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The interaction between pingao and marram on sand dunes

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DoC Investigation No.789

DSIR Land Resources Contract Report No.91/65

THE INTERACTION BETWEEN PINGAO AND MARRAM ON SAND DUNES

INVESTIGATION NO.: 789

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Contract Report No. 91/65

PREPARED FOR:
Director, Science and Research
Conservation Sciences Centre
Department of Conservation

June 1991

FINAL EXECUTIVE SUMMARY

KEY OUTPUT
INVESTIGATION NO: S/789

INVESTIGATION TITLE: The interaction between pingao and marram on sand dunes

STUDY VENUE: Canterbury, Westland

INVESTIGATION LEADER: T.R. Partridge, DSIR Land Resources

INVESTIGATION STATUS: Completed, except for small ongoing study

CLIENT: DoC, Science and Research Division

FINISH DATE: June 1991

INVESTIGATION OVERVIEW:

There has been considerable concern for New Zealand's remaining areas of native sand dune vegetation. Already devastated by induced instability, the few essentially unaffected dune systems now face a threat from the very species introduced to combat that instability; marram grass. This study examines the interaction between marram and the species most effected by it, the native sand binding sedge pingao. With such an understanding, it should be possible that appropriate conservation strategies can be put into place to protect the remaining areas of pingao.

OBJECTIVES:

To complete and report on four studies of this interaction.
1. To study the interaction of pingao and marram in relation to dune structure - the displacement process.
2. An examination of the process of pingao replacement by marram with time.
3. Pingao vs marram: the displacement interaction.

4. The effects of hand weeding of marram as a control measure.

METHODS:

The following techniques were used for the four studies.
1. A multivariate vegetation analysis of quadrat data from dunes at Kaitorete was used to examine where and how marram enters and spreads through the system.
2. Permanent plot studies on plant spread and displacement, in conjunction with dune building were carried out at Haast, New Brighton, and at three areas at Kaitorete.
3. Experimental and field studies at Kaitorete were carried out to examine how marram displaces pingao. Factors examined include allelopathic effects via poisons, and competition for light, water and nutrients.
4. Permanent plot studies were carried out at Haast and Kaitorete to examine the effectiveness of various weeding regimes on the behaviour and spread of marram.

FINAL RESULTS:

The results are too complicated to be presented in any detail.
1. The multivariate data analysis yielded 20 communities from which it was possible to draw conclusions regarding the behaviour of marram.
2. The permanent plot studies revealed many different situations involving pingao and marram. The outcome

of the interaction is varied and can be related to the situation involving the two species.
3. A pot experiment revealed no allelopathic interaction. Field studies suggested a possible competition for light, but this was not strong. There was no evidence of competition for nutrients from a pot experiment. There were considerable differences in upper layer moisture contents below marram and pingao. Marram seems to be able to deplete these layers.
4. In the first year, hand weeding of marram made no difference. In the second year six monthly weeding severely reduced marram recovery, but annual weeding did not.

FINAL CONCLUSIONS:

The studies on parts 2 and 4 are continuing, as the results for two years, although indicative, are not conclusive.
1. Marram spreads primarily by rhizome fragments. It therefore only establishes where there is disturbance, such as on the strand line and where dunes have been naturally or artificially activated. Spread from there is by lateral growth.
2. There are situations in which marram and pingao can co-exist, some are stable, others are not. In many situations however marram actively displaces pingao by first invading and then causing its demise.
3. Marram displaces pingao by competition, it is able to deplete moisture from the upper layers of sand around the root zone of the pingao, which then dies. Marram is however able to then exploit water at greater depth.
4. Hand weeding of marram needs to be carried out frequently and continuously. If it is not, then it will cause new problems by rejuvenating the marram.

RECOMMENDATIONS:

Marram is in many situations a threat to pingao. Areas where the two co-exist need to be identified and monitored, but left. In other situations immediate action needs to be taken before the problem becomes unmanageable and the remaining areas of pingao are lost. There is little that can be done to reverse the competitive interaction between the species. The only way to alleviate the problem is to control the spread of marram. This involves firstly checking valuable dune systems for newly established clumps, especially along the strand line. Secondly it involves controlling spread of areas that cannot be removed. Thirdly it involves removal of larger areas where possible. This can be done by hand weeding, but as this technique contains some risks, and must be maintained indefinitely, alternative methods of control need to be examined.

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GENERAL INTRODUCTION

In 1908, the Sand-Drift Act was added to the New Zealand statutes. This legislation was necessitated by the severe problem the country was facing from extensive amounts of mobile destabilised sand. In the time following European settlement, vast areas of coastal sand dunes had become destabilised, and were threatening rural and urban areas throughout. Added to this were areas of tertiary sands which had also become destabilised in parts of Northland, the Volcanic Plateau, and Central Otago. The exact cause of this instability is difficult to determine, but was probably mostly the result of land clearance for agriculture. The two indigenous sand binders, spinifex (*Spinifex sericeus*) and pingao (*Desmoschoenus spiralis*) were unable to cope with the instability and were overwhelmed by the vast quantities of sand. The Sand-Drift Act resulted in the testing of many adventive sand binders, with the European marram grass (*Ammophila arenaria*) being chosen. This species proved so successful that by the 1950s most of the problem areas had been stabilised by extensive plantings of marram. Only the infertile gumland sands of Northland remained a threat, but most of these have since been stabilised as well. Today, it is very much taken for granted that marram has played this crucial role.

The indigenous sand binders remained in areas where instability had not necessitated the planting of marram. Isolated areas in Fiordland, and near North Cape are examples. In other areas, varying amounts of the native binders remained along with the marram plantings. Whereas spinifex has generally survived quite well in the presence of marram, the remaining areas of pingao continue to contract when the two come into contact. In most of the South Island, pingao was the only indigenous sand binder, so the effects of this process are most strongly felt there. Although pingao is still quite widespread, its decline is of considerable concern to conservation. As well as the intrinsic value of pingao and the communities it forms, are traditional values to the Maori, especially as it is a valued material for weaving purposes.

Alleviation of the continued decline of pingao is now considered a priority for conservation in New Zealand. In recent years, the New Zealand Department of Conservation has supported a number of projects designed to understand the nature of the problem and to explore solutions. Such studies have included ecological studies and investigations of management techniques to halt the decline or to re-establish pingao. This study is one such project, and attempts to answer a number of questions regarding the interaction of pingao and marram. It firstly undertakes to understand the extent and nature of the displacement process, secondly it examines the competitive mechanism of interaction, and thirdly it studies the effects of one management option that might help to alleviate the problem. Most of the studies were carried out on the extensive pingao dominated dunes at Kaitorete Spit, Canterbury, with additional studies at New Brighton, Canterbury, and at Haast, South Westland.

This examination is made up of a number of different studies, each offering a different approach to a particular aspect of the problem. Each of these studies will be presented separately, to be tied together by a more generalised set of conclusions.

STUDY 1. THE INTERACTION OF PINGAO AND MARRAM IN RELATION TO DUNE STRUCTURE AND FUNCTION - THE INVASION PROCESS

INTRODUCTION

In most New Zealand dune systems there is little opportunity to view the process by which marram replaces pingao. Replacement is usually either complete or virtually complete, or in a few cases, marram is absent from the dunes. The dune system at Kaitorete Spit however, provides a rare opportunity to examine the establishment, growth and spread of marram into a dune system dominated by pingao. In particular, the section of the Kaitorete dunes that has been mined for sand allows an improved examination to be carried out, by providing a highly disturbed situation to compare with the essentially undisturbed unmined dunes. Also, as the time since mining is generally well known and spans a period of some 40 yrs, such an examination has a valuable temporal aspect as well. These opportunities exist because the replacement process is slow, probably the result of the dunes being composed of coarse sand that is not easily moved by wind.

This study therefore seeks to understand firstly, where marram starts its invasion in the dune system. Secondly, it examines the spread of marram on to the dunes, and thirdly, it examines how marram effects the plant communities of the dunes themselves. It should be mentioned that the techniques utilised in this study allow for another important conservation problem at Kaitorete to be examined; this being whether the mined dunes are recovering their vegetation following sand mining. This question is the subject of a separate report.

STUDY SITE

Kaitorete Spit is a sand/gravel barrier complex that separates brackish Lake Ellesmere from the Pacific Ocean, and is located immediately to the south of Banks Peninsula. The complex is only about 5-7000 years old, and the product of rapid growth, as it is now 28 km long and up to 3.2 km wide at the eastern end (Kirk 1969, Armon 1974). Continuous sand dunes occur on the seaward side at an average width of 220 m. Apart from three significant areas where marram dominates, the dune system is otherwise dominated by the native sand binder pingao (*Desmoschoenus spiralis*). The area examined in this study lies immediately to the north-east of Kaitorete Scientific Reserve in a zone of the dunes where there is slow seaward accretion of the dune margin. Inland of the dunes is a dry grassland dominated by introduced species, and especially the grass *Stipa nodosa*. The whole dune system is subjected to frequent strong winds from both the south and north-west. Tall woody vegetation is absent from the system.

Sand mining began on the dunes on a small scale in 1952, and has proceeded north-eastward. Records were started in 1964 with the granting of the first licence, and at that time some 6,000 m^3 were removed per annum. Removal of sand peaked in 1974 when 33,000 m^3 were extracted (Palmer 1980). Restrictions on amounts and areas available considerably reduced the extraction of sand in the 1980's. The total length of dunes mined by 1990 was approximately 1,300 m. Sand has been mostly removed from the middle of the dune system, but at the peak extended from close to the front dune, almost to the grass flats.

METHODS

Six sections of the dunes were chosen for detailed sampling. They include two unmined sections, at either end, and four that have been mined at various stages (Fig 1). Each section covers a 200 x 220 m area with the longer axis perpendicular to the shore. The wider dunes at section B necessitated increasing this to 240m. Each section was divided into 20 x 20 m squares, making a 10 x 11 sampling shape. Within each square a 5 x 5 m quadrat was randomly placed and species frequency measured within the 25 1 x 1 m subquadrats at the site.

