (except plants EC and GC). It seems that the small influx of sand onto the dune system is intercepted by the foredune so that very little of it reaches the reardunes. Plants EC and GC were both situated on the toe of the reardunes, and because of this gathered sand from the small amount of down-drift off the reardune flanks.

From the results of the sand deposition experiment at Site I, it seems that sand movement is the causal factor responsible for the differences found between the zones. Before the experiment began tufts onto which sand was to be intermittently deposited (I_s) were identical to the control tufts, (I_{ns}), and typical of other tufts of the reardune-grassland zone. After the experimental tufts had 14 cm of sand deposited on them over a one year period, their appearance noticeably changed to more resemble tufts of the foredune zone. This observation was substantiated quantitatively. The tufts had grown more robust and vigorous, i.e. longer and wider leaves and inflorescences, more spikelets per inflorescence, and more flowers and fruit per spikelet (Table 10). Their habits had changed orientation from horizontal to vertical, and their biomass had increased. Because of this sand deposition the tufts' rooting zones were subterranean and roots were growing into moist sand which held water that was available for uptake. Results from the control tufts indicate that before sand deposition, the experimental tufts were rooting into the top layer of sand which held very little available water.

Quantative results from site B support the view that sand deposition is the causal factor in determining vigour of pingao. This site is situated on the lee side of an eroding transverse dune. It has been found that sand was blown off the dune's eroding face and over its crest to be deposited on its lee side. Therefore, pingao tufts at site B were subjected to frequent deposits of sand. Consequently these tufts, when compared with tufts of the other sites, were the most vigorous (Table 10), were regularly dispersed, nearly all erect in habit, and had the highest biomass.

It appears that the effect of sand deposition on the growth habit of pingao, combined with other aspects of pingao's morphology, are responsible for the amount of water available to the roots for uptake, which ultimately determines the degree of plant vigour. This phenomenon has also been found to exist for other dune plants, (Marshall 1965). As was discussed in Section 2.2.3, *Desmoschoenus* is a 'migratory' species, i.e. the essential organs are being continually produced at the distal end of the rhizome to replace the organs that are dying at the rhizome's proximal end. These essential organs possess a short life-span relative to the potential longevity of the plant. Thus the zone of new adventitious root production migrates up the rhizome as the apex grows, the new roots replacing the senescent roots further down the rhizome. This zone of new root production occurs 5-10 cm behind the tuft apex, behind the zone of internode elongation. Continued development of new roots must take place if the plant is to survive, but this can only occur if there is sufficient moisture available at the site of root production.

On the dune system, especially during the summer, the only available water is held in the sand stratum 3-10 cm below the hot, dry layer of surface sand.

From the burial experiment (Section 6.4.5) it appears that the tuft apex of pingao is either negatively geotropic or positively phototropic, i.e. when the apex is covered by sand it grows vertically in an attempt to resurface. Because the apex is usually close to the sand surface very little sand is needed to bury it. If small amounts of sand are regularly deposited on a plant its rhizome will be vertically orientated and therefore the zone of new root development will lie below the buried apex and within the moist sand layer.

If sand deposition ceases the apex continues to grow. It reaches the sand surface and begins to turn from the vertical to eventually orientate itself horizontally and travel along the sand surface. New roots that arise from the rhizome's ventral surface grow into the surface layer of sand. If this layer is dry the roots do not develop and eventually die. With roots unable to be replaced there is insufficient water uptake, and plant vigour decreases. Only with new sand deposits can the rooting zone be buried enough to lie within the moist sand layer and produce functional roots.

This phenomenon is pronounced on the Kaitorete dunes due to the very small influx of sand, the coarseness of the sand (and hence low capillarity), and the very low rainfall. Vigorous leader plants have been observed on other dune systems where, as a result of various factors such as water table interactions, rainfall, and sand grain size, there is sufficient water present within the top layer of sand to enable root development.

In conclusion, as a consequence of pingao's morphology and growth pattern it is most suited to a dune environment onto which there is an influx of sand, because in this situation the rooting zone remains buried and adventitious roots are able to develop in the moist stratum below the dry surface layer of sand.

APPENDICES

APPENDIX I

PRESENT AND PAST *DESMOSCHOENUS SPIRALIS* DISTRIBUTION RECORDS IN NEW ZEALAND

This appendix records the occurrence, abundance and other data on pingao for all localities at which it is known to occur in New Zealand.

Mainland locality names may be found on the relevant map of the N.Z.M.S.1, 1:63,360 map series, and those for offshore islands from N.Z.M.S.219 (Stewart Island), N.Z.M.S.240 (Chatham Island), and N.Z.M.S.259 (Great Barrier Island). Map co-ordinates are also referable to these maps.

Literature records are identified by an asterisk after the author's name.

Abbreviations for herbarium specimens are as follows:-

AK	Auckland Institute and Museum
AKU	University of Auckland
WAIU	University of Waikato
MPN	Massey University, Palmerston North
WELT	National Museum of New Zealand
WELTU	Victoria University
CHR	Botany Division, D.S.I.R., Lincoln
CANU	University of Canterbury
OTA	University of Otago

NORTH ISLAND

West Coast, (North Cape to Cape Palliser).

Spirits Bay. 1975. A Esler. Small amounts.

Te Werahi Beach. 1975. A Esler. Small amounts
1982. S. Courtney. Common on foredunes and low dunes up to 1 km inland. Spinifex dominant. Marram present.

Twilight Beach. 1975. A Esler. Small amounts.

Te Paki Stream, (Kauaeparaoa Stream). 1975. A Esler. Moderate amounts.

Kahokawa Beach to Waikoropupunoa Stream, (N3+4/214388 to 271341). 1982. S Courtney. Scattered throughout at foredune bases and further inland on sand plains and amongst hollows of mobile dunes. Spinifex dominant. Marram present.

Waikoropupunoa Stream to Waimaharu Stream, (N3+4/271341 to 415170). 1982. S Courtney. Same as above but less common. Marram and lupin planted on dunes for pine plantations (N.Z.Forest Service). Dead pingao amongst marram and lupins.

Waimaharu Stream (N3+4/415170) to N6/494070. 1981. M Bellingham, A Davis. Frequent to scattered populations on mobile dune slacks and on sand plains and foredunes. No marram planted. Marram present. Spinifex dominant.

N6/494070 to N9/683700. 1981. M Bellingham, A Davis. Scattered. Pines and marram planted.

Waipapakauri Beach. 1975. A Esler. Scarce.

Near Ahipara. 1915. CHR288781.

Ahipara. 1920. CHR288782.
1975. A Esler. Scarce.

Hunahuna, (South of Tauroa Point). 1981. M Bellingham, A Davis. Abundant throughout.

North Herekino Head. 1981. M Bellingham, A Davis. Scattered.

Beach north of Mitimiti. 1981. M Bellingham, A Davis. Scattered.

Kawarua. 1975. A Esler. Small amounts.
1976. AK138994. Upper beach below Kawarua Hut.

Maunganui Bluff Beach. 1975. A Esler. Small amounts.

Glinks Gully. 1975. A Esler. Small amounts.

South Dargaville Beach to Karaka Creek (N27/51-33- to N32/54-24-). 1981. M Bellingham, A Davis. Abundant.

Kaipara Head, (South of Glinks Gully). 1975. A Esler. Accumulating sand favours spinifex.

North Kaipara Head. 1981. M Bellingham, A Davis. Scattered on low dunes (Figure 74). Mounds of dead plants. Marram and pines being planted by Poutu Forest Farms Limited.

Figure 74. North Kaipara Head, Northland

Figure 75. Waikato River Mouth

Pouto, North Kaipara Head. 1968. AK119920.

South Kaipara Head. 1975. A Esler. Small amounts.

Muriwai North. 1975. A Esler. Small amounts.

Muriwai Beach. 1973. CHR261073. On young dunes.

Muriwai South. 1975. A Esler. Small amounts.

Bethells Beach. 1965 AK128907.
1977. AK141101.

Anawhata. 1936. AK109439.

Waitakere West, (probably Bethells Beach). 1883. AK2147.

Piha Beach. 1939. MPN10626.
1956. AK44419.
1960. AKU6627.
1974. CHR274350.

Manukau North Head. 1981. G Loh. Infrequent. On hummocks on sand plains. Very vigorous.

Whatipu, Manukau North Head. 1973. CHR246571.
1981. A Esler.
1981. G Loh. Lupin present with pingao growing amongst it and exceeding it in height.

Kariotahi Gap, Waiuku. 1902. H Carse.* Common on sand-hills.

Waikato River Mouth, North Bank. N51/238967. 1982. G Carlin. Four small unhealthy colonies. Spinifex, marram and lupin present.

Waikato River Mouth, South Bank. 1982. F Overmars. Colonies sparsely scattered over a wide area on inner side of sand spit behind marram, lupin, gorse and spinifex. Forms small dunes. Marram being planted amongst pingao (Figure 75).

Raglan Harbour to Manu Bay. 1981. P de Lange. Weak population of 8 colonies. Marram present.

South Aotea Harbour. 1974. P de Lange. Present. Lupin and marram.
1981 P de Lange. Extinct.

Te Motu Island. 1982. P de Lange. Healthy population of 100+. Pines present.

Te Maika to Arohaki Bay. 1976. P de Lange. Very large population.
1981. P de Lange. Two small plants. Marram present.

Kawhia Coast, (from Nihinihi to Karewa Beach). 1981. P de Lange. One small clump on edge of eroding dune. Marram and lupin present.

Taharoa Coast. 1977. P de Lange. Abundant.

Waipingao Stream. 1981. B Clarkson. N99/085140.

Waitara, (between Epiha and Turangi Roads). 1981. B Clarkson. N99/086012 - 088012.

Brixton. 1959. AKU6626.

New Plymouth, Shore. No date. AK109440.

Kaupokonui River. 1964. CHR131413.

Castlecliff Beach. 1942. CHR37077. Uncommon.
Once abundant.

Himitangi. 1958. MPN10623, MPN10624.
1970. A Esler.*

Foxton Beach. No date. CHR85849.
1956. CANU963
1974. MPN12541.

