

AN ABSTRACT OF THE THESIS OF

Ellen Deehan Clark for the degree of Master of Science in

General Science presented on 6 October, 1989.

Title: Aspects of the Ecology and Morphology of *Lupinus littoralis*
Dougl.

Redacted for Privacy

Abstract approved: _____

John H. Lyford, Jr.

Lupinus littoralis Dougl. had a distinct pattern of distribution, in relation to the active foredune, on a recently prograded shoreline near the mouth of the Yaquina River on the Oregon coast. Personal reconnaissance revealed that L. littoralis grew at the lee base of the active foredune (as well as inland) where less sand burial took place than on top of the foredune. The objectives of this study were to determine the following: where L. littoralis occurred in the pattern of topography and soil organic matter accumulation relative to a recently prograded shoreline; what plants were found in association with L. littoralis; the gross morphology of L. littoralis; and whether the subterranean morphology of L. littoralis changed with distance from shore.

Transects showed L. littoralis to occur where percent soil organic matter was minimal (at the lee base of the active foredune), as well as where percent soil organic matter was slightly greater (inland on the hummocky plain and at the windward base of the inactive foredune). L. littoralis grew in two plant communities: the

foredune community, and the hummocky plain community. The distribution of L. littoralis was similar to that of Fragaria chiloensis (L.) Duch.

L. littoralis was discovered to be nonclonal. Multiple underground stems (each of which supported a cluster of leafy, trailing stems at the sand/soil surface) were connected to a single taproot. Two different subterranean stem morphologies appeared to correspond to relative amounts of sand burial on the research site. Plants growing at the lee base of the active foredune had more and longer underground stems, as well as thicker and deeper root crowns, than plants growing in the stable sand/soil at the windward base of the inactive foredune.

Aspects of the Ecology and Morphology of
Lupinus littoralis Dougl.

by

Ellen Deehan Clark

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed 6 October, 1989

Commencement June 1990

APPROVED:

Redacted for Privacy

~~Professor of Biology~~ (General Science) in charge of major

Redacted for Privacy

Chair of Department of General Science

Redacted for Privacy

Dean of Graduate School

Date thesis is presented 6 October, 1989

Ellen Deehan Clark

DEDICATION

To the Lupine Banquet of 1918,

Hamburg, Germany.

(Sator 1983)

ACKNOWLEDGEMENTS

In addition to providing a teaching assistantship, the Department of General Science contributed funds to this research. These funds covered photography supplies, histological chemicals, and laboratory costs for the final stages of soil analysis.

Much gratitude goes to my major professor, Dr. Jack Lyford, for his consistent encouragement and clarity of perception.

Many thanks to David B. Deehan Clark for his hard work, and patience, as my scientific technician ("donkey") and ^{co-parenting} life partner.

Numerous other people have contributed to this thesis through their encouragement, consultation, time, and expertise. I thank the following people: Dr. Mary E. Kentula, committee member (sand dune ecology); Dr. Patricia Muir, committee member (plant ecology); David Felstul (aerial photographs); Stephanie Gwin (mapping techniques); Keith King (photography techniques); Dr. Bruce McCune (data summary); Dr. Fred Rickson (anatomy); Betty Rullman (soil analysis); Dr. Donald Zobel (subterranean morphology); my family (believing in me); General Science graduate students (science and humor); and the General Science Department office staff (everything).