Six dune profiles of the areas sampled demonstrate the extent of mining and its effect on the dune structure (Fig 2). Of the two unmined sections, A has a single, and F a double dune ridge system. Section B was mined in the 1950s-1960s, but not to a great depth, while in the most recently mined section E (late 1980s), mining has been restricted to only a narrow part of the dune sequence. The most extensively mined dunes are in the

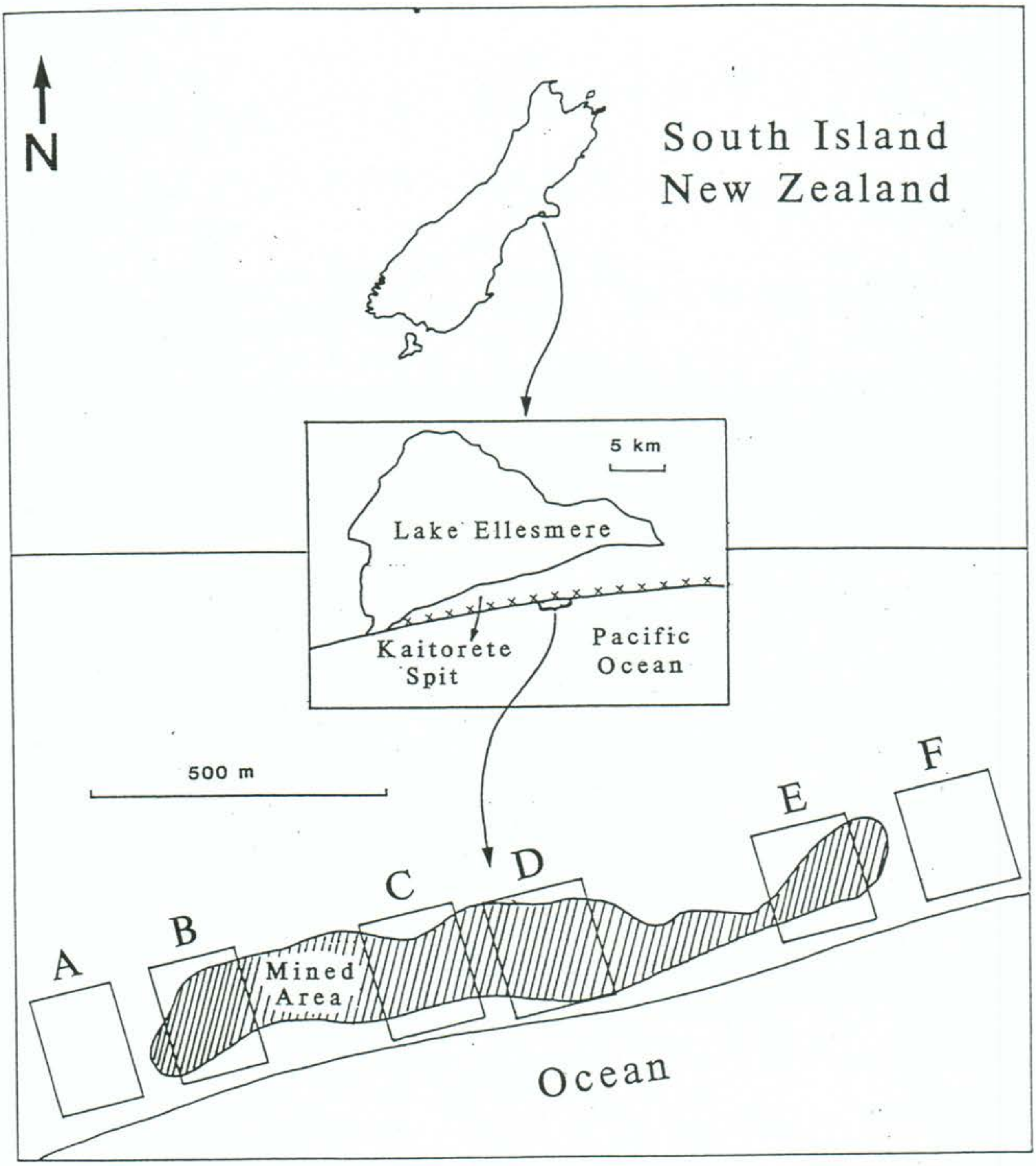
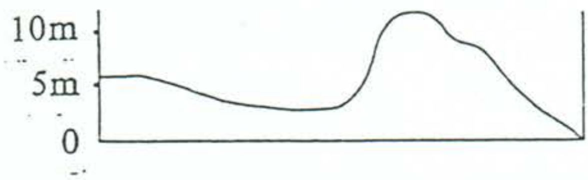


Fig 1. Location of the six sample areas at Kaitorete.

A

Inland → Coast

8	7	7	5	3	3	15	13	19	15	11
7	5	7	6	4	3	3	15	1	11	1
8	5	5	7	7	7	2	3	2	2	2
8	6	7	7	8	7	3		1	2	2
8	8	6	7	7	1	3	4	4	2	11
8	8	7	7	7	5	5	4	16	16	16
8	7	7	7	7	5	3	3	2	16	11
8	8	8	8	6	7	3	4		2	2
6	7	7	7	7	8	5	5	14	1	4
7	6	7	7	8	5	1	1	2	4	2

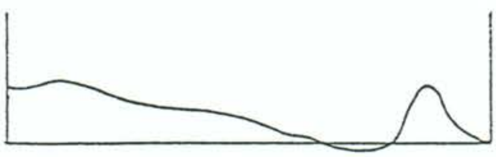


B

8	5	5	7	7	14	12	12	18	20	4	19
8	8	8	7	7	16	12	13	20	19	2	1
8	8	7	16	16	12	12	15	20	20	-	20
8	8	7	16	16	12	17	20	18	20	20	20
8	7	7	5	16	11	-	20	15	17	-	16
7	5	7	7	16	16	16	17	15	-	20	16
8	7	5	8	7	15	16	14	17	-	-	-
9	5	7	7	16	16	17	16	16	-	3	4
7	7	7	7	7	16	20	15	15	18	19	17
7	7	7	7	16	16	15	-	19	-	-	15

C

10	10	12	-	-	-	-	1	3	2	15
10	10	12	12	12	12	12	15	2	4	15
9	9	10	12	12	17	19	13	-	2	20
9	9	10	12	12	1	15	14	-	-	19
10	10	10	12	7	13	15	17	14	-	2
9	10	10	12	12	15	15	15	13	-	19
9	10	10	11	12	15	14	15	17	-	2
9	6	6	6	4	-	11	15	13	-	17
8	7	6	6	5	14	15	15	15	-	19
8	8	5	15	14	14	15	15	15	20	20

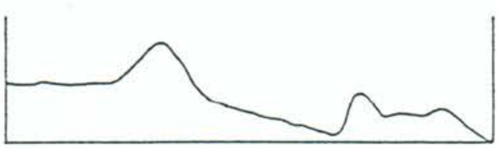


D

9	10	12	10	12	13	13	17	13	20	17
9	10	10	12	13	13	13	15	17	-	2
9	10	10	12	12	12	12	-	18	2	17
9	10	9	10	12	12	1	19	-	17	19
9	10	10	10	12	12	17	17	17	17	17
9	10	10	10	10	12	13	17	17	-	19
9	10	11	12	13	13	13	17	17	19	17
10	10	10	11	12	12	12	13	17	18	17
9	12	12	13	13	12	13	1	17	19	
9	10	12	15	13	13	13	-	-	-	19

E

8	5	6	5	-	-	11	11	5	3	2
9	5	5	-	18	-	19	14	14	2	11
5	5	15	5	-	15	11	14	14	4	17
9	3	5	5	5	11	-	15	1	2	17
9	5	5	5	5	11	11	15	2	3	17
9	5	5	5	11	5	17	1	15	2	1
9	9	5	5	5	5	2	14	1	4	2
9	5	6	5	5	5	5	15	2	1	15
9	5	10	5	14	1	5	17	2	1	17
9	5	10	4	5	14	14	-	2	2	15



F

9	5	5	5	5	5	4	1	3	4	18
9	5	5	6	5	5	5	5	4	4	2
9	5	5	5	3	5	4	3	15	3	16
9	7	5	4	5	5		3	3	4	2
9	9	5	3	14	11	13	1	3	3	18
8	7	5	6	4	14	14	2	4	4	2
5	6	4	5	4	1	1	3	15	2	2
9	6	5	3	4	4	1	4		15	2
9	6	6	5	3	3	4	1	3	2	2
9	6	5	5	5	3	4	15	15	2	15

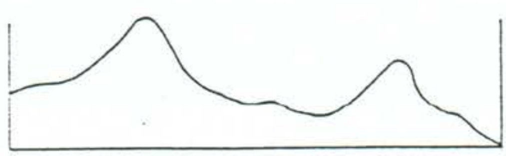


Fig 2. Dune profiles and community layout at Kaitorete.

central sections C and D, where almost the entire dune sequence was removed during the 1970s, often including the whole front dune, and to below mean sea level.

From the sampling data, sites and species were classified by Cluster Analysis. The association measure was Canberra Metric and the sorting strategy Flexible with beta set at -0.25 to create groups of comparatively even size (Clifford & Stephenson 1975). Analysis was performed using the PATN software package (Belbin 1989).

RESULTS

Twenty communities were discriminated by Cluster Analysis. Table 1 summarises frequency (within community) and mean site cover (sample site frequency) of the major species for the communities, and Fig 2 is the community maps of the six sections.

Communities 1 to 10 occur almost exclusively on unmined sites and represent the typical dune sequence. Communities 1 to 5 are dominated by pingao and represent subtle changes from the front of the foredune (1) to the front face of the backdune (5). The remaining communities 6 to 10 occur from the back of the back dune (6), on to the flats behind (8, 9), including deflation dunes (7), and back dunes invaded by bracken (*Pteridium esculentum*) (10).

The sites of communities 11 to 20 occur mostly on mined sites (73%), but a number also occur on unmined dunes, especially where they occur nearest the sea. They include sparsely vegetated communities including weedy sites (11), recently mined sites (12), sites with active sand (18, 19), and pavement with scabweed (*Raoulia australis*) (13, 14). More densely vegetated communities include new dunes on older mined areas (15, 16), and dense marram (20). Excluded from the analysis were sites with bare sand.

Pingao was found in all communities, at high cover in the unmined sites (except the grass flats and bracken) and at low cover in the mined sites. It is the characteristic dominant or co-dominant of 15 of the 20 communities and is therefore the main species of the dune system. Marram was found in 13 communities, including all 10 of the mined ones. It was however a characteristic dominant of only 4 communities, all in the mined grouping. It is found as dense stands in only 2 communities, firstly 16, where other species including pingao are found and 20, where it occurs virtually alone. In communities 12, 15 17 and 18 it occurs at lower density.

In the unmined section A, marram is confined to a single continuous dense patch on the front face of the foredune down to the strand line. In the similarly unmined section F it is confined to small patches of communities 16 and 18 that occur along the strand line. In the oldest mined section B marram is an important constituent of the vegetation. Firstly it occurs on the remaining unmined front faces of the foredune as communities 16, 17 and 20. The mined area behind has much marram represented by sites in communities 11-18 and 20. Much of this is dense marram (16, 20), but includes sparser mixtures with pingao as well. The area of communities 12-14 at the eastern end are in a segment of the dunes that was previously marram but which was re-mined in the late 1980s. Behind the mined section on the back dunes are sites of dense marram on unmined dunes, where it has spread from the mined sites.