Waitarere Beach. 1951. CHR83932, CHR83934.

Paraparaumu Beach. 1969. CANU019137. Amongst marram.

Between Paraparaumu and Paekakariki Beaches. 1933.
WELT19953.

North-west of Sinclair Head. 1981. P Marcroft. N164/133275.

Red Rocks. 1964. WELTU505.
1973. WELT51336.

Island Bay. 1948. CHR63936. Sand dune on beach.

Lyall Bay. 1950. Aerodrome Road.

Seatoun. 1981. J Simmons. Two patches.

Worcer Bay, (N164/38-18-). No date. WELT10039.

Days Bay. 1921. CHR1644.

Eastbourne. 1951. WELTU504.

Pencarrow Point. 1961. CHR307028.
1966. MPN10622..

Fitzroy Bay, (N164/42-10-). 1978. CHR323823.
On sand at cliff base.

Mukumuku Stream, Palliser Bay. 1951. CHR73612.
One colony on coastal terrace forming west bank at mouth.

Lake Ferry Spit. 1907. WELT48364.

East Coast

Kokota Spit, Parengarenga Harbour Mouth. 1982.
S Courtney. Covering coastal dunes and scattered throughout slacks. Abundant. Dominant. No marram. (Figure 76).

Great Exhibition Bay. 1982. S Courtney. Moderate sized populations scattered on foredunes throughout. Spinifex dominant. Middle section of bay planted in marram and pines behind foredunes.

Paxton Point. 1975. A Esler. Moderate amounts.

Henderson Bay. 1981. M Bellingham, A Davis. Very scattered.

Kowhai Beach. 1981. M Bellingham, A Davis. Very scattered.

East Beach. 1982. S Courtney. Abundant at west of beach. Otherwise common with spinifex dominant. Also scattered on sand plains behind dune with gorse, marram and lupin.

Figure 76. Kokota Spit, Parengarenga Harbour, Northland

Kaimaumau. 1975. A Esler. Small amounts.
1982. S Courtney. Very scarce.

Walker Island, Rangaunu Harbour, (N7/792946). 1982. S Courtney. Few patches of moribund plants in centre, surrounded by low spinifex-covered dunes.

Karikari Bay East. 1981. M Bellingham, A Davis. Scattered. Little marram.

Tokerau Beach. 1975. A Esler. Small amounts.
1979. D Given,* J. Bartlett. Scarce.

Marsden Point. 1891. CHR109730.
1898. CHR288779.
1899. AK2145.

Marsden Point to Ruakaka River. 1973. A Esler. Small amounts on 5 metre dunes. Marram and spinifex present.

Ruakaka River to Waipu River. 1973. A Esler. Moderate amounts. On foredunes and dune leeslopes with spinifex. Marram planted. Lupin and gorse present.

Waipu River, South Spit. 1973. A Esler. Moderate amounts on isolated mounds with spinifex.

Waipu Cove Beach. 1973. A Esler. Small amounts on foreshore, and vigorous on blowouts. Spinifex dominates. No marram.

North Pakiri. 1973. A Esler. On isolated mounds and on the foredune of 30 m high dunes. Marram inland.

South Pakiri. 1973. A Esler. Thin covering. Spinifex present.

Mangawhai, (south of Poutawa Stream to Te Arai Point). 1973. A Esler. Small amounts.

Te Arai Point. 1973. A Esler. Moderate amounts.

Whangateau, (N34/28-21- to 30-25-). No date. R Gardner.

Great Omaha Bay. 1863. WELT19947.

Takatu Point. 1975. AK136011.

Long Bay, Northshore. 1980. CHR362212. At mouth of creek.
1981. A Esler.

Kennedy's Bay, Coromandel Peninsula. 1876. AK2148.

Whangapoua Beach. 1981. G Loh. Three colonies of 5 m x 10 m. Marram present.

Matarangi Beach. 1981. P Johnson. Rare. Spinifex, *Pennisetum clandestinum* (Kikuyu grass), lupin and marram present.

Otama Beach, (N40/250780). 1981. P Johnson. Frequent. 20% cover on front face of 4 m dunes. Spinifex, lupin and gorse present. No marram.

Opito Bay, (N40/290770). 1981. P Johnson. Occasional. Spinifex dominant. Lupin and kikuyu present. No marram.

Hot Water Beach, (N44/312570). 1981. P Johnson, T Partridge. Frequent at base of 4 m spinifex dunes. Marram abundant. Lupin, kikuyu and gorse present.

Ocean Beach, (N44/350434). 1967. AK127421.
1981. P Johnson, T Partridge. Occasional.
Spinifex dominant.

Opoutere, (N49/375315). 1981. P Johnson, T Partridge.
Frequent. Often overtopped by lupin. Marram
spread is also a threat. Spinifex dominant.

Whitiporirua, (N49/368245). 1981. T Partridge. Occasional
patches at centre of beach. Spinifex abundant.
Kikuyu present. No marram.

Whangamata, (N49/367172). Two rows of 3 m high foredunes
dominated by spinifex with abundant pingao on the
toe slopes. Kikuyu and lupin present. No marram
or gorse.

Te Ramarama River Mouth, Whitiroa. 1981. G Loh. Small
amount. Sparse lupin and marram.

Waihi Beach to Bowentown foreshore. 1976. A Esler.
Scattered along last 3 km. Lupins and marram present.

Matakana Island. 1978. WAIU2335.

Sulphur Point, Mount Maunganui. 1982. G Taylor. Several
healthy clumps. Marram dominant. Dredging for
reclamation.

Mount Maunganui Beach. 1976. A Esler.

Papamoa Beach. 1982. G Taylor. Scattered 5 m x 5 m
colonies for 12 km except near domain. Interspersed
or surrounded by marram and lupin. 20-100 m gaps
between colonies. Best population in the Bay of
Plenty.

Maketu Channel to Kaituna Cutting (old Kaituna River Mouth).
1976. A Esler. Present.
1982. G Taylor. Four plants observed. Mixed
marram and lupin.

Maketu Beach, east of Channel. 1982. G Taylor. 18 plants
on 50 m long beach. Unstable due to changing channel.

Little Waihi Beach, (Bledisloe Park to Newdicks Beach).
1982. G Taylor. One plant seen. Marram and lupin
present.

Pukehina Beach. 1982. G Taylor. Very little. Marram
dominant.

South Rogers Beach. 1982. G Taylor. No pingao. Large
dunes of marram, lupin and *Muehlenbeckia complexa*.

Rogers Beach to Otamarakau. 1976. A Esler.

Otamarakau Beach. 1982. G Taylor.
Small clumps, 5 m x 5 m, on grass interface with
sand. Very scattered. Introduced grasses invading
sand.

Kohioawa, between Herepuru and Pikowai Streams, (8 km).
1982. G Taylor. Very sparse and discontinuous.
Growing on beach interface out of lupins. Marram
and lupins dominant.

Matata, (2.5 km). 1982. G Taylor. On lip of dune in
5 m^2 to 10 m^2 patches. Very scattered. Lupins
and marram dominant.

Between Tarawera and Rangitaiki River Mouths. 1982. G Taylor. Moderate sized colonies but very widely scattered. Marram predominant.

Whakatane Beach. 1976. A Esler.

Rangitaiki River Mouth to Whakatane. 1982. G Taylor. Large colonies, dominant in places, east of the river mouth. Small scattered colonies east of Coastlands subdivision.

Ohope Beach. 1982. G Taylor. Present 4 km from channel. Very scarce. Bracken, gorse and lupin on sand hummocks. Individual pingao plants scattered amongst marram at end of spit.

Ohiwa Harbour Sandspit. 1983. G. Taylor. 5 m x 2 m clump and several scattered tufts. Marram and lupin dominant.

Opotiki to Tirohanga, (Hikuwai Beach). 1983. Two plants seen at the Waioeka River mouth. Lupin dominant.

Whangaparoa Beach, (Cape Runaway). No date. M Heginbotham. Occasional. 1983. G. Taylor. No plants seen.

East Cape Lighthouse. 1965. CHR182635.

Castlepoint, Wairarapa. 1964. MPN756.
1980. J Simmons. Marram dominant.

White Rocks, Wairarapa. 1980. J Simmons. Scattered. Marram dominant.

East Coast Offshore Islands

Stephenson Island. 1869. J Buchanan.*

Moturua Island, Bay of Islands. No date. A Esler.

Motumuka Island, (Lady Alice of the Hen and Chickens Group).
1964. AK103831.
No date. A Esler.
1982. A Davis. Small population.

Near Tapuwai Point, Great Barrier Island. 1977. CHR321476.

Whangapoua Beach, Great Barrier Island. 1965. AK122181.

Kaitoki Beach, Great Barrier Island. 1963. AK104030. Marram present.

Great Mercury Island. No date. A Esler.

Onetangi, Waiheke Island. 1972. AKU10530.

SOUTH ISLAND

West Coast, (D'Urville Island to Riverton)

Browns Beach, Torrent Bay. No date. G Rennison. Marram present.

Farewell Spit. 1965. CHR148892, CHR167560.
1977. AK143113.
1981. G Loh. All along western side on flanks of steep dunes and on mounds in slacks. Also growing amongst lupins and overtopping them.

Archway Islands. No date. W Burke.

Wharariki Beach. 1976. CHR312017. S1+3/08-23-.

Turimawiwi River. 1974. CHR277794. S2/75-96-.

Kahurangi River. 1965. CHR177812.

Kahurangi Point, (S7/66-90-). 1970. B MacMillan, G Collett.*

Scotts Camps. 1981. A Dobson. Shingle beach north of Kohaihai Bluff. S12/555530.

Stony Creek. 1981. A Dobson. S12/555476.

Oparara River Mouth, North Bank, (S12/553400). 1981. G Loh. One small clump. Marram dominant.

Westport. 1982. A Dobson. On moles of Buller River.

Tip Head, near Westport. 1924. CHR60508.

Charlston. 1979. G Loh. S30/958562 and S30/958578. Scattered plants on beach front. Being eroded. Marram and lupin dominant.

Porarari River Mouth, South Bank. 1982. S Courtney. One 2 m x 2 m healthy colony. Marram present.