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1. Seashore lupine, <u>Lupinus littoralis</u> Dougl. (a) Foliage, inflorescences, and fruits. (b) Habit of <u>L. littoralis</u> .	4
2. Early aerial photographs of deflation plain south of South Jetty. (a) 1939. (b) 1958.	8
3. Aerial photographs of research area before and after extension of South Jetty. (a) 1965. (b) 1973.	9
4. Aerial photograph of research site in front of deflation plain	10
5. View of hummocky plain looking southeast from young foredune	12
6. Topography of research site with landform types identified	14
7. Map of research site showing Transects 6, 9, and 12 used for soil sampling and elevation measurements	16
8. Map of research site showing Transects 1 - 20 used for community vegetation sampling	18
9. Map of research site showing Transects A and B used for morphology sampling of <u>Lupinus littoralis</u> Dougl.	21
10. Elevations in research site, relative to the lowest point measured. (a) Transect 12. (b) Transect 9. (c) Transect 6.	24
11. Typical morphology of mature <u>Lupinus littoralis</u> Dougl. summarized from over 100 samples of mature plants at research site	30
12. Correlations and scatterplots between morphological measurements of <u>Lupinus littoralis</u> Dougl. (a) Length of underground stem and depth to root crown. (b) Number of underground stems and diameter to root crown.	33
13. Cross-sections of root of <u>Lupinus littoralis</u> Dougl. (a) Young root. (b) Mature root.	35
14. Relationship of species composition to topography along Transects 1-10	39

LIST OF FIGURES (continued)

<u>Figure</u>	<u>Page</u>
15. Comparison of subterranean morphology of <u>Lupinus littoralis</u> Dougl. relative to proximity of plants to foredune. (a) Relative position of Transects A and B. (b) Underground stem morphologies averaged for Transects A and B.	46

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1. Total carbon in sand/soil as determined by LECO dry combustion method	25
2. Means of percent cover values within m ² quadrats by landform type for Transects 1-10	26
3. Morphometrics and comparisons of <u>Lupinus littoralis</u> Dougl. at two locations on research site	32
4. Characteristics of environment and <u>Lupinus littoralis</u> Dougl. in two locations on research site	47

LIST OF APPENDIX TABLES

<u>Appendix</u>	<u>Page</u>
I. Record of construction of North and South Jetties at Yaquina Bay, Newport, Oregon	56
II. Means of percent cover values (one standard error in parentheses) within m ² quadrats by landform type for Transects 1-10.	57
III. List of plant species at research site.	59
IV. Estimated phenology of <u>Lupinus littoralis</u> Dougl. at research site, based on observations from June 1987 to June 1989.	61

TABLE OF CONTENTS

INTRODUCTION	1
STUDY AREA	7
METHODS	13
Relationship of Seashore Lupine to Topography and Soil	15
Plants Associated with Seashore Lupine	15
Gross Morphology of Seashore Lupine	17
Differences in Subterranean Morphology of Seashore Lupine	20
RESULTS	23
Relationship of Seashore Lupine to Topography and Soil	23
Plants Associated with Seashore Lupine	23
Gross Morphology of Seashore Lupine	28
Differences in Subterranean Morphology of Seashore Lupine	31
DISCUSSION	36
Relationship of Seashore Lupine to Topography and Soil	36
Plants Associated with Seashore Lupine	38
Gross Morphology of Seashore Lupine	43
Differences in Subterranean Morphology of Seashore Lupine	45
CONCLUSIONS	52
LITERATURE CITED	54
APPENDICES	56

ASPECTS OF THE ECOLOGY AND MORPHOLOGY OF
LUPINUS LITTORALIS DOUGL.

INTRODUCTION

Seashore Lupine, Lupinus littoralis Dougl. (nomenclature follows Hitchcock et al. 1984) had a distinct pattern of distribution in relation to the active foredune on a recently prograded shoreline. Personal reconnaissance revealed that L. littoralis grew at the lee base the active foredune, as well as inland, where there was little sand burial. Because L. littoralis had previously been described as clonal by Kumler (1969), its restriction to areas of minimal sand burial seemed unusual. Other clonal sand dune legumes, such as beach pea (Lathyrus japonicus Willd.), thrived on the upper lee side of the foredune where burial by sand was more common.

Sand dune plant species play an active role in the establishment and development of sand dunes (Cooper 1958). In addition to accumulating sand which builds sand dunes, sand dune plants stabilize sand behind the foredune, building soil and allowing other species to invade and grow. Distribution of sand dune species in relation to the shoreline is influenced by the physical components of wind, saltspray, and sand deposition. These physical factors decrease in intensity as one moves inland from shore (Boyce 1954, Byrd 1950, Barbour et al. 1985).