At section C the unmined foredune remnants are tiny, but have some dense marram (20). The mined area behind has some sites with marram (mainly 12, 15, 17), but usually denser stands than at section B. There are some signs that marram is beginning to establish at the base of the backdunes behind the mined area. Only one of the tiny foredune fragments of section D has marram, while it is found only scattered and at low density through the extensive mined area behind. Marram is completely absent from the mined part of section E, but does occur at two sites on the strand line.

DISCUSSION

The results clearly demonstrate the role of disturbance to the establishment of marram. Indeed virtually every site containing marram can be traced to a probable origin at an unstable active part of the dunes. On the unmined dunes, this active area is the strand line along the front of the foredune. At this line plants establish, ble 1 - Frequency and abundance within the 20 communities. Only the 31 most abundant species are included. For each species the first mber is frequency within the community (F=100%, 9=90-99%, 8=80-89% etc) and the second is mean site abundance (expressed similarly as frequency in the 25 bquadrats). L indicates locally abundant, and + present but rare.

Community

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
No of Sites	25	41	30	31	78	20	55	31	36	35	18	40	24	21	44	24	34	8	16	16
Acaena agnipila		+		9-1	4-1	8-1	7-2	9-4	F-5	5-2		+				3-1				
Trifolium arvense					+	+	8-3	9-7	6-2	3-1	+	+		+		5-1				
Zoysia pungens					2-+	L	9-6	F-8	3-1	L			+			L				
Rytidosperma clavatum							+	5-2	9-5	+										
Stipa nodosa					+	+	+	7-3	9-6	+										
Aira caryophyllea					+	+	L	5-1	+							+				
Silene gallica			+		+	+	2-1	3-+	4-1											
Trifolium glomeratum								3-1	5-1		+									
Bromus diandrus	L	L	7-1	6-2	9-5	9-5	7-2		4-2	8-4	L	8-3	+	+	+		+			
Rumex acetosella		L	8-2	8-2	9-4	9-3	F-7	F-8	9-8	9-4	6-3	3-1		9-2	+					
Desmoscheonus spiralis	F-5	F-8	F-8	F-8	F-6	9-4	9-4	+	2-1	+	3-1	8-2	F-2	F-3	9-3	8-3	9-3	F-1	F-4	+
Hypochoeris radicata	F-2	F-5	F-3	9-5	9-2	7-2	9-5	F-6	9-3	9-3	4-1			F-2	9-1	F-4				
Lagurus ovatus	F-4	F-6	F-8	F-8	F-8	F-8	F-9	F-9	9-8	9-6	7-3	7-3	+	9-2	5-1	F-5	4-1			+
Calystegia soldanella	7-2	9-5	9-4	9-4	5-1		9-4	3-1	+	+	6-2		+	+	3-1	9-3	7-1			
Ammophila arenaria	+	L					+			L	3-1	5-1	L	3-1	5-2	F-7	5-1	6-2		F-6
Raoulia australis	4-1	L			1-+	+	5-1	9-6	6-2	+	+	6-2	F-2	7-3	5-2	+	+			
Erodium cicutarium	L					+	+		+	L	+	9-4	6-2	+	+	L	+			
Carmichaelia appressa					1-1	5-2	L	L	L	L										
Muehlenbeckia complexa	L			L	L	F-7	L	+	+	L					L					
Melicytus alpinus					L	L			+											
Holcus lanatus		+		+			+		L	L	+	+			+					

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
o of Sites	25	41	30	31	78	20	55	31	36	35	18	40	24	21	44	24	34	8	16	16
oa cita						5-1	+	·	9-2	5-1		L	+		+					
eridium esculentum				L	L	L	L	+	4-3	F-8	L	L								
arex breviculmis								L												
eudognaphalium teoalbum	+	3-+		+	+	+	+					3- +		+	+	+				
nagallis arvensis											+	L								
oeniculum vulgare												L								
olium perenne						+	L			+	+	+								
rsium arvense										L		L			+					
arex pumila											L				L					
ymus rectisetus									L	L										

and if these are sand binders, commence the process of dune building. It is here where marram first establishes and from this point spreads slowly up the front face of the foredune displacing the pingao as it advances. These establishment sites occur along the entire sampled area (Fig 3), and indeed along much of the actively prograding north-eastern end of Kaitorete Spit. The largest of these stands occurs within the sample area at section A, and its slow rate of vegetative spread is evidenced by the fact that this stand was present as a small patch on aerial photographs from the 1960s. It is probable that the now truncated marram dominated foredunes at section B were of similar size before mining. It is to be expected that if left unchecked that the many small patches of marram along the strand line will spread if left.

The extensive disturbance caused by the sand mining has created a much greater opportunity for the establishment and spread of marram. Instead of being confined to a narrow zone, there is now an extensive area of disturbance in which marram can invade. Seedlings of marram are seldom encountered, while most new plants can be shown to have arisen from stem fragments. Therefore, for marram to spread it must not only have disturbance, but a ready supply of stem material from nearby. In the oldest mined section marram stem fragments have probably originated from the stable marram covered foredunes that have been truncated from behind by sand mining. Within this area, large amounts of sand remained, this further promoting the lateral extension of marram. Pingao, which clearly established at the same time, has mostly been displaced, and now exists as unhealthy plants amongst the marram.

A similar situation exists at section C, but here the supply of sand is limited, so although well established, marram has not spread as successfully nor has it built dunes as it has at section B. At section D, the process is at an even earlier stage. Here there is no direct supply of rhizome fragments from the foredune (mining has not effected the one patch of marram on the foredune), so fragments of marram have probably had to come form sections B and C to the west. Spread of marram is again probably severely limited by the supply of sand.

At section E, mining has been kept well back from the foredune, so supply of rhizome material from there is unlikely. Furthermore, there is a short area of dunes left between sections D and E, primarily for the protection of a stand of an unnamed species of *Asperula* (*Galium*) which has been fenced off. This has severely restricted the opportunity for marram to enter the most recently mined area, but it is likely that within time rhizome fragments will enter this area and establish marram there.

Behind the mined area on sections B and C, there is evidence that marram is invading the unmined backdunes. Here the line of contact between mined and unmined dunes is probably acting very much like the strand line, and the invasion process occurring very much as it occurs on the front of the foredune elsewhere. This means that the back dune system is favourable to marram and that as a result of mining is being invaded. Within the present regime it is however unlikely that marram will be able to invade pingao dominated foredunes from behind. As shown on Fig 2, there is a wide unvegetated zone at the front of the mined area where plants find it difficult to establish in the unstable sand derived from the retreating foredune fragments.

CONCLUSIONS

1. To invade stable dunes dominated by pingao marram first requires an area of unstable sand.
2. This unstable area is provided by the actively accreting strand line where this occurs.
3. Invasion of stable dunes from this point proceeds, but is generally slow and by lateral spread.
4. In spreading, marram displaces pingao from the dunes.
5. If the dune system is destabilised in any way, the opportunity for marram spread is greatly enhanced.
6. Spread is primarily by rhizome fragments and is optimised if a ready supply of both these and active sand for binding are available.
7. Such instability frequently provides new opportunities for further spread.

STUDY 2. AN EXAMINATION OF THE PROCESS OF PINGAO REPLACEMENT BY MARRAM WITH TIME.

INTRODUCTION

It is clear that throughout New Zealand, and especially in the South Island, that sand dunes once occupied by pingao are now covered in marram. What is not always clear though is the process by which this change has taken place. For instance a statement that is frequently heard is that marram has displaced pingao by building dunes of steeper slope. Such statements are usually unsubstantiated, indeed Esler (1978) illustrates the different dune profiles (his Fig 33), but nowhere does he state that this involves a displacement process, nor does he suggest that the different dune building processes are responsible.

The evidence seems to suggest that for many of New Zealand's dune systems, and especially those built out of finer sands that the two species may have never been in contact (Cockayne 1911). In these situations, induced instability removed the entire pingao vegetative cover to create bare sand upon which marram was later planted. In other situations however, it is clear that the two species come into contact and the pingao is being replaced by marram.

This study attempts to answer some important questions regarding the physical process of replacement using permanent quadrats. At this stage (1991) these quadrats have been in place for only three years to yield two years results, and although trends can be seen, they are by no means certain, and further sampling for at least two more years will be necessary to verify these. There are a number questions that this study attempts to answer. Firstly, does marram replace pingao in all the situations where they come into contact? A further development of this question is whether pingao and marram can actually co-exist in certain situations. If they can, then identification of these situations is crucial for optimising active conservation efforts. Secondly, there is the question of how fast the process takes place, that includes the mode by which marram invades and by which pingao departs. Thirdly, the study examines the role of sand accumulation in the invasion process, this being an indication of whether differences in dune structure play a role as suggested earlier.

STUDY SITES

Plots were set up at three locations: Kaitorete Spit and New Brighton Beach, Canterbury, and at Hannah's Clearing, Haast, South Westland. At New Brighton the dune system is dominated by marram, with only a few small areas of pingao on the front face of the foredune. This situation is similar to many North Island dune systems, where pingao occupies only small areas above the strand line on dunes dominated by either or both of spinifex and marram (Partridge 1991). At Haast, the beach has a poorly structured system of very low dunes with about an even mixture of marram and pingao. Rather than building tall dunes, the binders create hummocks, the system grading into short forest/scrub behind.

Three parts of the extensive Kaitorete dunes were chosen for examination. In the north-east, near Birdling's Flat, there is a low two ridge dune system with a hollow between. On the seaward ridge a front of marram meets the pingao at a very obvious boundary. Additional small outliers of marram have also established in the pingao along the strand line. Although close to doing so in a number of places, marram has not yet reached the stable inner ridge by vegetative spread. At the south-western end, near Black Huts, the dune system consists of a single low dune ridge, with a long back slope down to Lake Ellesmere. The narrow front face has pingao, while the larger area of back face has large 'islands' of marram with narrow bands of pingao between. The third area is that which has been used for sand mining and adjacent unmined dunes, and has been described in Study 1.

METHODS

The sites for location of the permanent quadrats were chosen to represent as many different situations involving mixtures of pingao and marram as possible. At New Brighton, one plot (6 m x 2 m) was set up.

This plot grades from dense marram, through a zone of pingao, to dense marram again. At the time of setting up there were areas of bare sand between the two species on both sides. At Haast, six plots were set up. Two were used for a dual purpose, being controls for a marram pulling experiment that will be reported on in another study in this report. Unfortunately, one of these (plot 5) was mistakenly weeded of marram in May 1990. Two new plots, one being part of the marram pulling study were set up in 1991, and will not be reported on here. Plot 1 (8 m x 6 m) covers a section of the narrow dune system from bare sand to the margin of woody vegetation behind. Plot 2 (4 m x 3.5 m) was set up in a mixture of equal amounts of pingao and marram, the two species being in contact. Plot 3 (5 m x 5 m) was set up on a flat area where pingao seedlings were establishing, but where marram was commencing spread from the side. Plot 4 (6 m x 2 m) consisted of two patches of pingao on sloping sand with marram spreading towards one of the patches. Plot 5 (3 m x 3 m) was set up in dense vegetation consisting of only slightly more marram than pingao. Plot 7A (4 m x 2 m) (plots 6 and 7B were used for the weeding study) was set up in dense marram with only a little pingao remaining.