Punakaiki Beach. 1982. S Courtney. Three very small patches on stabilized sand bank amongst sedges and introduced grasses, and on beach with marram.

Point Elizabeth, near Rapahoe. 1945. CHR301216.

Greymouth, near Motorcamp. 1968. CHR177085.

Greymouth, near Grey River Mouth. No date. CHR1718.

Rocky Creek Mouth, Totara Lagoon. 1981. F Overmars.

Shearers Swamp, (S57/320310). No date. P Wardle.

Saltwater Beach. 1982. S Courtney. Moderate sized populations on small dunes and sand plain. Gorse and marram dominant. (Figure 77).

Okarito Beach. 1982. S Courtney. Small solitary tufts on inland side of south spit and small healthy population at south side of beach.

Three Mile Beach. 1981. F Overmars. Scattered individuals in a narrow strip on exposed foredune toe. Gorse and marram present on main dunes. Gold dredging along beach and foredunes.

Five Mile Beach. 1972. P Wardle. Present on the sandy beach towards Waiho Bluff. One of the best developed dune areas in South Westland. Marram present.

Gillespie Beach. 1965. CHR123550.
1980. S Courtney. Few scattered plants. Marram and gorse present.

Ohinetamatea Beach. 1980. Few scattered plants. Gorse dominant. Marram present.

Sandy Beach, (south of Makawhio River). No date. P Wardle.

Maori Beach, (north of Mahitahi River). No date. P Wardle.

Ohinemaka Beach. No date. P Wardle.

Figure 77. Saltwater Beach, South Westland

Figure 78. Sandhill Point, Waitutu, Southland

Murphy Beach. 1982. G Loh. Few scattered 20 cm high seedlings on gravel. No marram. Gorse present.

Ship Creek. 1980. P Johnson. Gravel beach.

Waita River Mouth. 1977. OTA037221. Occasional plants on small dunes.
1982. C O'Donnell.

Arawata River Mouth, West Bank. 1982. S Moore. One patch 200 m back from coast. Marram thick along coast.

Okuru, Mussel Point. 1964. CHR151402.

Near Jacksons Bay. 1972. WAIKU736.

Smoothwater Bay. 1980. P Johnson.

Homminy Cove. 1980. P Johnson.

Stafford Bay. 1980. P Johnson.

Cascade River Mouth. 1978. P Johnson. Very abundant on raw sand on foredune fronts. Gorse present. Marram planted. Rabbits present.

Barn Bay. 1978. P Johnson. Very abundant on unstable 4 m high dunes, at entrances to blowouts, and in dune hollows. No marram. Gorse and rabbits present.

Big Bay. 1978. P Johnson. Very abundant on foredunes and large inland dunes behind. Two clumps of marram. Gorse and rabbits present.

Martins Bay. 1978. P Johnson. Very abundant on dunes 4-6 m high along sand spit. Monoculture. On mounds in dune hollows. Marram and rabbits common. Gorse present.

Head of Lake McKerrow. 1980. P Johnson. Abundant in sand and gravel. (19 km from the coast).

Kaipo River Mouth. 1978. P Johnson. Very abundant on 3 m foredunes. No marram or gorse. Rabbits present.

Madagascar Beach - Yates Point Coast, (S112/832374). 1977. OTA037280. Occasional plants on sand dunes.
1980. P Johnson. Occasional on grit and gravel beaches. No marram. Gorse present.

Transit Beach. 1978. P Johnson. Frequent on foredunes south of river mouth on dune hummocks. Marram present.

Poison Bay. 1974. OTA035215. Occasional plants on sand dunes at head of the bay.
1978. P Johnson. Frequent on foredune face. No marram or gorse present.

Southerland Sound. 1978. P Johnson. Very abundant on sand constriction in the middle of the fiord on large young dunes. No marram. Gorse present.

Catseye Bay. 1970. CANU70067. On unstable dunes.
1978. P Johnson. Very abundant on outlying dunes and on faces of main dunes. Fire has killed some pingao. No marram. Gorse present.

Pandora River Mouth, Thompson Sound (S139/118464). 1980. P Johnson. On front slope of 3-4 m high dune.

Neck Cove, Thompson Sound, (S139/113442). Common on 3 m high dunes.

Coal River. 1978. P Johnson. Very abundant. Dense on front faces of young dunes. Monoculture. Also scattered behind dune crests on low dunes in dune hollows. Marram present on foreshore and fairly well established. Gorse present.

Disappointment Cove, Resolution Island. 1978. P Johnson. Rare. No marram. Gorse present. Evidence of recent fire.
1978. CHR253959.

Breaker Point. 1982. K Morrison. S165/78443.

Northport, (Fisherman's Bay), S165/810468. Rare. No extensive foredune. No marram or gorse.

West of Sealers Bay, Chalky Island, S165/786387. 1978. P Johnson. One clump on foredune. Marram established. No gorse.

Lee Bay, (Southport), S165/856372. Occasional on gravel beach.

Seek Cove, S165/864366. 1978. P Johnson. Rare on forest edge. Gravel beach. No marram or gorse.

Te Whara Beach, (Spit Islands), S165/884358. 1969 CHR198608.
1978. P Johnson. Very abundant. On large dunes 15 m high. Marram present. No gorse.

Welcome Bay, S165/843340. 1978. P Johnson. Abundant on top of beach. No large dunes. No marram or gorse.

Otago Retreat, (Observation Point), S173/908289. 1979. P Johnson. Common on 1.5 m high dunes.

Beach near Puysegur Point, S173/879265. 1963 CHR145447.
1979. P Johnson. On very small dunes.

Sealers Creeks, S173/885245. 1978. P Johnson. On open dunes. No marram or gorse seen from the air.

Kiwi Burn, S173/969194. 1978. P Johnson. Abundant on small foredunes. No marram or gorse.

Grace Burn Mouth, S174/014184. 1978. P Johnson. Abundant on small dunes west of mouth. Marram present. No gorse.

Green Islets, south of Grace Burn. 1978. P Johnson. Abundant on sand blown over sedimentary rocks.

Big River Mouth, S174/142198. 1966 CHR172155.
1978. P Johnson. Abundant on low dunes 2-4 m high. Marram on west bank. No gorse.

Waitutu River Mouth. 1978. P Johnson. Abundant. On gravel beach and dense on face and crest of low dune. No marram or gorse.

Sandhill Point. 1982. S Pearce. Abundant. (Figure 78).

Blue Cliffs Beach, S175/522404. 1982. S Pearce. Two small clumps. Marram dominant.

East Coast

Cloudy Bay. 1978. A Dobson. Scattered sparsely throughout length of bay. Marram present.

Wairau River Bar, S22/328009. 1970 CHR229610. Marram and spinifex present.

Awatere, Marlborough. No date. AK2149.

Lake Grassmere. No date. G Walls. Common on seaward dunes.

Whites Bay. No date. CHR109731. Marram abundant.

Near Cape Campbell. 1970. CHR911912. Abundant on back of beach on shingle.

Flaxbourne River, Chancet Rocks. 1981. P Williams.

Near Kekerengu, S42+43/27-38-. 1975. CHR274906.

Twenty miles north of Kaikoura, (Hapuku?). 1975. T Partridge. On large dunes of coarse sand.

Between Hurunui and Blythe Rivers. 1981. T Partridge. Very rare on shingle beach. Marram present.

Motunau Beach. 1982. D Given. Few plants amongst marram.

Amberley Beach. 1969. CHR204886.
1982. S Courtney. Two small colonies seen. Marram dominant.

Waimakariri River Mouth South Spit to Spencer Park. 1981. S Courtney. Eight small healthy clumps on toe of foredunes. Marram dominant. Browsing evident.

Spencer Park, South Beach. 1982. S Courtney. Two small clumps. One on foredunes and one behind crest.

Waimairi Beach, South. 1982. S Courtney. Small moribund clumps on steep dune face. Marram dominant.

North New Brighton Beach. 1982. S Courtney. Two patches. On patch quite healthy on steep dune amongst marram. Other patch of four tufts. Very unhealthy.

New Brighton. 1956. CANU7717.

South New Brighton Beach. 1982. S Courtney. Seventeen small to moderate sized colonies throughout. Mainly confined to foredune below marram dunes. A few clumps on ridge and some colonies forming their own dunes at mouth of blowouts. (Figure 79).

Southshore Beach. 1982. S Courtney. Frequently scattered throughout north of beach. Monocultural dunes in middle section of beach (Figure 18). None in south. Marram present.

New Brighton Spit. 1982. S Courtney. One small patch at south-east end. Marram dominant.

Sumner. 1938. CHR223783.
1982. S Courtney. Extinct. Marram present.

Taylors Mistake. No date. CANU965.
1982. S Courtney. Extinct. Marram present.

Tumbledown Bay, Banks Peninsula. 1982. S Courtney. Dominant on unstable dunes. Pasture grasses invading. Marram present. Browsing evident.

Figure 79. New Brighton Beach, Canterbury

Figure 80. Tautuku Beach, Catlins, Southland

Hikuraki Bay, Banks Peninsula. 1982. S Courtney. Very small clump and scattered moribund plants on beach grass interface. Sand being stabilized by pasture grasses. Cattle trampling evident.

Birdlings Flat. No date. CHR290800.

Poranui 10 miles west. 1961. CHR144174. Dominant sand-binder.

Kaitorete Spit. 1979. CHR357405A. S94/96-19-. On fixed coastal dunes.
1982. S Courtney. Pingao dominant three kilometres from Poranui Point (Birdlings Flat), to the dunes near the mouth of Lake Ellesmere. Scattered patches of marram present, increasing in abundance towards the western end of the spit.

Caroline Bay. 1956. CHR93285. Small clumps only.

Aramoana. 1981. T Partridge. Dead tufts seen on inland side of the spit.

Alans Beach. 1950 OTA018165
1951. OTA004770
1981. P Johnson. One small patch.

Sandymount. 1953. OTA001735.

Sandfly Beach. 1978. P Johnson. (Now rare on Otago beaches).
1981. G Loh. Two clumps, 10 m x 10 m, on steep dunes eroded by cattle.