Most studies of Oregon sand dune communities have been conducted either on deflation plains, or on disturbed sand dune systems where storm erosion has created patches of disturbance among the dunes

(Boyce 1954, Byrd 1950, Cooper 1958, Kentula 1973, Kumler 1963 and 1969, Wiedemann 1966). When stabilizing vegetation is not present, or has been killed by fire, erosion, or sand burial, dry sand is free to blow away, leaving wet sand at the water table exposed. This process is called deflation. The wet sand provides a moist seedbed for subsequent species (Wiedemann 1966).

Succession can be described as a biologically controlled process (Barbour et al. 1980); however, in sand dune ecosystems, physical factors play a large role. In deflation plains of sand dune complexes, succession begins as dry sand collects around herbaceous vegetation rooted in the moist sand. In time, these discrete hummocks accumulate more sand and connect to form large areas dominated by shrubs and trees. On non-deflated sand dunes, the course of succession has been inferred through studies of the zones (bands) of vegetation that lie parallel to shore (Kumler 1969). The strand occurs along the shore, and consists of the beach and foredune communities (Barbour et al. 1985). Inland from the strand, a herbaceous plant community grows.

Physical factors influencing species composition in non-deflated sand dune areas dramatically change with distance from shoreline. Plants of the beach community grow in a harsh environment washed by storm waves. Above storm line, a foredune is created by beach grasses collecting windblown sand. European beach grass, Ammophila arenaria (L.) Link, introduced to the west coast in 1896, thrives with sand burial, sending its rhizomes up into the newly deposited sand (Wiedemann et al. 1969). This vigorous adventitious growth results in foredunes higher than those previously created by the less vigorous

endemic American beach grass, Elymus mollis Trin. On the lee side of the foredune, the windforce decreases, and plants tolerant of xeric conditions and minimal sand burial grow here (Wiedemann et al. 1969, Barbour et al. 1985). Inland from the base of the foredune, a herbaceous plant community develops. This community thrives in an environment of less wind, saltspray, and sand burial than on the foredune. In time, soil organic material builds up, allowing less xeric species to invade and thrive. Eventually the early herbs and grasses are shaded out by taller shrubs and trees (Wiedemann et al. 1969).

Plant species of foredunes must tolerate more water stress, wind, saltspray, sandblast, and sand burial than do species restricted to inland habitats (Kumler 1963). Because of broad ecological tolerances, many of these foredune plants also survive and compete in the more stable sand environments inland from the foredune. Plasticity of morphology and anatomy allow for survival in more than one habitat (Seliskar 1985).

Lupinus littoralis is an endemic legume of sand dunes and deflation plains from northern California to British Columbia (Hitchcock et al. 1984). This perennial herb has purple flowers and trailing stems that form prostrate mats (Fig. 1). The above ground portion of the plant dies back in winter (Schwendiman 1977). Its stems, leaves, and sepals are covered by fine, white, appressed hairs. Pubescence is a common characteristic of plants inhabiting xeric habitats with high light intensities (Barbour et al. 1985).

L. littoralis has been encountered in ecological studies of Oregon coastal dunes, though it has not been studied specifically. In



(a)



(b)

Figure 1. Seashore lupine, Lupinus littoralis Dougl. (a) Foliage, inflorescences, and fruits. (b) Habit of L. littoralis shown with Ammophila arenaria (L.) Link and Elymus mollis Trin.

sand dune systems observed by Kumler (1969), L. littoralis was present on and to the lee of dunes in the pioneer and herbaceous communities. In deflation plains studied by Wiedemann (1966), L. littoralis was found in the dry meadow community which exists at an average distance of 253 cm above mean water table (Kentula 1973), as well as in the meadow community. The communities in which L. littoralis occurs represent the early stages of sand dune and deflation plain succession (Kumler 1969, Wiedemann 1966).