At the Birdling's Flat part of Kaitorete, two plots (each 5 m x 3 m) were set up. Both straddle the pingao to marram boundary. At the Black Huts site Plot 1 (4 m x 3 m) was set up to straddle the seaward pingao boundary, while Plot 2 (7 m x 2 m) extended from dense marram, across a zone of pingao that extended from the shore to the lake, and back into marram again. Eight plots were set up in the vicinity of the mined area at Kaitorete. Plots 1 and 2 (each 5 m x 3 m) straddle the pingao to marram boundary on unmined dunes. Plots 3 and 4 (each 4 m x 4 m) were set up on the strand line in equal mixtures of pingao and marram) In plot 3 the two species occurred together, while in plot 4 they commenced as discrete separate clumps. Plot 5 (5 m x 5 m) was set up on an area previously dominated by marram, that had been originally mined in the 1960s and again in 1987. At the time of setting up the plot was being colonised by pingao seedlings and by a few marram plants from stem fragments. Plot 6 (5 m x 5 m) was also set up in an establishment area, but on an area that had previously been pingao without any marram. Plot 7 (4 m x 4 m) was on an area of dunes mined in the 1960s and now dominated by marram with some remnant pingao. Plot 8 (6 m x 6 m) was on an area mined in the 1970s and consisting of patchy pingao with some more recently established marram.

At each plot pegs were placed to locate the plot boundary. In addition pegs were placed, usually inconspicuously, a measured distance away from the plots in case pegs went missing. At least two of the pegs were levelled with a surveyors level to establish a datum for each plot. Measurements of vegetation and sand accumulation were made at yearly intervals. Tapes were placed across the plots at 0.5 m intervals and sample points established at each 0.5 m along these tapes. At each point presence of all species was recorded in a 10 cm x 10 cm square, and the sand surface was levelled and related to the datum level. In the plots set up to examine seedling dynamics, the position of each seedling was plotted.The plots were set up in October to November 1989.

RESULTS

New Brighton.

There was little change at this site (Table 2). Pingao declined slightly, marram remained stable, and the bare area between stayed bare. None of the transformations involved one species displacing another, but were gains or losses to bare ground. Changes in sand level were slight. Pingao and bare areas had a slight loss of sand, while marram had a slight gain.

Table 2. Changes in pingao and marram 1989-1990, New Brighton plot.

	1988	1989	1990
pingao	11	9	8
marram	29	31	30
both	0	0	0
bare	25	25	27

what do no's relate to? No. plants?

Haast

Plot 1.

In this large plot there have not only been major changes in pingao and marram, but in other species as well (Table 3). The greatest changes were between 1988 and 1989, when most species showed a considerable increase in cover. Only tree lupin (*Lupinus arboreus*) declined, this being attributed to attack by the fungal pathogen *Colletotrichum* that devastated this species throughout New Zealand at that time (Molloy et. al. 1991). The slowest of the increasing species was pingao. Between 1989 and 1990, however, the process stabilised for many species, including both marram and pingao. Sheep sorrel (*Rumex acetosella*) continued to increase, while shore bindweed (*Calystegia soldanella*) suffered a decline. The transformations (Table 4) indicate that for marram in particular, this stability is not real. Between 1988 and 1989, marram colonised many bare areas, and indeed continued to do so to 1990. Between 1989 and 1990, however, it disappeared from an equal number of sites. Sites containing both species are rare. Between 1988 and 1989, marram was able to join pingao, but did not replace it, while from 1989 to 1990, the picture is less clear with former sites containing both species loosing either, or both marram and pingao.

Table 3. Changes in pingao and marram 1988-1990, Haast, plot 1.

	1988	1989	1990
pingao	39	48	47
marram	42	78	81
Carex	59	77	77
Calystegia	29	56	36
lupin	24	-	1
sorrel	9	49	65
Rubus	-	9	6

Table 4. Transformations for pingao and marram 1988-89 (first value) and 1989-90 (second value), Haast, plot 1.

	composition from			
	neither	pingao	marram	both
to				
neither	97,71	5,7	3,21	-,1
pingao	14,6	26,27	-,-	-,3
marram	30,25	-,-	36,46	-,2
both	-,2	4,3	-,1	4,2

Plot 2.

Between 1988 and 1989, pingao declined slightly, while marram increased by much more, while between 1989 and 1990, marram continued its increase, albeit more slowly, while pingao remained stable (Table 5). There has not been a great deal of mixing of the two species and most of the change are unrelated to interactions (Table 6).

Table 5. Changes in composition 1988-1990, Haast, plot 2.

	1988	1989	1990
pingao	10	8	9
marram	10	18	23

Table 6. Transformations for pingao and marram for 1988-89 (first number), and 1989-90 (second number), Haast, plot 2.

	composition from			
	neither	pingao	marram	both
to				
neither	46,41	1,2	1,3	-,-
pingao	1,-	3,3	1,1	1,-
marram	9,7	1,1	4,10	2,-
both	-,-	1,-	-,2	1,2

Plot 3.

Colonisation of this plot has been remarkably slow (Table 7). Survival of pingao seedlings present in 1988 is about 50%, but these have hardly grown over the two years, the largest being a plant of 35 cm height and 3 shoots, and the next a single shoot plant of 15 cm. All plants have however been severely browsed. Of the seedlings established in 1989, only one has survived, and in 1990 only a small number of additional seedlings were added. Marram, absent in 1988, is slowly invading along one side and is now well established as a small patch.

Table 7. Changes in composition from 1988 to 1990, and the fate of pingao seedlings at Haast, plot 3.

	1988	1989	1990
pingao	1	1	2
marram	-	2	5
pingao			
seedlings	11	17	10
(88 sl)	11	8	5
(89 sl)		9	1
(90 sl)			4

Plot 4.

The situation in this pingao dominated plot has been relatively stable (Table 8, 9). In the absence of marram, pingao has changed little. However, marram is invading one of the pingao patches and will soon come into interaction with it.

Table 8. Changes in composition from 1988 to 1990 at Haast, plot 4.

	1988	1989	1990
pingao	15	13	17
marram	-	1	5

Table 9. Transformations for pingao and marram from 1988-89 (first number) and 1989-90 (second number) for Haast, plot 4.

	composition from			
	neither	pingao	marram	both
to				
neither	42,41	7,1	-,1	-,-
pingao	6,6	7,11	-,-	-,-
marram	1,4	-,-	-,-	-,-
both	-,-	-,-	-,-	-,-

Plot 5.

There has been a slow increase in pingao with time, and a rapid increase in marram between 1989 and 1990 (Table 10). The failure of marram to increase in 1990 was probably effected by the accidental weeding during this period. The situation is however very dynamic and unpredictable (Table 11). There are no apparent trends in species replacement, with for instance, marram disappearing from mixtures as easily as pingao (the large loss of marram from mixtures in 1989 to 1990 is again probably a weeding effect).

Table 10. Changes in composition from 1988 to 1990 at Haast, plot 5. * Between 1989 and 1990, the marram was mistakenly weeded out.

	1988	1989		1990
pingao	14	16		20
marram	19	29	*	31

Table 11. Transformations in composition from 1988-89 (first number) and 1989-90 (second number) at Haast, plot 5.

	composition from			
	neither	pingao	marram	both
to				
neither	10,3	1,-	3,2	-,1
pingao	1,1	2,3	1,2	2,6
marram	7,8	2,-	9,13	2,1
both	3,1	4,3	1,3	1,1

Plot 7A.
Of all the Haast plots, this is the most stable in regard to the sand binders, but like plot 1, has been invaded by sheep sorrel (Table 12). Gorse (*Ulex europaeus*) is also spreading on to the plot. Marram is fairly stable, dominating most of the plot, but its interaction with the remnant pingao is very dynamic. Indeed, pure pingao has never remained at the same site for two measurements, while mixtures change readily to either species (Table 13).

Table 12. Changes in composition from 1988 to 1990 at Haast, plot 7A.

	1988	1989	1990
pingao	10	8	9
marram	34	39	36
sorrel	-	5	17
gorse	-	2	4

Table 13. Transformations for pingao and marram from 1988-89 (first number), and 1989-90 (second number), at Haast, plot 7A.

	composition from			
	neither	pingao	marram	both
to				
neither	4,1	-,1	-,4	-,-
pingao	-,-	-,-	-,-	2,2
marram	4,3	2,-	23,25	3,3
both	-,-	-,1	3,4	3,1

Kaitorete - Birdlings Flat.

Plot 1.

In this densely vegetated plot the replacement process is very clear (Table 14). The movement of marram through the plot is matched by a decline in live pingao and an increase in dead pingao plants (recorded as such where the whole plant was dead). Also of note is the disappearance of the annual grass *Lagurus ovatus*) following the advance of marram.

Table 14. Changes composition from 1988 to 1990, Plot 1, Birdlings Flat.

	1988	1989	1990
pingao	38	34	29
(dead)	10	15	20
marram	35	43	51
Lagurus	41	36	30

Pingao decreasing
Marram increasing.

Plot 2.

Between 1988 and 1989 there were considerable changes (Table 15). Marram spread rapidly into the plot, and there was a noticeable decline in both pingao and *Lagurus*. This trend slowed considerably during the 1989 to 1990 period with only minor changes taking place. The transformations (Table 16) clearly demonstrate that the main process of replacement over two years is pingao, to both together, to marram, and not an immediate replacement of pingao with marram.

Table 15. Changes in composition between 1988 and 1990 at Birdlings Flat, plot 2.

	1988	1989	1990
pingao	49	40	35
(dead)	6	14	16
marram	35	50	55
Lagurus	60	44	47
sorrel	8	11	15
catsear	2	1	1

Pingao decr
Marram incr

Table 16. Transformations between pingao and marram from 1988-89 (first number) and 1989-90 (second number) at Birdlings Flat, plot 2.

	composition from			
	neither	pingao	marram	both
to				
neither	7,7	1,1	1,1	-,-
pingao	-,-	18,11	1,-	-,2
marram	2,2	1,-	14,26	7,4
both	-,-	9,6	-,-	12,16

Kaitorete - Black Huts

Plot 1.

The composition and positions of the plants remained remarkably stable over the two years (Table 17, 18). Furthermore there was a clear and consistent separation of the two species by a distinct bare zone.

Table 17. Changes in composition from 1988 to 1990 at Black Huts, plot 1.