Lawyers Head. 1981. G Loh. One hundred metres up, in sand on cliff. Marram present. Construction site.

St. Kilda. 1890. WELT19948.

Cannibal Bay - False Islet. 1982. S Courtney. Rare. Restricted to south-west of bay on lower slopes of False Islet at grassland/dune interface. Marram abundant and dominant.

Tahakopa Bay. 1978. P Johnson.
1982. S Pearce. Scattered throughout in small patches. Marram dominant. Coastal forest also on dunes.

Tahakopa River Mouth, Northbank. 1982. S Pearce. Small clumps amongst marram.

Taukuku Bay. 1965. OTA013602.
1982. S Pearce. Scattered throughout on toe of dune. Dense clumps also with marram and flax on semi-stable dunes. Moribund in places. Marram dominant. Figure 80.

Waipati Beach. 1978. P Johnson. Very scarce.

Wallace Beach. No date. P Johnson.

Long Beach. No date. P Johnson.

Dummy's Beach. No date. P Johnson.

Shades Beach. No date. P Johnson.

Little Beach. No date. P Johnson.

Waipapa Point. 1981. W Burke. Common.

Waituna Lagoon. 1968. G Kelly.* Rare on gravel spit.

Tiwai Point. 1982. T Partridge. Small scattered plants on foreshore mound. Marram dominant.

South-east of Barracouta Point. 1982. T Partridge. Dominant on dunes up to 150 m. In full blast of southerlies. Marram present although not healthy.

STEWART ISLAND

Murray Beach. 1979. H Wilson.

Smokey Beach. 1979. H Wilson.
1979. CHR355446.

East Ruggedy Beach. 1979. H Wilson.

Sealers Bay, Codfish Island. 1911. Poppelwell.*
On unstable foredunes. No Marram.
1979. H Wilson.
1980. L Merton. Marram present (first recorded 1966).

Big Hellfire. 1979. H Wilson.

Little Hellfire. 1979. H Wilson.

Mason Bay. 1940. AK109442.
1964. MPN10625. Marram present.
1977. S Courtney. Extensive dunes spreading inland and dotted with pingao throughout (Figure 81)
1979. H Wilson. Dominant over a wide area. Coming inland where sand is encroaching onto red tussock.

Island Hill Lake. 1981. S Courtney. Small unhealthy patches.

The Gutter. 1979. H Wilson.

Doughboy Bay. 1979. H Wilson.
1979. S Courtney. Gorse and marram present.

Port Adventure. 1979. H Wilson.

Chew Tobacco Bay. 1979. H Wilson.

The Neck. 1979. H Wilson.

Back Beach. 1979. H Wilson.

Note: Marram is present at most of the Stewart Island localities and is expanding apparently at the expense of pingao in some places. Pingao is still abundant, (H Wilson, pers.comm.)

CHATHAM ISLAND

Wharekauri. 1954. CHR96649. Three plants seen. Marram dominant.
1982. D Given.

Kaingaroa. 1967. CHR176532. Marram present.
1982. D Given.

Waitangi West Beach. 1980. F Overmars, A Davis. Small colony of unhealthy semi-buried plants (Figure 82). Marram dominant.

Figure 81. Mason Bay, Stewart Island

Figure 82. Waitangi West Beach, Chatham Island

ADDENDA TO APPENDIX I

Karekare Beach. (W. Coast Auckland). 1968. C. Ogle. On sand below rocks. Spinifex present.

Waikawau Bay. 1983. S. Pearce. One hectare of healthy pingao at the north end. Marram, spinifex and lupin present.

N40/203757, unnamed beach east of Rings Beach. 1983. F. Overmars. Healthy plants in 24 scattered clumps over 100 m of beach and mostly behind a small lagoon.

Kuaotunu Beach. 1983. F. Overmars. Three small clumps on western end at base of small terrace. Healthy scattered patches along the mid-beach concentrated around blowout. At the eastern end scattered amongst dominant spinifex, with marram behind. Also a patch on both sides of the lagoon.

Wharekaho Beach. 1983. F. Overmars. One plant found beside road and three healthy tufts beside a fence on a sandy lawn about 8 m from the terrace edge. Housing development on the old dune system along the length of the beach.

Buffalo Beach. 1983. F. Overmars. None observed. Marram and spinifex dominant.

Heihei Beach. 1983. F. Overmars. None observed. Low dune system covered by housing development.

Otara Bay and Te Karo Bay. 1983. F. Overmars. No pingao seen. No dune system.

Ocean Beach. 1983. F. Overmars. Healthy patches throughout foredune. Some patches reaching 4-5 m in length. Scattered 'runners' on foredune. At the southern end an undeveloped housing section on the reardunes is covered by pingao on the dune ridges. Common south of the beach. Spinifex dominant and lupin present.

Pauanui Beach. 1983. F. Overmars. Very small scattered patches, at the north end, amongst spinifex. Mainly on the edge of the foredune.

Kapuni Stream Mouth, 1970. C. Ogle. Near old stream mouth.

Whenuakura River Mouth (just south of Patea). 1978. C. Ogle.

Waitotara Beach. 1977. C. Ogle. About 2 km south of Waitotara River mouth.

Himitangi Beach, north and south. 1954. DSIR Soil Map of Oroua Downs, N148 Sheet 5. Occasional clumps scattered throughout most of the dune system. Also scattered marram, spinifex and lupins.

Hokio Beach, south of Hokio Stream. 1982. C. Ogle. Very common with marram and lupin behind spinifex-dominant foredunes. A monoculture over large areas, most of which has been fenced for pine planting. *Pimelia arenaria* also present.

Waikawa Beach (between Otaki and Levin Beaches). 1972. C. Ogle. Present with spinifex.

Paekakariki North, Queen Elizabeth Park. 1982. C. Ogle. Very small amounts. Dying out. Much marram and lupin disturbance.

Tongue Point (near Karori lighthouse), N164 23-15-. 1982. R. Parrish. Small patch.

Red Rocks (between Ohiro Bay and Sinclair Head). Early 1970's. C. Ogle. Small pockets on semi-fixed dunes with *Raoulia hookeri* and *Coprosma acerosa*. May have been destroyed as a result of quarrying.

Fitzroy Bay. Recent record. C. Ogle. Large area, 2-300 x 50 m just east of Lake Kohangatera. Healthy on steeply sloping sand up against cliff. Lupin and marram present but not abundant.

Te Humenga Point to Otakaha Stream, Palliser Bay. 1980. C. Ogle.

Washdyke Stream, (north of the Clarence River). 1983. F. Overmars. Uncommon to rare along one kilometre each site of the stream mouth, on one metre high dunes. Marram dominant.

Greymouth. Recent date. C. Ogle. Between airstrip and coast on gravel. Sparse. Marram and introduced grasses present.

APPENDIX II

SURVEY OF *DESMOSCHOENUS SPIRALIS* DISTRIBUTION IN NORTH CANTERBURY

Results from surveys made during 1981 and 1982 are presented in this Appendix. The areas covered include the coastline of Pegasus Bay (from Omihi State Forest at the northern end to Taylors Mistake in the south), the bays between Akaroa Heads and Birdlings Flat, and the coastline of Kaitorete Spit.

The surveys have been divided into fifteen sections, A to O, and localities where pingao was found to occur are enumerated and refer to Figures 14 to 17.

A. Omihi State Forest to Waipara River. 28/4/82. Sandy beach with pebble and gravel overlay. Dunes 1-2 metres high, very steep, and stabilized with marram. No pingao observed.

B. Waipara River to North Amberley Beach. 28/4/82. Sandy beach, or sandy with gravel overlay. No dunes. The beach is a semi-stable sand terrace.

(1) Twelve tufts of pingao scattered along North Amberley beach. Not vigorous and scattered amongst dominant marram. One hundred and thirty inflorescences.

C. Amberley Beach. 28/4/82. Sandy substrate. No dunes. The beach is a wide semi-stable sand terrace.

(2) Pingao present amongst scattered marram. Two clumps. Not vigorous. Marram dominant. Eleven inflorescences.

D. Amberley to Leithfield Beach. 28/4/82. Sandy beach with overlying gravel restricted to high tide region. No dune. Sand plain covered with marram. No pingao.

E. Leithfield Beach to Ashley River. 28/4/82. Sandy beach. From the north to the south the sand plain becomes progressively narrower and a dune system behind it becomes more developed. Substantial dunes at the Ashley River lagoon, 5-10 metres high, very steep. Sand plain and dunes covered with marram. *Cassinia vauvilliersii* and *Pinus radiata* also present. No pingao.

F. Ashley River to Waimakariri River. 10/3/82. Beach of gravel overlying sand south of Ashley River mouth, otherwise sandy. Dunes more or less continuous, 3-5 metres high. Steep and densely covered with marram. *Pinus radiata* plantations behind. No pingao observed.

G. Waimakariri River Mouth to Spencer Park. 10/11/81. Sandy substrate. Small dunes at river mouth increasing to 3-4 metres high further south. Marram dominant. Dunes steep. Marram planted on blowouts. Seaward faces eroding, and frequent wind channels. *Cassinia vauvilliersii* and *Phormium tenax* also on dunes. Eight colonies of pingao found, listed from north to south.

(3) Amongst marram on eroding foredune face of three metre dunes. Unhealthy with curling leaves and few tufts. No inflorescences..

(4) Large healthy colony forming its own three metre high dune, adjacent to the mouth of a blowout channel. Flanked by 3-4 metre marram-dominant dunes. More than 200 inflorescences.

(5) Small healthy colony at the toe of a deflating steep marram-dominant dune. Half buried with sand from adjacent wind channel. Twenty-two inflorescences.

(6) Small healthy colony forming embryo dune at the base of an eroding steep marram-dominant dune face. Twenty-one inflorescences.

(7) Small healthy colony on open sand in front of three metre high dune covered with scattered marram. Nineteen inflorescences. Leaves browsed.

(8) Two healthy tufts. As for (7).

(9) Small healthy colony on toe of dune. Rhizomes of dead pingao behind. Marram dominating dune behind colony. No inflorescences. Leaves browsed.