Plants living on the foredune tolerate burial and tend to be clonal (Kumler 1969). Kumler (1969, p.703) described the morphology of L. littoralis as clonal, stating, "There were numerous seedlings from [L. littoralis], but there was much reproduction by vegetative means." However, Wiedemann (1966) noted that L. littoralis had limited tolerance to sand burial, which is unusual for clonal sand dune species. Therefore, questions remain as to the overall morphological strategy of L. littoralis since it was described as clonal, yet it did not tolerate abundant sand burial. In addition, the distribution of L. littoralis in a sand dune area where sand burial is a major factor, and not sand deflation, has not been documented. This study attempted to address these issues.

A young sand dune system, located at the mouth of the Yaquina River, Oregon, was formed after the southern jetty was extended in 1972, and sand was deposited south of the jetty. This area of sand accretion provided an opportunity to study the ecology of L. littoralis in sand dune communities unaffected, as yet, by sand deflation, where sand burial during foredune building was a dominant abiotic factor. During a reconnaissance trip, L. littoralis was noted

to have a distinct pattern of distribution in relation to the active foredune on this prograded shoreline. L. littoralis grew at the lee base of the active foredune (as well as inland) where less sand burial took place than on top of the active foredune. Research was undertaken to describe and explain the distribution pattern.

This study examined a prograded area in an early stage of succession where sand deflation was not taking place, and documented the distribution and morphology of L. littoralis. The specific objectives were to answer the following questions:

Relationship to Environment of Active Sand Burial

- * Where does L. littoralis occur in the pattern of topography and soil organic matter accumulation relative to a recently prograded shoreline?
- * What plants are found in association with L. littoralis?

Morphology

- * What is the gross morphology of L. littoralis?
- * Does the subterranean morphology of L. littoralis change with distance from shore?

STUDY AREA

The study area was located at the mouth of the Yaquina River in Lincoln County, Oregon ($44^{\circ}37'N$, $124^{\circ}4'W$). History of the site was linked to jetty construction. To increase harbor use, rock jetties were constructed north and south of the entrance to the estuary over a period of time beginning in 1880 (Appendix I). The jetties were constructed in stages, with sand deposition occurring south of the southern jetty.

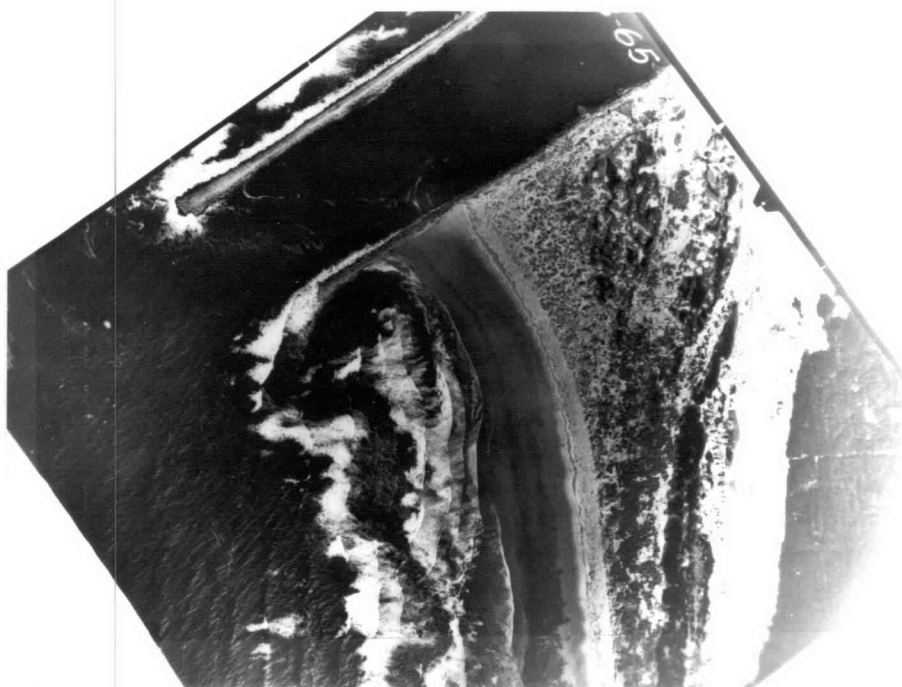
The U.S. Army Corps of Engineers took aerial photographs of the mouth of the Yaquina River from 1939 to 1985. For this study, these photographs were interpreted, enlarged to similar scales, and cropped to show changes in the beach and dune area south of the mouth of the Yaquina River (Figs. 2, 3, and 4).