	1988	1989	1990
pingao	10	13	11
marram	20	20	21
Lagurus	6	4	9
Calystegia	3	8	2
Salsola	-	1	-

Table 18. Transformations from 1988-89 (first number) and 1989-90 (second number) at Black Huts, plot 1.

	composition from			
	neither	pingao	marram	both
to				
neither	29,28	-,2	1,1	-,-
pingao	3,-	10,11	-,-	-,-
marram	1,2	-,-	19,19	-,-
both	-,-	-,-	-,-	-,-

Plot 2.

The two stands of marram at either side of the pingao differed in density and interaction with the pingao. On one side the marram was dense and the two species mixed, while the other side was of lower density and the two species were separated by a bare area. The composition (Table 19), remained stable however and there were few transformations (not presented). All transformations involved adding to create mixtures and there were no displacements.

Table 19. Changes in composition from 1988 to 1990 at Black Huts, plot 2.

	1988	1989	1990
pingao	18	14	16
marram	41	42	43
Lagurus	6	2	1
lupin	-	-	2
catsear	2	1	3

Kaitorete - Central

Plot 1.

Marram spread rapidly through the plot (Table 20) and after two years there was little pure pingao left (Table 21). However, as the vegetation is generally sparse, mixtures and bare areas persist. Between 1988 and 1989 a small steep section containing marram collapsed, hence the four marram to nothing readings. The spread of *Acaena agnipila* is the result of the growth of a single large patch.

Table 20. Changes in composition from 1988 to 1990 at Kaitorete, plot 1.

	1988	1989	1990
pingao	31	30	23
(dead)	4	6	9
marram	31	40	48
Lagurus	22	19	14
Calystegia	6	6	4
catsear	3	2	2
Acaena	2	4	7

Table 21. Transformations for pingao and marram from 1988-89 (first number) and 1989-90 (second number) at Kaitorete, plot 1.

	composition from			
	neither	pingao	marram	both
to				
neither	17,20	1,1	4,1	-,1
pingao	1,0	12,3	-,-	-,2
marram	7,4	0,1	16,21	2,4
both	-,-	9,7	1,0	7,11

Plot 2.

In contrast to plot 1, the replacement process is very slow (Table 22). Only a few sites previously occupied by pingao have had marram added, and only a few with both have had pingao disappear (Table 23). Marram seems to be advancing only very slowly across the plot, and it might take some time for longer term trends to become clear. The larger than usual number of associated species is because this plot was located on the back dune system.

Table 22. Changes in composition from 1988 to 1990 at Kaitorete, plot 2.

	1988	1989	1990
pingao	26	24	24
(dead)	17	17	21
marram	35	39	43
Lagurus	46	52	51
brome	9	10	14
catsear	5	4	3
sorrel	4	8	1
Acaena	-	-	1

Table 23. Transformations for pingao and marram from 1988-89 (first number) and 1989-90 (second number) at Kaitorete, plot 2.

	composition from			
	neither	pingao	marram	both
to				
neither	14,10	2,2	3,2	-,-
pingao	2,4	18,14	-,-	-,1
marram	2,4	-,-	29,32	1,2
both	-,-	3,3	-,-	3,2

2

Plot 3.

At this active establishment zone, both pingao and marram have spread vigorously (Table 24). During the first year they barely came into contact, while in the second year mixtures occurred, but there was no sign of species replacement (Table 25).

Table 24. Changes in composition from 1988 to 1990 at Kaitorete, plot 3.

	1988	1989	1990
pingao	24	31	33
marram	17	26	32
Calystegia	11	15	8
Lagurus	1	5	7
catsear	-	1	1
Salsola	1	-	-

Table 25. Transformations for pingao and marram from 1988-89 (first number) and 1989-90 (second number) at Kaitorete, plot 3.

	composition from			
	neither	pingao	marram	both
to				
neither	25,19	2,3	-,1	-,-
pingao	9,4	19,19	-,-	-,1
marram	7,2	-,-	16,21	-,1
both	-,1	2,5	-,2	1,1

Plot 4.

Although the overall totals for pingao remain stable, while those for marram increase (Table 26), these somewhat hide the two processes taking place. Originally the marram was a dense patch surrounding some pingao, while other pingao was present around the periphery. This central pingao has declined from 8 in 1988 to 5 in 1989 to 2 in 1990. It is this decline that has contributed to the dead pingao counts. Around the margin pingao spread has compensated for this loss, but these areas have also come into contact in 1990. The processes of replacement are however clearer in the transformations, with half the sites containing both species loosing their pingao each year (Table 27).

Table 26. Changes in composition from 1988 to 1990 at Kaitorete, plot 4.

	1988	1989	1990
pingao	16	16	17
(dead)	3	5	8
marram	27	35	40
Lagurus	3	-	2

Table 27. Transformations for pingao and marram for 1988-89 (first number) and 1989-90 (second number) at Kaitorete, plot 4.

	composition from			
	neither	pingao	marram	both
to				
neither	34,26	1,-	1,2	-,-
pingao	4,4	6,9	-,-	-,-
marram	7,7	-,-	19,26	3,3
both	-,-	3,1	-,-	3,3

Plot 5.

Initially, this plot contained a large number of pingao seedlings and a few marram patches that had established from rhizome fragments (Table 28). The area in which the plot was located had been mined in 1987, so these plants had only recently established. The pingao performed poorly, the numbers of new seedlings declined with time and survival was poor. In contrast, marram survival was good, and the plants were spreading. Surviving pingao plants were showing signs of severe grazing, most probably by rabbits and hares, which are both common on the dunes. By 1990, the plot already seems destined to become pure marram.

Table 28. Changes in composition and in plant numbers from 1988 to 1990 at Kaitorete, plot 5.

	1988	1989	1990
pingao	3	1	-
marram	2	5	6
pingao (sl)	18	7	4
(88 sl)	18	2	1
(89 sl)		6	1
(90 sl)			2
marram (pl)	5	6	6
(88 pl)	5	4	4
(89 pl)		2	2
(90 pl)			0

Plot 6.

The numbers of pingao plants has remained stable, those that are lost each year being replaced by new recruits (Table 29). The plants are spreading slowly and the trend suggests that the plants present now should probably dominate the plot, albeit at a slow rate.

Table 29. Change in frequency and plant numbers of pingao from 1988 to 1990 at Kaitorete, plot 6.

	1988	1989	1990
pingao	2	3	5
pingao (sl)	14	16	14
(88 sl)	14	9	6
(89 sl)		7	5
(90 sl)			3

Plot 7.

This plot showed remarkable stability over the two year period (Table 30). Both pingao and marram were showing no spread into either bare sites or into areas occupied by other species. The plot consists of two clumps of marram, one clump of pingao, and on clump where the two occur together. Even where together there is little sign of any displacement.

Table 30. Changes in composition from 1988 to 1990 at Kaitorete, plot 7.

	1988	1989	1990
pingao	11	11	11
marram	28	29	29
Lagurus	26	24	21
catsear	4	2	3
Calystegia	11	14	9

Plot 8.

Although it occupies only a small proportion of the plot, the pingao is stable and probably moribund (Table 31). Much of the area between the isolated tufts is scabweed, a species indicative of areas where there is no movement of sand.

Table 31. Changes in composition from 1988 to 1990 at Kaitorete, plot 8.

	1988	1989	1990
pingao	14	13	13
scabweed	22	24	25
Erodium	11	13	8
Lagurus	5	8	2
Bromus	7	11	10

Changes in sand level.

The results for these are not presented here, firstly because they so far show no trends, and secondly because the changes in all plots have been small. Early indications suggest that at Haast, there are differences in the amount of sand being added each year. From 1988 to 1989 in plot 1, each point rose by an average of 0.52 cm, while between 1989 and 1990, each point fell by 2.30 cm to make a total drop of 1.78 cm. The readings suggest that both pingao and marram accumulate slightly more sand or tend to loose less sand than bare sites, but these differences are not significant for the two years data.

At Haast plot 2, which was one of the most dynamic for vegetation change, the mean annual point changes from 1988 to 1990 were insignificant (<.01 cm). From 1989 to 1990, of the nine points that accumulated larger than normal amounts of sand (>2 cm), six had no vegetation, one went from pingao to pingao, one from marram to marram and one from pingao to bare. This pattern is no different from that expected from a random sample.

At Kaitorete-central, apart from the two strand line plots (plots 3 and 4), sand hardly appears to have moved at all. Rapid (plot 1) and slow (plot 2) marram spread and the maintenance of moribund stands of both pingao (plot 8) and marram (plot 7) all occur without the addition of sand. On the strand line, there is greater activity within plots, but at present there are no differences between bare sites and those vegetated by either species. At the other Kaitorete areas, (Birdlings and Black Huts) sand changes were minimal.

DISCUSSION

Although the results cover too short a time period to make definitive conclusions, some tentative and generalised statements can be made. Firstly, in the areas examined, there appear to be only two of the three possible outcomes of the interaction between pingao and marram; stability, and pingao being displaced. Nowhere was there evidence that pingao was able to displace marram. Indeed, in brief examinations of dune systems in New Zealand (Johnson 1991, Partridge 1991), only one situation was cited (Pakiri Beach, North Island) in which marram was being displaced by pingao, and that was on a dune where marram had been recently planted.

It is of extreme importance that stable situations be distinguished from those involving displacement. If conservation effort is to be put into managing marram, then the primary target needs to be situations in which pingao is actually threatened. During New Zealand's period of massive dune instability, there probably never was any great displacement through interaction, instead pingao disappeared first with the increase in dune instability, and marram appeared later through planting and natural spread on to unvegetated dunes. The active displacement process recorded in this study is much slower, but is nonetheless significant. For instance, apart from a few areas such as at Black Huts, there is reason to expect that marram will eventually displace pingao from the whole of Kaitorete Spit.

A number of situations in which the two species seem to co-exist have been indicated from the results. These situations can be divided into stable and dynamic.

The first stable situation occurs at New Brighton where remnants of pingao exist on marram dominated dunes. Similar situations exist throughout New Zealand where stable patches of pingao occur on the front face of foredunes otherwise dominated by marram, or more frequently by spinifex. This stability may however be only temporary at New Brighton, where the whole dune system has been subjected to frequent erosion and building phases. During the building phase pingao probably establishes at the strand line along with marram, but as marram frequently seems unable to completely colonise the building front foredune face, there is the opportunity for pingao to persist. In the absence of pingao, such 'gaps' in the marram remain bare, and indeed seem to be prime sites for the commencement of dune blowouts. In the situation that exists at New Brighton, there is little that can be done to manage the system to preserve or enhance pingao on such dunes. Plantings of pingao have been carried out, with some success, but the potential for instability, especially during an erosion phase, leaves the plant very vulnerable. That it has been able to remain at all is indicative of pingao's ability to re-establish provided a seed source is available. On the New Brighton dunes however, there is so little pingao left that this ability is even threatened.