(10) Small unhealthy colony amongst marram on a steep eroding north face of a wind channel. No inflorescences.

H. Spencer Park to Waimairi Beach. 22/1/82. Sandy substrate. Continuous 2-3 metre high steep dunes densely covered with marram. *Lupinus arboreus* and *Pinus radiata* plantation behind.

(11) Pingao present just south of Spencer Park Beach. Small colony on toe of foredune in front of low marram-dominant dune. Also amongst marram further back. The foredune plants are healthy with inflorescences. Browsed. Plants on marram dune not healthy, with dead plants around them indicating their numbers are decreasing. Browsing evident.

I. Waimairi Beach to Central New Brighton. 22/1/82. Sandy substrate. Beach backed by steep three to four metre high dunes dominated by marram. Two colonies of pingao present at South Waimairi Beach.

(12) Moderate sized colony on steep coastal face of dune, surrounded by marram and extending to the toe of the dune. Plants amongst the marram on the top of the dune face were moribund. Tufts at the dune base were

healthy but threatened by marram invasion. One hundred and twenty-six inflorescences.

(13) Four very healthy tufts on eroding face, below steep marram-dominant dune which have slipped from higher up the face due to deflation of sand. No inflorescences.

J. <u>Central New Brighton to Southshore</u>. 22/1/82 and 20/5/82. Sandy beach backed by steep 2-4 metre high dunes. Marram-dominant for most of their length. Wind tunnels frequent and are in the process of forming blowouts. Used as thoroughfares by people seeking access to beaches. Many colonies of pingao of varying sizes found, listed from north to south.

(14) Small healthy colony of toe of steep eroding marram dune. Small sward of marram within colony. Twenty-nine inflorescences.

(15) Twelve metres from (14). As for (14) except no inflorescences.

(16) One hundred metres from (15). Moderate sized colony extending from toe of dune to its crest and on the flanks of small adjacent erosion gully. Dunes marram-dominant and steep. Plants at toe of dune healthy. Plants on the dune face and amongst marram moribund. Eighty-six inflorescences. Browsing evident.

(17) Sixty metres from (16). Small healthy colony on toe of deflating marram dune. Five inflorescences.

(18) Three metres from (17). Small healthy toe slope colony, backed by steep eroding marram dunes. Nineteen inflorescences. Once spread back along blowout face but only dead rhizomes remain.

(19) Four small colonies associated with a blowout channel. Colony forming northern foredune is very healthy. One hundred and twenty-five inflorescences. Colony on marram-dominant dune face behind it is unhealthy with associated dead rhizomes. No inflorescences. The foredune on the south side of the wind channel is covered with a small colony of vigorous plants. Seventy-eight inflorescences, some very robust. A one metre high sand hummock on the south side of the channel entrance contained undermined, dead or dying plants of pingao. On the second survey the whole hummock had deflated and all pingao were dead.

(20) One hundred and thirty-five metres from (19). Isolated dune, at entrance to small blowout, two metres high and nearly as steep as surrounding marram dunes. Rounded crest. Dead pingao flanking the sides and healthy pingao on the crest. One hundred and eighty inflorescences. Marram colonizing dune base. Three small healthy patches of pingao in front of dune. Also a small isolated healthy patch three metres up the face at the end of the blowout on unstable sand. One hundred and thirty inflorescences.

(21) Twelve metres from (20). Small colony on toe slope of a steep deflating marram-dominant dune. Healthy but no inflorescences.

(22) Moderate sized colony on small eroding channel, surrounded by steeper deflating marram dunes. Healthy pingao plants occupying lower dune face behind marram on toe slope. Orange, moribund plants and dead rhizomes on upper face associated with marram. Healthy plants also on crest of dune. Inflorescences mostly restricted to healthy plants, (one hundred and eight in total).

(23) On north side of blowout associated with South New Brighton Surf Club building. Small isolated steep two metre high dune with dense unhealthy pingao on north flank. None on crest. Eroding south flank with dead rhizomes. Marram on south flank and at base of north flank. More than one hundred inflorescences.

(24) Pingao forming the coastal dunes for 10 metres, from the south side of blowout associated with South New Brighton Surf Club building. Mostly unhealthy plants on steep faces and crests. Healthy plants in colony in front of dunes and on less steep faces. Dunes surrounded by steep eroding marram dunes.

(25) Moderate sized population associated with stabilizing blowout. Tufts very scattered on open sand, and reaching the two metre high crest. More than one hundred inflorescences. Surrounded by steeper and higher marram dunes.

(26) Small healthy colony on south side of the same blowout as (25). At toe of eroding marram dune. Fifty-two inflorescences.

(27) Two metre high hummock in the middle of large blowout. Covered in dead rhizomes of pingao and marram. Small clump of pingao behind hummock and on foreshore in front of it. Both healthy. No inflorescences.

(28) On crest and toe of steep marram-dominant foredune on north side of re-colonizing blowout. Dead rhizomes on eroding face. Plants healthy at toe. Sand fence erected in front. Six inflorescences.

(29) Solitary tuft on south side of same blowout as (28). Healthy. No inflorescences.

(30) Small isolated colony on re-colonizing blowout surrounded by colonizing marram and steep eroding four metre high marram dunes. Very healthy. Sixty inflorescences.

(31) Moderately large scattered population associated with blowout. Sand fence erected. Healthy colonies at toe slopes on north and south side, also on small hummocks on blowout. Unhealthy plants and dead rhizomes on steep south faces where pingao is being undermined. Marram on crest. Inflorescences mainly restricted to healthy plants (more than one hundred in total).

(32) Moderate sized scattered colonies associated with blowout,100 metres from (31). Similar to (31). Small pingao hummock on south of blowout and two colonies on exposed face further back. Two foreshore

colonies below dead rhizomes, and healthy crest colony, all on north side.

(33) Large scattered population associated with a double sand erosion fence, and gently inclined dunes in front between steeper marram dunes. Moribund and dead plants at marram-pingao interface. Healthy hummocks on exposed sand. Dead pingao rhizomes on steep eroding faces of marram dunes.

(34) Moderate sized population associated with blowout. Sand fence erected. Dense healthy colony on toe of slope. Less healthy, more scattered plants further back on north side. Interspersed with marram and *Senecio elegans*. Dead rhizomes on steep sloping facing sea on north. Surrounded by steep eroding marram dunes. *Cassinia vauvilliersii* on south crest.

(35) Similar to (34). Moderate sized population associated with small active blowout and double sand fence. Moribund plants on flanks of steep eroding marram dunes. Low elongated hummock behind fence with healthy scattered plants.

(36) More than one hundred continuous scattered colonies, mainly confined to the toe slopes and lower faces of 2-4 metre high steep marram dunes, the upper faces of which are eroding. The healthiest plants and the plants that have the most inflorescences are on the toe slope. At wind channels and blowouts, pingao is usually found on the side flanks, the crests and the seaward facing toe slopes of the north and south sides. The colonies increase in frequency towards Southshore.

K. Southshore to New Brighton Spit Nature Reserve. 22/1/82. Sandy substrate. Steep eroding 2-4 metre high marram dunes, continuous to spit. Pingao colonies scattered along dunes south of Southshore and on one colony on the spit.

(37) Thirty metres of pingao-dominant coastal dunes between marram-dominant dunes. Plants sparsely scattered and healthy. Much more open appearance than the dense swards of marram. Plants associated with the pingao are marram and *Senecio elegans*. On the rear dunes, pingao is confined to a sand hollow with *Lupinus arboreus*, *Senecio elegans*, *Chrysanthemoides monoiifera*, and is very unhealthy. Surrounded by stable marram-covered dunes.

(38) Moderate sized scattered colonies associated with blowouts. Sand erosion fence erected. Healthy plants forming foredune, on hummocks and on north face further back. Dying and unhealthy plants on steep north dune face. Healthy plants on its crest.

(39) Twenty metres from (38). Scattered colony on face of marram dune. Healthy plants towards toe. Forty-four inflorescences, restricted to the toe slope.

(40) Five metres from (39). Small healthy colony on lower face of two metre marram dune. Nine inflorescences. Marram amongst the colony. Dunes not steep.

(41) Healthy solitary tuft five metres from (40). Below marram sward on face. No inflorescences.

(42) Large scattered population associated with a series of wind channels and a blowout. Six sand fences erected. Pingao restricted to north and south flanks, crests and seaward toe slopes.

(43) Ten metres from (42). Small moribund colony mainly on upper slope and crest of marram-dominant dune. Two inflorescences.

(44) Moderate sized very healthy colony ten metres from (43). Restricted to slower slope toe of face that is less steep than the surrounding eroding marram dunes. Marram amongst some of the colony. Thirty-five inflorescences.

(45) Thirty metres from (44). Quite healthy moderate sized colony on rear face of small blowout behind sand fence. Forty-five inflorescences. Amongst *Senecio elegans* and marram.

(46) Twenty metres from (45). Small population associated with small blowout and two sand fences. Unhealthy plants on steep hummocks and the south side of blowout. Dead and dying tufts.

(47) Sixty metres from (46). Small healthy colony on deflation hollow, between steep eroding marram dunes. Behind sand fence.

(48) Small colony of pingao amongst marram on crest of 1-2 metre high dunes at Brighton Spit. A few moribund plants and one vigorous plant.

L. <u>Sumner Beach and Taylors Mistake</u>. 3/5/82. Very small sand dunes and small patches of marram found. No pingao.

M. <u>Akaroa Heads to Birdlings Flat - South Coast of Banks Peninsula</u>. 21/8/82. Most of the bays have a rocky or stony substrate and no associated dune system. Low coastal terraces composed of basaltic and loess-based river sand are present at a few bays but are usually covered with pasture grasses. Pingao was found on the small dunes system at Tumbledown Bay and on a semistable sand terrace at Hikuraki Bay.

Horseshoe Bay. Stony foreshore and wide driftwood zone below small sandflat stabilized by pasture grasses. No marram. Three dead detached tufts of pingao were found amongst drift debris. The zone in which they were found and the lack of suitable habitat suggest they were washed up after being sea-bound. Their most likely source was Kaitorete Spit.