At the Black Huts plots at Kaitorete, the entire pingao and marram interaction appears to be stable. The two species do not however co-exist, suggesting that they persist together by mutual exclusion, probably the result of a non overlap of realised niches. It has generally been regarded that pingao and marram occupy the same ecological niche, that is any site that is suitable for one is suitable for the other. Ecological niches are best envisaged as a set of environmental gradients along which the particular species can survive. The realised niche is the part of the gradient along which the species is actually found, once interactions with other species are taken into account. It can therefore be said that pingao appears to have a niche that so overlaps that of marram that the two actively compete for the same sites. As suggested, this usually involves marram displacing pingao. However, the Black Huts sites suggest that the overlap is not complete and that there are situations to which pingao is better suited than marram. There is little doubt that the situation here is relatively stable as there is no sign of recently dead pingao amongst the marram, nor is there evidence of marram spreading into the pingao. Pingao occupies the front face of the low foredune and narrow bands through to the lake behind, whereas marram occupies the back face of the dune. Sea water is frequently washed on to the foredune front face and down the narrow low-lying areas to the lake, these being the areas occupied by pingao. It is difficult to envisage much sea water reaching the marram. This suggests two effects that might influence vegetation patterns. First, pingao is more salt tolerant than marram (Sykes & Wilson 1989), and second the sea water deposits coarse gravel where it flows. The areas of marram are on finer sand. Therefore, either salinity or sediment type or both may be producing conditions suitable to only pingao. This would suggest that the niche of marram does not completely overlap that of pingao, and that there are sites in which

(1) pingao > salinity tolerance.
(2) pingao on coarser gravel, marram on finer sand

pingao is better suited. There is no need for immediate action to be taken to control marram in this situation provided the present situation persists.

The third situation in which the two species co-exist is at the mined area at Kaitorete. In many of the areas sampled, pingao appears to be stable and indeed moribund, but at plot 7, Kaitorete-central, marram appears moribund as well. In the earliest mined areas, sufficient sand was left for dune building and on these marram has colonised at the expense of pingao. On the dunes that were mined in the 1970s however, there was limited sand available, so the marram and pingao mixture has stabilised at an earlier stage. On the nearby plot 8, where marram is absent, the dune building has stopped even earlier, there being now scattered clumps of pingao barely beyond the seedling stage, but moribund and in poor health. Between the plants the surface has lost all movable sand and is now a pavement dominated by scabweed. The absence of any interaction in plot 7 is therefore the result of both species being trapped by an inability to spread and come into contact. This suggests that for active displacement to occur, there needs to be sufficient sand within the system for at least marram to spread. Again in this situation, there is little need for active management of marram as this species has lost its ability to spread. This situation applies not only to mined dunes, but to situations where sand supply is very limited.

In contrast to these highly stable mixtures, the dunes at Haast suggest a maintenance of the pingao/marram mixture because of instability. The results demonstrate that marram is spreading rapidly at the expense of pingao, although there is so far little evidence of replacement. It is known from discussions with local residents that marram has been on these dunes for a long time, so the question arises as to why these dunes are not covered in marram, with or without associated pingao. Indeed, the vegetation on these dunes is very sparse. The limited data on sand movement may provide a clue. Sand appears to move in and out with great frequency and indeed the whole dune system may be very unstable. Results from the seedling plots both at Haast and Kaitorete show that following disturbance, a large number of pingao seedlings establish along with some plants of marram, mostly from stem fragments. The marram grows and spreads at a much faster rate, and over time comes to dominate on mature dunes. However, if the building dune system is completely flattened and returned to the start, then pingao will be favoured again because of its superior initial colonising ability. The mixture of species will thereby be maintained only if the system is frequently disturbed and not allowed to reach its end point of pure marram. At Haast, this instability is of low scale, trends can be observed but only over small areas. Indeed, some of the plots are close to being threatened by a receding step to the unvegetated beach. With the destruction being small scale, there is always a seed source available for the recolonisation of bared surfaces. Such situations require no help through management. The two species will continue to interact in the way described, the only threat being a change in conditions that would result in total stability, and domination by marram.

The situation of most concern is however, that in which marram is displacing pingao. Unlike it has often been suggested, there is no evidence that this process is one related to dune building. Invasion by marram was unrelated to differentials in rate of sand accumulation. If indeed marram is able to trap sand at a faster rate, then it has no real influence on the displacement interaction. The most vulnerable stands of pingao are those that are stable and perhaps moribund, provided they are on sand. In these situations, the replacement is fairly rapid. An active front of marram consists of vigorous shoots that start widely spaced amongst the pingao. Other shoots arise from these and marram density and height increases. Once a dense stand has formed, the pingao declines in vigour to eventually die. The boundary between pingao and marram therefore has four zones; pure pingao, pingao with extension shoots of marram, dense marram with unhealthy pingao, dense marram with only dead pingao. Irrespective of whether the process is rapid (plot 1) or slow (plot 2), the whole process typically covers less than three metres, an indication of how effective the replacement process is. At Kaitorete, some of the associated species disappear with the pingao, most notably *Lagurus ovatus*, catsear (*Hypochaeris radicata*) and *Acaena agnipila*. The displacement of pingao is of great concern. Although marram is easily managed while small, its spread provides considerable problems if left unchecked. Even if removed from the dunes, there is little prospect of pingao re-establishing unaided. Areas where marram has been removed show no sign of colonising, a situation similar to dunes from which tree lupin has been eliminated by disease (Molloy et. al. 1991). It is this situation where most control effort for conservation purposes needs to be placed.

The two Kaitorete plots on the strand line have had insufficient interaction for any conclusions to be drawn. With pingao being fairly vigorous, it may be harder to displace, much as at the situation at Haast, but the marram in these sites is also equally more vigorous and probably eventually able to displace pingao. However, irrespective of the outcome, these areas are important for control, as has been indicated in the first study, this is the establishment site for marram, and the point from which it commences its attack on the dunes.

The three seedling plots show considerable differences. At Haast, seedling survival of pingao is minimal, apparently because of grazing. Growth is also very slow, but this can possibly be attributed to the non addition of sand over the two years, and indeed sand has been removed from the plot. At Kaitorete-central plot 5, grazing has been so severe that pingao has been virtually eliminated. Marram in contrast, appears to be unpalatable. There are dense stands of marram adjacent, and it may be that these provide cover for rabbits and hares, in contrast to open pingao (plot 6), where there is limited cover from hawks, and where pingao seedling survival is greater.

CONCLUSIONS

1. Marram can either co-exist with pingao or displace it, depending upon conditions.
2. Stable situations in which the two can co-exist include:
   a. the front face of the foredune where marram spread is restricted
   b. where environmental factors favour pingao (e.g. salinity, sediment type)
   c. where both species are moribund.
3. Unstable situations can occur in which co-existence is maintained through re-starting of the establishment phase, which favours pingao.
4. Displacement of pingao by marram is most severe on stable dunes with moribund pingao.
5. The replacement process is unrelated to that of dune building and the shapes of different kinds of dunes.
6. As soon as marram invades, pingao starts to loose vigour and dies, leaving pure marram.
7. Pingao establishment can be severely restricted by grazing, while marram is unpalatable.
8. To conserve stands of pingao, effort needs to be put into controlling marram, but firstly only where it is actually displacing or threatening to displace pingao.

STUDY 3. PINGAO v MARRAM; THE DISPLACEMENT INTERACTION

INTRODUCTION

The potential for marram to displace pingao in certain situations has been clearly demonstrated in the previous study. The important question that follows from this is by what mechanism does it do so. An understanding of the process may lead to the possible management option of interfering with the process and thereby stopping it or even reversing it.

There are two kinds of interactions that may be taking place between pingao and marram. The first involves allelopathy, in which marram has a direct influence on pingao, by producing toxic substances that actively kill it or retard its growth. Once a popular concept (Rice 19), allelopathy has been shown to be difficult to demonstrate, especially in the field. Chemical exudates almost always have an effect on growth, but this can usually be attributed to osmotic effects on water uptake, and indeed inert chemicals frequently have the same effect. Allelopathy will be examined in this study, but only at a crude level, and the results will be interpreted with a great deal of caution.

The second interaction involves competition, in which marram deprives pingao from one or more of the resources it requires to survive. Such competition may take place in either the shoot or root zones. Shoot competition is most likely to be for light, in which marram might shade the pingao. Root competition is most likely to be for nutrients or water, in which marram takes these from the soil more effectively than the pingao, thereby starving it. There are many nutrients that may be important, and investigating each and in combination is a difficult and onerous undertaking. The technique employed in this study will not be able to indicate which nutrients are limiting, but will use the species involved as phytometers to directly indicate if this is the source of the competition. Although not particularly sensitive, the phytometer method should indicate any effects in this situation because the competitive effect is so strong.

The aim of this study is to investigate the possible mechanisms by which marram is able to displace pingao by examining changes in the field across a pingao to marram boundary, in conjunction with glasshouse experiments to further test the various hypotheses.

METHODS

a. Shoot and root profiles across the boundary.

Much can be learned regarding possible interactions between species from studies of their physical structure. Although in many ways similar, pingao and marram have different growth forms, and these differences may provide clues to their behaviour when they interact. Also, there may be important but unseen differences below the sand surface, and these may be critical.

At the central part of Kaitorete, two areas were selected for the construction of shoot and root profiles across the pingao marram boundary. Profile 1 was located on stable dunes with moribund pingao but actively invading marram. Profile 2 was located on the strand line where both species are actively spreading.

At the stable profile site, six plots were set up, two in pure dense marram (with dead pingao), two in the mixing zone, and two in pure pingao. Each plot was 2 m x 0.5 m with the shorter side in the direction of the vegetation change. The six plots formed a non-contiguous series across the change in composition. At the strand line site, only three plots were possible, one in each zone, and they were not located in a continuous series, but where the vegetation best fitted the criteria required.

At each plot height profiles were measured at each of twenty randomly located points. If only bare sand was located at a point, this was noted and another point substituted. This gave twenty vegetated points per plot and a number of bare points. At each point a 10 cm x 10 cm quadrat was used to measure plant frequency at ground level and at height intervals of 10 cm for both pingao (live and dead) and marram. Depth profiles for buried material were constructed at ten randomly located points in each plot. Pits were dug and sampled at both ground level and 10 cm depths. Cubes of sand and root material were extracted from a contiguous series of samples. Extracts were 10 cm^3 in volume. These were each washed and live material extracted, identified (which was very easy), separated into root and shoot, and dry weighed after within site pooling of the material.

b. Allelopathy.

Seeds of pingao were collected and germinated in seed trays. Regrowth shoots of marram were collected from a recently mined area and planted into pots. Once the pingao seedlings were 5 cm tall 30 plants of even size were selected. Ten marram plants of even size and of similar size to the pingao were selected as well. Twenty pots were made up with Kaitorete sand from the most recently mined area. Into 10 of these, two randomly selected plants of pingao were planted and in the other ten a single plant of pingao was planted with one of marram. The pots were kept well watered with plentiful nutrient for a period of 8 months. They were then harvested, and all plants divided into root and shoot before dry weighing.

c. Competition - shoot

It was considered that the only possible form of shoot competition would be for light. Additional plots were set up adjacent to the profile studies as described in 'a.' above. In each plot 50 random points were located and at each a light meter was used to measure light intensity at firstly the maximum height of the vegetation, secondly at the height at which pingao was found or might be expected to be found, and thirdly at ground level. This set of measurements were made on four occasions; morning, midday and evening on a cloudless summer day, and midday on a cloudy summer day. All lower level readings were converted to percentage of that at the top.

d. Competition - root

1. Moisture

This study was set up adjacent to the profile studies described above. In each plot pits were dug and sand samples collected from four depths; just below the surface, and at 15 cm, 30 cm and 45 cm depths. The procedure was repeated over 10 months from August to May, and therefore covered one summer. Moisture content of a sample of approximately 100 g was determined by wet weighing followed by drying and dry weighing, moisture being expressed as a percentage of dry weight.

2. Nutrients

Seeds of pingao were collected and germinated in seed trays. Once the seedlings were about 5 cm tall forty plants of even size were selected, washed out and planted into individual pots of Kaitorete sand collected from the mined area. The pots were randomly allocated to one of two treatments and one of two replicates, giving ten plants per treatment per replicate. The labelled pots were randomised within each replicate and maintained in a glasshouse for a period of eight months from September to April.

Each month subsurface sand samples were collected from beneath both pure pingao and pure marram. The samples were balanced by wet weight to 1 kg, and 500 ml of water was added. The solution was gravity filtered and used to water the allocated plants, once a week for a month. At the end of the experiment, all plants were separated into root and shoot and dry weighed.

RESULTS

a. Profiles across the pingao marram boundary

The above ground profile for the stable sand area is presented in Table 32. In pure pingao (plots 1 and 2) the pingao grows to a height of 20 cm, with only the occasional shoot reaching up to 30 cm. In plot 3, marram enters, and although not abundant demonstrates an immediate height increase over the pingao. In plot 4, the marram thickens considerably, as well as increasing its height, and the pingao, unaffected in plot 3, shows a decline. In pure marram (plots 5 and 6), pingao is confined to a few dwarfed plants and much dead material, while the marram reaches a greater density and height than the pingao ever did.

Table 32. Above ground height profiles for the six plots located across pingao marram boundary at the stable sand site. Values for pingao in brackets represent dead material.

		Plot					
		1	2	3	4	5	6
0cm	Pingao	65(10)	75(5)	60(20)	35(20)	5(30)	10(25)
	Marram			15	40	85	90
10cm	Pingao	30(5)	45	35(10)	15(10)	(15)	(5)
	Marram			15	40	75	85
20cm	Pingao	5	10				
	Marram			10	35	70	70
30cm	Pingao						
	Marram			5	15	55	60
40cm	Pingao						
	Marram				10	40	45
50cm	Pingao						
	Marram					25	35
60cm	Pingao						
	Marram					5	10

The change across the pingao marram boundary is even more clearly marked below ground (Table 33). Pingao shoot material never reaches below 10cm depth and root material stopped at about 20cm. As marram invades it establishes a much deeper profile with shoot material down to 50 cm, and root material to at least 60 cm. The biomass at each level is also much greater than for pingao, and once there is more marram than pingao, the latter disappears rapidly from the profile.

Table 33. Below ground profiles for the six plots located across the pingao marram boundary at the stable sand site. Each pair of values is the dry weight of root (g) and the dry weight of shoot.

		Plot					
		1	2	3	4	5	6
0-10cm	Pingao	41:157	56:218	37:112	15:44		
	Marram				61:69	126:394	296:679
10-20cm	Pingao	28:-	39:-	15:-	3:-		
	Marram				24:44	59:141	198:521
20-30cm	Pingao		3:-				
	Marram				14:-	37:96	110:224
30-40cm	Pingao						
	Marram					15:35	55:96
40-50cm	Pingao						
	Marram					8:-	35:54
50-60cm	Pingao						
	Marram						16:-

The strong displacement process evident at the stable sand site does not occur at the strand line site (Table 34, 35). Pingao survives in dense marram, although there is some indication of a poorer performance there. Pingao grows taller at this site and its roots tend to go down a little further. The depth to which marram stems and roots are found is much lower here, stopping at 40 cm, although it may have not had as much time to penetrate as far.

Table 34. Above ground profiles for the three plots across the pingao marram boundary at the strand line site . Value in brackets is for dead material.

		Plot		
		1	2	3
0cm	Pingao	40	45	30(5)
	Marram		35	75
10cm	Pingao	35	30	20
	Marram		20	65
20cm	Pingao	15	10	5
	Marram		20	60
30cm	Pingao			
	Marram		15	45
40cm	Pingao			
	Marram		5	30
50cm	Pingao			
	Marram			15
60cm	Pingao			
	Marram			10

Table 35. Below ground profiles for the three plots across the pingao marram boundary at the strand line plot. The first value is root dry weight (g) and the second value shoot dry weight.

		Plot		
		1	2	3
0-10cm	Pingao	36:220	49:301	26:101
	Marram		77:256	203:428
10-20cm	Pingao	21:-	27:-	41:-
	Marram		55:114	220:339
20-30cm	Pingao	5:-	18:-	
	Marram		26:92	45:23
30-40cm	Pingao			
	Marram			17:21

b. Allelopathy

Accumulative dry weights for the ten plants in each treatment combination is presented in Table 36. The presence of marram had no significant effect on the growth of the associated pingao plants.

Table 36. Cumulative dry weights (g) of the groups of ten plants assigned to the two allelopathic interaction treatments.

Treatment	Marram/Pingao		Pingao/Pingao	
	Marram	Pingao	Pingao	Pingao
Dry weight	377.6	243.1	226.4	309.2

c. Competition - shoot.

Pingao stands are very open and there is little reduction in light intensity at ground level (plots 1,2) (Table 37). As marram invades there is a distinct reduction in light levels, firstly at ground level, and secondly at the height of the pingao (plots 3,4). By the time pingao has been replaced the light intensity at ground level is about half that above the stand, and at the top of the dead pingao it is approximately 75% (plots 5,6).

Table 37. Changes in light intensity at two levels (m = top of pingao, b = ground level) relative to that above the stand (expressed as percentages), at the stable sand site.

	Sunny Day			Overcast Day
Plot	Morning	Midday	Afternoon	Midday
1 m	1.0	1.0	1.0	.98
b	.83	.91	.93	.95
2 m	1.0	1.0	1.0	.96
b	.79	.88	.85	.90
3 m	1.0	1.0	.98	.95
b	.81	.90	.82	.85
4 m	.89	.95	.91	.90
b	.87	.83	.83	.77
5 m	.84	.84	.88	.82
b	.81	.79	.77	.61
6 m	.66	.72	.73	.70
b	.55	.66	.69	.58

At the strand line site the pattern is similar (Table 38). However, at the dense marram of plot 3, the ground light levels are extremely low, and indeed much lower than at the pingao height. The higher light levels for the afternoon reading are probably the result of the orientation of the plots to face the afternoon sun.

Table 38. Changes in light intensity at two levels (m = pingao height, b = ground level) at the strand line site (expressed as percentages).

	Sunny Day			Overcast Day
Plot	Morning	Midday	Afternoon	Midday
1 m	1.0	1.0	1.0	1.0
b	.83	.81	.92	.86
2 m	.95	.94	1.0	.92
b	.81	.77	.85	.79
3 m	.64	.71	.77	.62
b	.33	.43	.51	.29

d. Competition - root.

1. moisture

Mean percentage sand moisture for the ten months is presented in Table 39. Below pingao, moisture levels increase with depth, but as marram invades, the amount of water in the upper layers decreases considerably. Analysis of variance shows a significant difference between both plots with pingao and both with marram at the 0 and 15 cm depths ($P<.01$), but not at lower depths, which are beyond the pingao root zone. There were no significant differences between either species and the intermediate plots. This pattern was particularly evident in summer. In August and September there were no obvious differences, and the pattern was first established in October. In January the difference was greatest, with the top layer containing no moisture under marram. By April and May the pattern had again disappeared.

Table 39. Moisture levels (percentage wet weight) at four depths below the six plots at the stable sand site. Values are means for 10 months.

	Plot					
Depth	1	2	3	4	5	6
0 cm	6	8	8	4	3	2
15 cm	11	14	12	8	5	3
30 cm	15	18	17	16	14	7
45 cm	19	19	21	18	15	18

This pattern was not repeated at the strand line site (Table 40). The addition of marram made no significant difference (P=.01) at any of the levels. Overall moisture levels were higher than the stable sand site, and there were no seasonal effects. This site regularly receives water from the dunes behind and from the high tides, so differences are not expected.

Table 40. Moisture levels (percentage wet weight) at four depths below the three plots at the strand line site. Values are means for 10 months.

	Plot		
	1	2	3
Depth			
0 cm	14	11	9
15 cm	20	16	14
30 cm	16	18	20
45 cm	15	14	13

2. Nutrients.

There were no significant differences (p=.05) between the treatments (Table 41). The plants did not grow as well as those of similar starting size in the allelopathy experiment (Table 36) indicating a nutrient stress, but there is no evidence that sand from below marram contains less nutrients than that below pingao.

Table 41. Cumulative dry weights of the 10 pingao plants per replicate when watered with extracts from below marram and pingao.

	Marram		Pingao	
	R1	R2	R1	R2
Dry Weight	141.6	163.9	171.3	129.7

DISCUSSION

The profiles demonstrate a critical morphological difference between pingao and marram. Above ground marram rapidly overtops pingao, growing to about twice the height. Below ground the difference is even greater, with marram stems and roots extending to much greater depths of sand. Indeed, pingao is a relatively shallowly rooted plant, although it holds on to its sand tenaciously, as can be evidenced if attempts are made to pull it out. These morphological differences lead to clear competitive advantages for marram which can explore greater volumes of air and sand. This is however not a case of niche separation, as marram also fully exploits the space utilised by pingao. The implication is therefore that in the zone of interaction marram directly effects pingao, and its greater size probably gives it the ability to do so.

The results demonstrate no evidence of an allelopathic effect. Marram is therefore not directly killing pingao, but is displacing it by severe competition for resources. Three resources were examined in the study; light, water, and nutrients. The experiment involving watering with nutrients from below both species indicated no nutrient limitation, so light and moisture are implicated. It is felt that the evidence for light playing an important role is weak. Certainly below marram the amount of light reaching ground level is low, but at the height of pingao, this reduction is not great. Also, this large reduction in available light occurs only after pingao has gone, and the displacement zone is not so severely stressed. Furthermore in the strand line site, where light levels are lowest under the tallest marram, pingao still holds on, suggesting that light is not the primary factor.