(49) Tumbledown Bay. Sandy foreshore in front of small dune system. An active blowout has cut through the dunes, and there are moderate amounts of loose sand. Pingao dominant on these dunes. Healthy on the lee side of the blowout faces. Being undermined in places. Inflorescences present. West side of dune system being stabilized by pasture grasses. Marram present at front of dune system.

(50) Hikuraki Bay. Stony foreshore below a small terrace of basaltic sand. Mostly stabilized by pasture grasses. Very small population of moribund pingao made up of

two colonies. Many dead tufts around existing colonies. No inflorescences. Trampling by cattle, and browsing evident.

N. Kaitorete Spit Coastline. 7/10/81 and 4/5/82. Gravel foreshore occasionally overlying coarse sand. No dunes within three kilometres of Birdlings Flat, but increasing in size after this for about seven kilometres and widening to include sandy flats behind. The dunes along the last third of the spit taper towards the Lake Ellesmere outlet. The dunes are composed of coarse sand.

(51) Pingao is found on all the dunes along the spit and is the dominant plant, forming a dense cover on the foredunes and on much of the semi-stable mature dunes. Isolated plants are found colonizing the blowout zones and sand plains. Towards the Lake Ellesmere outlet pingao is found on mounds between natural storm channels where the sea has breached the spit to the lake. Healthy plants are generally restricted to the foredunes. Small colonies of marram have naturally established from planted seed sources, and are scattered throughout the length of the spit amongst pingao on the foredunes. At the eastern end bracken *(Pteridium esculentum)* competes with pingao on the semi-stable mature dunes.

O. Lake Ellesmere outlet to three kilometres west. 4/5/82. Shingle beach backing onto marram dominant sand terrace. No pingao.

APPENDIX III

MISCELLANEOUS

Table 22 Incubation of 'Floatation Experiment' Fruit

Treatment	Fruit incubated A	Fruit incubated B	Seed germination
Freshwater sunk	21	25	0
Freshwater unsunk	59	55	0
Seawater sunk	51	50	0
Seawater unsunk	29	30	1

Table 23 Viability of Fresh and Stored-dry Seed

Seed Age	Seeds viable* A	Seeds viable* B	Ave.% seeds viable	Standard Error
Fresh	45	44	89	1
6 months	39	43	82	4
10 months	34	32	66	2

* N = 50

Table 24 Viability of 'Floatation Experiment' Seeds

Treatment	Seeds Tested A	Seeds Tested B	Seeds Viable A	Seeds Viable B	Ave.% seeds Viable	Standard Error
Freshwater unsunk	25	29	12	16	51.6	3.60
Freshwater sunk	55	51	10	9	17.9	0.30
Seawater unsunk	52	61	28	27	49.1	4.74
Seawater sunk	28	19	4	2	12.4	1.90

Table 25 *t* Test[1] of Seed Viability between 'Floatation Experiment' Treatments

	Freshwater unsunk	Freshwater sunk	Seawater unsunk
Freshwater sunk	9.33*		
Seawater unsunk	0.42 n.s.	-6.57*	
Seawater sunk	9.63*	2.86 n.s.	7.19*

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[1] with data from Arcsin √% transformation.

Table 26 Leaf Production and Browsing Frequency of Seedlings of *Desmoschoenus*, Site M, (from December 1980 to January 1982), N (tuft) = 85

L = Leaf Production, B = Browsing, D = Dead, I = trampled, II = undermined, III = uprooted, IV = buried

Seedling Tuft	Browsed Initially	Dec L B	Jan L B	Feb L B	Mar L B	Apr L B	May L B	Jun L B	Jul L B	Aug L B	Sep L B	Oct L B	Nov L B	Dec L B	Jan L B	No.o time Brow
A 1			1	2	1	✓				1	1	1 ✓	1 ✓	D		3
2		1	1	1	1	✓		✓	1		1	2 ✓	1 ✓	D		4
														I		
B 1				1	D											
C 1				1 ✓							1		1	2	1	1
2				1 ✓							2			2	1	1
3				1 ✓					1		1		1	✓		2
4				1 ✓							2	1		2	1	1
5				1 ✓						1	1			2	1	1
D 1	✓		D													1
E 1				1 ✓	D											1
F 1		1		1	1		1	✓		1	2	1	1	3	1	1
													1a	1	1	0
													1b	1	1	0
														1c	1	0
2		1	1	2	1		1	✓		1	1			3	2	1
													2a	1	1	0
														2b	1	0
3		1		1	1	1		✓			1	1	1	3	2	1
			3c	1				1		1	2	2 ✓	2	D		1
										3b	1		1	3	1	0
													3c	3	1	0
G 1		1	2	4	2	2	1				3	1	1	2 ✓		2
										1a	1		1	1 ✓		1
								✓				1b	2	1 ✓		1
														II		
H 1	✓			2	1	1		✓		1		1	1	2 ✓	1	3
				1a	2 ✓	1			1		2	1	1	1	1	1
2				2	1	2		1		1	2	1	1	2 ✓	2	2
3	✓			2	1	1			1		1	1	1	1 ✓	1	2
4	✓			2		1		✓			1	2	1	2 ✓	2	3
												4a	2	2	2	0
I 1		1		1	1	2			1		1	1	1 ✓	2	1	1
								I								
J 1			1	1	1	1 ✓	D									1
2				1	1	1	D									1
K 1		1	2	2	✓	1				1	2	1	1 ✓	2	2	2
2		1	1	3	✓			1			2	1	1 ✓	1	1	2
3		2	2	2	✓					1	1	1	1 ✓	2	1	2
4			1	1	✓						2	1		1	2	1
5		2	1	2	✓						2	1	1 ✓	1	1	2
6		1	2	2	✓						1	1	1 ✓	1	1	2
7		1	2	1	✓				1		2	1	1 ✓	1	1	2
8		2	1	2	✓	1			1		D					1
										8a		1				0
													I			
L 1			1		✓	1	✓			1		2	✓	1 ✓	2	4
2		1	1		✓	2	✓	1			1	1	1 ✓	3	2	3
3				1	1 ✓	1	✓	1			1	2	✓	1 ✓	1	4
4			1	2	1 ✓	1	✓						D			2
5				1	1 ✓	2	✓				2	1	✓	1	1	3
6					1 ✓		✓	1			1	2	1 ✓		2 ✓	4
7			2	1	1 ✓	1	✓				2	2	✓	2 ✓	1	4
		7a	1			2		1			1	1	✓	1	1	2
												7b	1	2	2	0
													II			
M 1	✓			1		1					1					1
N 1			✓	D												1
O 1			✓	D												1
P 1	✓	1	1	1	1	2	✓		1		1	2 ✓		1	2 ✓	4
		1a	2			1	✓				1	1 ✓	1 ✓	1 ✓	1	3
2	✓			1	2	2	✓	1		1	2	1 ✓		3	2	3
3	✓	1	1		2	2	✓	1			1	2 ✓	1	2	2	3
4	✓	1	1	1	2	2	✓				1	1	1	2	2	2
										4a	1	1		2	2	0
5	✓		1	1	2	2	✓				1	2 ✓	1 ✓	3	2	4
											5a	1		1	1	0
6	✓	1		1	2	2	✓		1		1	2 ✓		2	1	3
Q 1		2	1	2	✓	D										1
2		1	2	3	✓	D										1
3		1	1	2	✓	D										1
4		2	2	1	1 ✓	D										1
5		2	2	3	2 ✓	D										1
6		1		2	1 ✓	D										1
R 1		1		2	1	2	1	1			2	2	1	2	2	0
											1a	2	1	3	3	0
													1b	2	2	0
													1c	2	2	0
													1d	1	3	0
														1c	2	0
														1f	2	0
S 1			2		1		2		1		1	2	D ✓			1
													III			
T 1			1	1	1 ✓	1					1		D			1
2				1	D ✓											1
3			1	1	1 ✓	1		1			2	✓	D			3
4			1		2 ✓	1					2	✓	D			3
5		✓		D												1
6		✓		D												1
													IV			
U 1		1	1	1		1		1			1		1	1	1	0
V 1		1		2		1		1	✓	1	1	1		1	1	1

Table 27 Frequency of Tuft Occurrence at Sites A-H

Site	NUMBER OF TUFTS IN EACH QUADRAT																							
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23 ..	30
A	2		7	7	6	1	4	7	6	6	1	3													
B			2	1	4	6	11	11	9	5	1														
C	5		6	3	2	6	6	4	2	3	1		2		2	1	3			1	3				
D	7	3	5	5	4	6	3	4	3	1	2	2	2	1	1		1								
E	28		1		6	1	1	3	3	2			2				1				1	1			
F	23	3		1	5	2	3	2	1	1	1	2	2	1	1		1								1
G	31		1	1	1	1	2	1	1	1	2				1	2	1	1		1		1		1	
H	20	3	2	2	3	2	2	4	1	1	1	1	1	2	1		1		1	1			1		

N = 50 quadrats per site

quadrat = 60 cm diameter

Table 28 Analysis of Variance of Tuft Biomass between Foredune Sites (A-D) and Reardune-Grassland Sites (E-H)

Source of Variation	dfs	SS	MS	F_s
Between A-D and E-H	1	871.12	871.12	101.45***
Among A-D and E-H	6	262.89	43.82	5.10***
TOTAL	7	1134.01	162.00	
Within Groups	232	1992.00	8.59	

Table 29 Analysis of Variance of Tuft Biomass among Habit Types

Source of Variation	dfs	SS	MS	F_s
Among Groups	3	1130.66	376.89	10.83***
Within Groups	256	8906.93	34.79	

Table 30 *t* and *t'* Tests for Tuft Biomass between Sites A-D, E-H, I_s and I_{ns}

	A-D	E-H	I_{ns}
I_s	1.34 n.s.'	-3.94***	-4.90***'
I_{ns}	9.34***'	1.67 n.s.'	
E-H	27.01***'		