In the stable sand site the invasion of marram has a severe effect on sand moisture content over the summer. As soon as growth starts the marram seems to be able to lower the moisture level of the upper sand layers to what is probably below a critical value for pingao. Marram is able to survive this because it alone can exploit moisture from lower sand levels. The shallow rooted morphology of pingao clearly disadvantages it in this situation. At the strand line site there is abundant moisture in the upper layers throughout the summer. In this situation pingao is able to survive with marram for longer, despite the improved vigour of the marram. It is therefore considered that marram out-competes pingao primarily by reducing moisture levels in the upper layers of sand. The process may be accentuated if marram is able to trap water held then lost by pingao roots during the night, a process that has been recorded in some desert plants (Caldwell 1990) as water parasitism.

Much of the pingao at Kaitorete is on stable sites, and is moribund as evidenced by the poor health of the plants. In this situation such plants must be particularly susceptible to any additional stress, even by a slowly invading species such as marram. Nutrients on these dunes seem to be low which means that the whole displacement process takes place only very slowly. On active sites where nutrients are plentiful, both marram and pingao have improved vigour, and both grow and spread at a faster rate. In this situation, pingao holds out for longer, but eventually succumbs. In this situation light may be playing a more important role, especially when the marram becomes very dense and tall. It appears that the outcome of this displacement occurs after a much longer time than the moisture stress driven replacement on stable dunes.

CONCLUSIONS

1. Marram most frequently displaces pingao through root competition for water.
2. Pingao is shallowly rooted while marram has deep roots and rhizomes that allow it to exploit water at greater depth than the upper layers that it has depleted.
3. In active sites with abundant moisture there appears to be some competition for light, although this appears less effective at displacing pingao.
4. There is no evidence for allelopathic interactions or competition for nutrients.

STUDY 4. THE EFFECTS OF HAND WEEDING OF MARRAM AS A CONTROL MEASURE

INTRODUCTION

The most commonly used technique for the removal of marram from mixtures with pingao is hand pulling. Despite its ability to explore greater depths of sand, marram comes out rather easily, although rhizome material is invariably left behind. Many areas seem to have been weeded once, such as a large stand at Kaitorete, while in other locations, such as at Ship Creek on the West Coast north of Haast, it is known that weeding of a single patch takes place frequently. In the first situation it is hard to tell whether the hand pulling has had any effect, while in the second, pulling has had a considerable beneficial effect, but has not eliminated the marram altogether.

The aim of this study is to gain a more accurate idea as to the effects of pulling by monitoring various plots in which marram is removed at various frequency.

METHODS

At six sites (four at Kaitorete and two at Haast), pairs of permanent plots were marked out and frequency of marram, pingao, and other species plotted as in the interaction study described above (Study 2). All plots are 3 m x 3 m except for Haast site 7 which is 4 m x 2 m. The pairs were chosen to be as even as possible and were in most cases adjacent. At each site one of the pair was randomly assigned to be weeded. The two plots at Haast were weeded then again after one year, then at six monthly intervals, giving 3 weedings over two years. The four plots at Kaitorete were divided into two frequencies, yearly and six monthly. The first have therefore received two weedings in two years and the second four. Measurements were made annually before the weeding.

RESULTS

1. Haast Sites 5,6.

The unweeded site was accidentally weeded between the 1989 and 1990 readings. The first weeding made little difference, marram continued to increase in the plots (Table 42). The two six monthly readings show a considerable difference however, with little marram left in the weeded plot. The accidental weeding has temporarily slowed the rate of marram spread. Weeding seems to make little difference to the pingao.

Table 42. Changes in composition in weeded and unweeded plots at Haast (sites 5,6).

	1988	1989	1990
Unweeded			
Pingao	14	16	20
Marram	19	29	* 31
Weeded			
Pingao	26	23	22
Marram	21	34	3

2. Haast Site 7.

The pattern seen at the previous site is repeated here Table 43). In 1988, marram had a high cover in both plots and remained fairly stable in the unweeded plot. In the weeded plot the first weeding made no difference, but the two that followed have considerably reduced the cover of marram. There is no indication so far that pingao has benefited from the weeding.

Table 43. Changes in composition in weeded and unweeded plots at Haast Site 7.

	1988	1989	1990
Unweeded			
Pingao	10	8	9
Marram	34	39	36
Rumex	-	5	17
gorse	-	2	4
Weeded			
Pingao	9	6	10
Marram	28	28	7
Coriaria	6	5	8
Calystegia	-	5	4

Kaitorete Site 1 (weeded annually)

Annual weeding has made no difference to the dense marram at this site (Table 44). Pingao continues its slow decline while marram is barely held at a stable cover.

Table 44. Changes in composition in weeded and unweeded plots at Kaitorete site 1.

	1988	1989	1990
Unweeded			
Pingao	19	14	8
Marram	27	35	39
Lagurus	20	13	19
Weeded			
Pingao	16	14	10
Marram	29	34	31
Lagurus	14	18	18

Kaitorete Site 2 (weeded six monthly)

In comparison with the annual weeding, the six monthly weeding shows a considerable decline in marram between 1989 and 1990 (Table 45). In the first year however, there was no indication that this decline was likely to happen. Pingao has so far shown no response to this change.

Table 45. Changes in composition in weeded and unweeded plots at Kaitorete site 2.

	1988	1989	1990
Unweeded			
Pingao	16	13	9
Marram	24	28	31
Lagurus	16	17	11
Weeded			
Pingao	21	19	19
Marram	30	29	9
Lagurus	24	20	27

Kaitorete Site 3 (weeded annually)

The pattern seen here is similar to that at site 1, with no noticeable decline in the marram. (Table 46)

Table 46. Changes in composition at weeded and unweeded plots at Kaitorete Site 3.

	1988	1989	1990
Unweeded			
Pingao	19	14	13
Marram	29	34	37
Lagurus	16	14	23
Weeded			
Pingao	14	15	11
Marram	22	29	29
Lagurus	31	30	17

Kaitorete Site 4 (weeded six monthly)

The decline in marram in the second year is similar to that at site 2 (Table 47).

Table 47. Changes in composition in weeded and unweeded plots at Kaitorete site 4.

	1988	1989	1990
Unweeded			
Pingao	14	11	10
Marram	19	25	29
Lagurus	19	17	15
Weeded			
Pingao	18	19	19
Marram	25	19	5
Lagurus	16	24	35

DISCUSSION

The six sites examined show a remarkably similar pattern of response to weeding. Between 1988 and 1989 weeding had no effect on marram. Indeed, this species frequently appeared even more vigorous the following year, probably because the sand surface was disturbed and because a large amount of dead material was removed. That marram should recover in such a fashion demonstrates its rapid growth rate and the supply of reserves stored in the remaining underground parts. Indeed it seems that such a treatment may be beneficial to the marram as it removes the large amount of dead above ground material that shades the newly emerging shoots, allowing them to grow more vigorously. A large portion of above ground dead material may be the reason that marram so readily becomes moribund at high density, long established stands frequently appear this way.

The second year of hand weeding shows major differences. In the two plots weeded only annually at Kaitorete, marram has continued to recover with the same vigour as before, but in the other plots that were weeded twice in the second year the decline in marram has been remarkable. It appears that this frequency of weeding is sufficient to change the balance between reserves created and destroyed. This does not mean that the remaining marram is unhealthy, it simply appears less vigorous.

Pingao response has so far been minimal. Weeding has not resulted in its recovery, continuation of the experiment will be necessary to determine whether this will happen.

Weeding of marram is therefore a process that needs to be undertaken frequently if it is to be successful. Infrequent weeding results in recovered vigour, and there should be no expectation that any response should be visible in the first year.

CONCLUSIONS

1. Weeding of marram is only effective if carried out frequently and continuously.
2. Failure to weed properly may be deleterious to the situation as it only rejuvenates marram growth.

GENERAL SUMMARY

These studies have revealed a great deal of the problem of how pingao and marram interact, although after only two years measurements it must be indicated that many of the results are as yet inconclusive. The studies show that marram can in certain situations not actually threaten pingao, these situations need to be understood and identified if inappropriate measures are to be avoided. In the situations where the two do interact, the most likely scenario is that marram will replace pingao, although this process may take place at different rates. In most situations this involves the deeply rooted marram depriving pingao of moisture in the upper sand layers, while it obtains moisture lower down. Competition for light may also take place where the species are more vigorous and moisture is abundant, but this appears less effective at displacing pingao. Where pingao is old and moribund the displacement process occurs extremely rapidly. In these displacement situations marram spread needs to be controlled. Hand weeding can be effective, but has risks and needs to be carried out frequently and continuously.

REFERENCES

Armon, J.W. 1974. Late quarternary shorelines near Lake Ellesmere, Canterbury, New Zealand. N.Z.J.Geol. 17: 63-73.

Belbin, L. 1989. PATN Technical Reference. CSIRO Division of Wildlife and Ecology, Canberra. 175p.

Caldwell, M.M. 1990. Water parasitism stemming from hydraulic lift: A quantitative test in the field. Israel J.Bot 39:395-402.

Clifford, H.T., Stephenson, W. 1975. An introduction to Numerical Classification. Academic press, New York.

Cockayne, L. 1911. Report on the dune areas of New Zealand, their geology, biota and reclamation. Appendix to the Journal of the New Zealand House of Representatives C13:1-76. Government Printer, Wellington.

Esler, A.E. 1978. Botany of the Manawatu District, New Zealand. N.Z. Government Printer, Wellington.

Johnson, P.N. 1991. The sand dune and beach vegetation inventory of New Zealand. II. South and Stewart Island. DSIR Land Resources Scientific Report No 16. DSIR Land Resources, Christchurch.

Kirk, R.M. 1969. Beach erosion and coastal development in the Canterbury Bight. N.Z.Geog. 25: 23-35.

Molloy, B.P.J., Partridge, T.R., Thomas, W.P. 1991. The decline of tree lupin (*Lupinus arboreus*) on Kaitorete Spit, Canterbury, New Zealand, 1984-1990. N.Z.J.Botany 29:

Palmer, J.D. 1980. The Kaitorete Dunes. Dept. of Lands and Survey, Christchurch.

Partridge, T.R. 1991. The sand dune and beach vegetation inventory of New Zealand. I. North Island. DSIR Land Resources Scientific Report No. 15. DSIR Land Resources, Christchurch.

Rice, E.L. 1984. Allelopathy. 2nd Edition. Academic Press, Orlando, Florida.

Sykes, M.T., Wilson, J.B. 1989. The effect of salinity on the growth of some New Zealand sand dune species. Acta botanica Neerlandica 38: 173-182.