Table 31 Example of Leaf Production Counts

Plant AA

Tuft						MONTH								
	1980 Dec	1981 Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	1981 Dec	1982 Jan
1	3	3	2	3	2	1			1	2	3	4	4	4
										[1]a	4	3	4	3
											b	6	4	3
2	2	1	1	1	1			1	1	2		2	2	2
3	1			1	1	1			1	2	2	3	4	2
4	INFLORESCENCE													
		a	9	1	1		1			1	1	3	2	3
5	3	5	2		3	1	1			1	1	2	3	2
6	1	2	1		2				1	2	2	4	3	4
7	1	1	1		1				1			2	1	2
8	3	1		1							2	1	1	D[2]
9	1	1	3	1	1				1	2	1	3	3	2
10	3	2	1	2	1	1		1	1	1	2	4	4	4
			TUFTS 11 - 17 DEAD											
18	3	2	1	1	2				1	1	2	3	3	3
19	3	3	1	1	1					1		2	3	2
20	1	2	1	1		1			1	1	1	4	2	3
21	3	2	1	1	1				1		2	1	3	2
22	3	2		1	2	1	2			1	1	3	3	4
			a	6	2					2	1			
										b	4	4	4	3
										c	4	4	6	3
23[3]	6	7	5	2	1					INFLORESCENCE				
										a	5	6	5	5
											b	5	5	5
												c	8	5

[1] New Tuft

[2] Dead

[3] Terminal Tuft

Table 32 New Tufts arising from Monitored Tufts (1981-82)

Plant	MONTH													No. of Tufts Monitored
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	
AA	1	1								2	3	1		16
AB		2								3	3			4
AC		1										1		2
AD														1
AE	1								2	2	6	2	1	7
AF	1	1	1						1	3	7	5	2	6
CA	3		2	1				1	1	1	2	5	4	6
CB												1	1	7
CC	2	1	1						1	1	2	5	3	8
EA											2			4
EB		1								3			1	15
EC	6	2							3	6	18	21	5	14
GA	2							2	1	2	8	6	3	7
GB				1					1		4			21
GC		3							2	1	10	3		9
HA		1								2	2			4
HB	1	1							1	1		2		6
HC	2								1		3	6	3	11
HD	1		1							1	7	2	1	25
TOTAL	20	14	5	2				3	14	28	77	60	24	173

Table 33 Increase in Length of Developing Culm-Peduncles (1981-82)

Tuft			MONTH				
	Sep	Oct	Nov	Dec	Jan	Feb	
AA23	5.5	9	17.5	12.5	4	2	
AB1	6	9	14	13	4	*	
AB2	5	7	18	13	8	2	
AB3	5.5	11	16.5	10	7	1	
AB4	6	10.5	16.5	13	5	*	
AB6	8	9	18	13	5	0	
AE1	5	9	20	12	2.5	*	
CC1	4	8	16	10	3	*	
CC2	5.5	11	16.5	15	3	*	
EB7	6	9	11	8	5	2	
HD18	4	6	13	10	0	0	
HD24	5	5.5	12.5	10	2	0	
Average Length	5.5	8.5	16.0	11.5	4.0	1.0	Total 46.5

* Could not be measured as harvested for growth analysis measurements at the beginning of February.

Table 34 Rhizome Growth (cm) (1981-82)

Tuft	MONTH												Total
	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	
AA25*	1	0	0	0	0.5	5.5	9	17.5	12.5	4	2	0	52
AB6*	2	0.5	0.5	0	0	8	9	18	13	5	0	0	56
AE7	1	2	0	0	2	1	1	5	5	7	4	3	31
AF6	2	2	1	1	1	5	5	9	10	5	5	2	48
CA6	1	1	0	0	0	0.5	0	1.5	1	2	2	1	10
CC8	2	1	1	0	0	1	1	3	4	1	2	1	17
EA4	0	0.5	0	0	0	0	0	0.5	0	0.5	0	0	1.5
EB15	2	0	0	0	0	1	1	2	1	1	1	0.5	9.5
EC14	3	2.5	0	0.5	0	4	5	10	13	7	4	2	51
GA7	1	0	0.5	0	0	0	0.5	0	1	0.5	0.5	0	4
GB21	1	1	0	1	1	2	2	4	2	1.5	1	0.5	18.5
GC9	3	2	0	0	0	1	4	6	4	5	4	2	31
HA4	0.5	0	0	0	0	0	0.5	0	0.5	0.5	0	0	2
HB6	0.5	0	0.5	0	0	1	0	1	1	1	1	0.5	6.5
HC11	1	0.5	1	0	0	1	0.5	2	1	1	1.5	0.5	8.5
Total	18	12.5	4	2.5	4	17.5	20.5	44	43.5	33	26	13	38.5
Average	1.5	1.0	0.5	0	0.5	1.5	1.5	3.5	3.5	2.5	2.0	1.0	19.0

* Rhizome growth due to inflorescence development. Not included in the average.

Plants AC, AD, CB and HC were not measured.

Table 35 Example of Lamina Die-Back Measurements

Tuft ACI

Leaf	1982 Jan	1981 Dec	Nov	Oct	Sep	Aug	Jun	May	Apr	Mar	Feb	1981 Jan	1980 Dec	Before De or Broken (
1										22	27			44
2														2#
3											10	34		51
4										9	26			32#
5														1#
6									23.5	34.5	36.5	41		
7										19.5	30.5			34#
8						8	15.5			28.5	37	42.5		48
9						8.5	16.5			30.5	32			37#
10										32.5	34.5	38		48
11						6	19.5		29					30#
12							20			31.5				39#
13				6	7	12	16.5		31.5	37.5				43#
14				5	6	13.5	19.5		29.5	35.5	39			40.5#
15			3	8	10		22.5			39	40			45.5
16			5	10	11.5	16.5	24.5		34.5	40	41			46
17		9	12	16.5	17.5	20.5	27			41.5				46.5#
18		13	15.5	18	20	22	32.5	39						49
19		20	21	23	24	27	29.5							39.5#
20		20.5	22	24	25	31	37.5							43.5#
21	18	27	28	30	31	35.5	41							53.5
22	18	31.5	32.5	35.5	36.5	41	45						55	
23	34	35.5	37	39	40	44	47.5						48.5	
24	32	39	40.5	42.5	43.5	44.5								45#
25	37.5	41	42	45.5	46.5	49						55		
a 1	18	21												
2	21.5	24												
3	21.5	24												
4	24	26												
5	21	23												
6	20													
7	16													
26	31	42.5	44	46.5	48.5							53.5		
27	38.5	44	45.5	48	49				54					
28	35	43	43.5	49.5	50				51.5					
29	41	46.5	47	49			50.5							
30	39	46	48	49		50								
b 1	18													
2	22													
3	19													
4	19													
5	15													
6	12													
31	40.5	46	47.5		50									
32	41	46	48	49.5	50.5									
33	40.5	44.5		48.5										
34	41.5	45		48.5										
35	40.5	45		48										
36	42.5		49											
37	40		48											
38	40		46											
39	38		43.5											
40	36	40												
41	34	38												
42	30.5	33												
43		30												
44	27													
45	22													
46	20													
	APEX													

APPENDIX IV

MANAGEMENT OF KAITORETE SPIT SCIENTIFIC RESERVE AND ENVIRONS

The Kaitorete Spit dune system is the least modified of Canterbury's dunes and as far as is known holds the largest dense continuous population of *Desmoschoenus spiralis* (pingao) in New Zealand. Although not without modification, the Spit is still largely representative of one end of the range of dune systems on which pingao occurs or once occurred in New Zealand. With appropriate management directed at retaining the *natural* dune system pattern of instability, the Spit offers the opportunity for the long-term survival of pingao as an ecosystem, and as a species evolving in response to its habitat.

There are about 127,000 ha of dune country in New Zealand, (Cockayne 1911) much of which continues to be modified and stabilized. Despite this, there are very few reserves that encompass any indigenous dune system outside Fiordland National Park. It is a much under-represented ecosystem.

The Kaitorete Spit Scientific Reserve (128.2 ha) was established in 1979, "for botanical purposes" (Mr. W.K. Higgins, Department of Lands and Survey 1982, pers. comm.). It is 4.7 km long (16.5% of the Spit's length) and tapers in width from 0.6 km at its eastern end to 0.2 km at its western end. Its southern (coastal) boundary is 200 m inland from the foreshore, (refer to Figure 19).

Unfortunately, the reserve does not include a representative sample of the *Desmoschoenus*-dominated dune system. Only the northern flanks of the reardunes fall within its boundaries.

A management plan is required for the reserve by 1984 and it is now under active consideration by the Department of Lands and Survey. During the course of fieldwork a number of deficiencies were noted in the reserve and its management, and these are discussed below for guidance in the preparation of the management plan. Some deficiencies have been rectified since fieldwork was completed and these are taken into account. It is hoped that research presented in this thesis will also assist the management of the reserve.

BOUNDARIES

The reserve does not include any part of the coastline from the mean high water mark to a line 200 m inland. The coastal boundary of the reserve more or less follows the crests of the reardunes, thereby excluding the southern flanks of the reardunes and the foredune, strand and foreshore zones. With respect to the protection of a representative example of the dune system this boundary is highly unsatisfactory.

All zones should be included in the reserve as together they are integral and closely inter-related parts of the dune system.

The present boundary is botanically, zoologically, and geomorphologically artificial; it does not delineate two ecologically distinct zones. The foredune holds the densest, healthiest population of *Desmoschoenus* found anywhere on the dunes and these are excluded from the reserve. Inclusion of these zones would mean that the complete successional sequence of the dune vegetation would exist within the reserve.

Only with such inclusions can the reserve be considered an adequate representative portion of the Spit's pingao population. However, its adequacy should be reassessed in terms of a national protected natural area system which is to represent, *inter alia*, the full range of New Zealand coastal ecosystems. The main opportunity at present to extend the reserve's other boundaries is to the west, because of the sand-mining operation on the eastern side.

Ideally the whole future human use and management of the Spit dunes should be assessed in conjunction with the adjacent Lake Ellesmere which is a Wetland of International Importance (C. O'Donnell, N.Z. Wildlife Service 1983, pers. comm.).

Recommendations

1. That the coastal strip of land adjoining the present southern boundary of the reserve, which includes the foredune and strand zones be included in the reserve.
2. That consideration be given to extending the reserve in future, in the light of its national importance as an example of an extensive *Desmoschoenus*-dominant dune system.

BROWSING, PLANT DAMAGE AND FENCING

At the time of fieldwork, browsing animals within the reserve were rabbits, hares, sheep and cattle. Since that time cattle have been removed, although a grazing licence for sheep still existed.

Rabbits and probably hares are the only animals that frequently browse pingao. They are most selective towards pingao seedlings although occasional browsing of adult tufts has been observed. Seedling studies show that the leaves of seedlings are soft enough to be very palatable and are therefore under high browsing pressure. Once the seedling becomes conspicuous (usually a year after emergence when auxillary tufts arise) it has a 90% chance each year of being browsed at least once (assuming the rabbit population remains as at present). One third of seedlings that are browsed die as a result. For these reasons there is no measurable net increase in seedling biomass and therefore no seedling establishment. The effect of continued seedling browsing will ultimately be to decrease the long-term viability of the pingao population and influence the future patterns of dune formation. It is hard to know how great these changes will be.

Rabbits and hares also browse other indigenous plants within the reserve, especially *Carmichaelia appressa,* a prostrate broom which is endemic to Kaitorete Spit. Rabbit burrows are also common on the grassland both undermining vegetation and damaging roots.

Control, or ideally, eradication of rabbit and hare populations within the reserve is required. Poisoning and shooting are traditional techniques of control. These methods at best can only temporarily decrease such populations unless regular intensive management is adopted which is both labour intensive and cost-inefficient.

The other alternative is the erection of a rabbit-proof fence. Once erected rabbit and hare eradication would be possible. It is very important, though, that the reserve remains unfenced along its southern (i.e. coastal) boundary. A fence here would almost certainly affect dune system dynamics with respect to sand movement and deposition, dune formation, stability etc. To exclude rabbits the fencelines of the eastern and western boundaries would therefore need to continue down to the foreshore and the sea be used as a natural boundary.

Sheep will resort to browsing pingao only if no alternative food source is available. Such a situation rarely arises. The harshness and high fibre content of the leaves of mature pingao tufts are the sedge's main deterrents against browsing. Instead, the sheep have been seen on the dunes browsing adventives such as *Hypochoeris radicata* (cat's-ear) and *Rumex acetosella* (sheep's sorrel), as well as indigenous plants such as *Calystegia soldanella* (sand convolvulus), *Carmichaelia appressa, Sophora microphylla* (kowhai), and *Hymenanthera crassifolia* (porcupine shrub).

Damage to pingao rhizomes as a result of trampling by sheep may indeed occur by the effects of such have not been observed. Seedling damage and erosion, on the dunes, of frequently used sheep tracks have been observed. Sheep also aid the dispersal of *Acaena agnipila* (an Australian bidibid) throughout the dune system, by catching and carrying its spiny fruit within their fleeces.

Overall, while sheep are useful within the reserve in checking introduced weeds, their other activities must be considered detrimental to the features the reserve was created to protect, (most being only slightly so due to low stocking rates).

It is important that cattle remain excluded from the reserve. When cattle grazed within the reserve the dunes were continually used as a thoroughfare from the grassland to the foreshore where washed up seaweed was grazed. Due to the sheer weight of cattle, damage to plants of pingao upon being trampled over was inevitable.

Damage to plants of *Desmoschoenus* has also occurred as a direct result of motorbike-scrambling amongst the dunes. Pingao rhizomes were crushed and/or disconnected from each other, leaving discrete trails of dead plants wherever the vehicle had been.

The fencing of the reserve would help to effectively decrease the amount of damage to pingao and other vegetation. At the time of fieldwork the only functional fence delimiting the reserve was along its northern boundary. The eastern and western boundary fences were in disrepair but during 1982 a new fence was erected along the eastern boundary.

It is important that no fence be erected along the southern (coastal) boundary. Instead, the east and west fences should extend down to the foreshore and the sea be used as a natural barrier.

Recommendations

1. That no cattle be permitted within the reserve.
2. That after expiration of the grazing licence sheep be exlcuded from the reserve for a trial period.
3. That the effects of the sheeps' removal on the vegetation be monitored and unless good reason can be found for their re-introduction after this time that they remain excluded.
4. That the reserve be fenced in such a way as to prohibit the entry of cattle, sheep and vehicles without erecting a fence along the southern (coastal) boundary, and that the feasibility be assessed of extending the eastern and western boundary fences down to the foreshore for this purpose.
5. That an investigation be undertaken to assess the feasibility of rabbit-proofing the proposed fence.

WEED CONTROL

In Section 21(a) of the 1977 Reserves Act it is stated: "Except where the Minister otherwise determines, the indigenous flora and fauna shall as far as possible be preserved and the exotic flora and fauna shall as far as possible be exterminated". With respect to the exotic flora no such management has yet been apparent apart from the grazing of sheep whose beneficial contribution in the long-term to the management of the reserve is questionable.

The abundance of some exotic herbaceous species makes their extermination impractical if not impossible but it is unlikely that these species threaten the features for which the reserve was created to protect. Introduced plant species that occur within or adjacent to the reserve and are a threat to the long-term viability of the pingao population (and the sand dune community as a whole) are *Ammophila arenaria* (marram grass), *Lupinus arboreus* (tree lupin) and *Ulex europaeus* (common gorse). These are either very localized or sparsely scattered throughout, or in the vicinity of, the reserve. Their total eradication should be attempted.

Marram has established as isolated colonies within the reserve and along the foreshore adjacent to the reserve. It is also scattered throughout the length of the Spit and is a well-established sand-binder within the sand-mining area and towards the outlet of Lake Ellesmere. Its ability to supplant pingao has been observed both within the reserve and on other dune systems throughout the country. For this reason it is of high priority that it be exterminated from the vicinity of, and within, the reserve.

The marram population of the nearby mining area poses a constant threat to the reserve as it produces copious marram seed that is capable of dispersing and germinating within the reserve. It is desirable that no more planting of marram occur anywhere on the Spit and that the eradication, if possible, of marram that has been planted in the sand-mining area be undertaken. The natural recolonization of the mining area by pingao could possibly be hastened by transplanting healthy tufts from the surrounding dunes. If the roots and rhizomes of transplants are kept as intact as possible and are well buried, transplanting should be successful.

Due to the small size of most of the marram colonies, a viable method of control would be to pull out swards of all living tillers and rhizomes by hand and repeat at 3-6 monthly intervals until no new tillers emerge. This has already been tested on two small colonies within the reserve. Three sessions of hand pulling were sufficient to kill the plants. Alternatively spraying with glyphosphate (the active ingredient in 'Round-up') works very well in controlling rhizomatous grasses. Unfortunately it may knock back pingao to some extent and should only be used on marram colonies that are too large to destroy by hand.

It is important that marram be distinguished from *Festuca littoralis* and *Carex pumila*, an indigenous grass and sedge, which are both sparsely scattered throughout the reserve dune system. Distinguishing characteristics of these plants should be sought from some botanical source.

A small population of lupin near the reserve's western boundary, a single prostrate plant of gorse (on the foredune about 100 metres from the eastern boundary), and a solitary pine tree, *Pinus* sp., near the western boundary should be eradicated while their numbers are manageable and before their range increases.

Upon the completion of the eradication of these adventives, the reserve and its environs should be thoroughly checked say every 2-3 years to prevent the re-establishment of the above weeds and the establishment of other introduced plants (e.g. *Pinus radiata* which is present west of the reserve).

Recommendations

1. That introduced flora both within and in the vicinity of the reserve, which threaten the special qualities of the reserve, be eradicated.
2. That an eradication programme be devised for marram within the sand-mining area adjacent to the reserve, and for other marram colonies along the Spit whose seed is able to reach the reserve.
3. That there be no future planting of marram (or other introduced species) on the Kaitorete Spit dunes unless future sand movement threatens neighbouring farmland and no other alternative to sand stabilization exists.
4. That the reserve be regularly checked for the establishment of marram, lupin, gorse and other troublesome adventives.

SAND-MINING

A sand-mining operation is working adjacent to the eastern boundary of the reserve and is gradually working towards Poranui. The reardunes, and in some places the foredunes, have been removed. A planting regime of marram and pingao has been adopted to vegetate the substrate after mining, although such a regime has been very cursory and sporadic.

It seems incongruous that such activity is occurring in the vicinity of the reserve and to a dune system that supports a threatened plant. Indeed, activities such as mining and marram planting have lead to the present "vulnerability" of *Desmoschoenus* in New Zealand, (a vulnerable species is a species which is believed to become endangered in the near future if the factors causing its depletion continue to operate, (Given 1981).

As well as the direct threat to pingao, the sand mining operation is almost certainly directly mining the sand resource at a rate far in excess of any sand input from southern onshore drift sources. Without study, the long-term effects of this can only be guessed. At worst, they could involve irreparable damage or loss of the Spit system.

Recommendation

1. That no sand-mining be continued on Kaitorete Spit dunes after the present operator's lease expires.

PUBLIC USE OF THE RESERVE

Although there is provision under Section 21 2(b) of the Reserves Act 1977 for prohibiting public access to scientific reserves, this has not been invoked yet for the Kaitorete Spit Scientific Reserve and nor is it considered appropriate or practical to do so.

The reserve is vulnerable to disturbance of the sand dune system. This is unlikely to be significant provided vehicles and stock are exlcuded and public use is low. Because the reserve is located well away from high public use areas and is hardly visible from any road, public visitors are likely to be only those who casually come across it in the course of fishing, walking, shooting or other activities.

The provision for allowing public access should be re-assessed if at some future time damage to the reserve becomes evident.

Public notices should be erected which aim to educate visitors of the purpose and value of the reserve. Information presented should include:

- reserve's name and designation
- administering department
- purpose and special features of the reserve

People should also be asked to enjoy and respect the reserve, and to refrain from activities which may damage it, e.g. lighting fires, trampling on or removing plants and animals, and removing sand.

Recommendation

1. That public notices be erected at public access points to the reserve displaying the above information.

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