The earliest aerial photograph of the jetties at the mouth of the Yaquina River was taken by the U.S. Army Corps of Engineers in 1939 (Fig. 2a). A large expanse of sand lay south of the South Jetty. By 1958 (Fig. 2b), this sandy plain was deflated and colonized by herbaceous and woody vegetation. A foredune established by Ammophila arenaria bordered the deflation plain (Wiedemann 1966).

In 1965 (Fig. 3a), the foredune had increased in size and was associated with a row of embryo dunes, small hummocks that form on the beach as sand collects around driftwood or rooted vegetation. Because they are close to the shoreline, embryo dunes wash away periodically during storms unless the shoreline progrades (Wiedemann 1966). In 1965 and 1966, the North Jetty was extended; consequently, some sand may have been deposited in front of the embryo dunes, stabilizing the



(a)



(b)

Figure 2. Early aerial photographs of deflation plain south of South Jetty. (a) In 1939, vegetation is sparse. (b) In 1958, vegetation dominates deflation plain. Scale approximately 1:34,000.



(a)



(b)

Figure 3. Aerial photographs of research area before and after extension of South Jetty. (a) In 1965, before research site was deposited, deflation plain is bordered by large foredune that runs along beach. (b) In 1973, South Jetty was extended. Sand collected south of jetty, and in front of old foredune, forming research site. Scale approximately 1:34,000.



Figure 4. Aerial photograph (1985) of research site (elliptical area with darker vegetation) in front of deflation plain (lighter colored vegetation). Note three trails running across deflation plain and into research area. Scale approximately 1:34,000.

vegetation.

In 1972, the South Jetty was extended 549 m (Hanson, U.S. Army Corps of Engineers, pers. comm.). Sand, transported north by the littoral current, was blocked by the jetty and collected south of the jetty (U.S. Army Corps of Engineers 1985). This shoreline accretion formed the research area in front of the foredune (Fig. 3b).

By 1985 (Fig. 4) the research area was a vegetated sand dune ecosystem composed of young embryo dunes, a young foredune, and a series of hummocks leading inland to the old embryo dunes and old foredune. The newly prograded shoreline, comprised of the young embryo dunes, young foredune, and series of hummocks, was fifteen years old when this study began in 1987.

The research area was bordered on the west by a young foredune and on the east by an old foredune. These two foredunes were connected at the southern end of the site and diverged as they ran north. Consequently, the research area was somewhat triangular. The northern part of the prograded area was a complex of dissected dunes, hummocks, and deflated patches. South of the middle trail a non - deflated hummocky plain lay in between the young and old foredune (Fig. 5).



Figure 5. View of hummocky plain looking southeast from young foredune (old foredune in background).

METHODS

The young and old portions of the research area were mapped using paces, meter tape, and compass. Landforms, forming zones in relation to the shoreline (Fig. 6), were identified as follows:

1. beach
2. embryo dune
3. windward slope of young foredune
4. top of young foredune
5. lee slope of young foredune
6. lee base of young foredune
7. hummocky plain
8. windward base of old foredune
9. windward slope of old foredune
10. deflation plain

Two types of transects were used on the research site. Twenty transects ran from the beach across the research site to the base of the old foredune, and were used to estimate percent cover of Lupinus littoralis and its associates in m² quadrats. Three of these transects (Transects 6, 9, and 12) were also used for sand/soil collection, elevation measurements, and L. littoralis morphology reconnaissance. Two transects of another type were laid south to north along the bases of the young and old foredunes to contribute information about differences in the subterranean morphology of L. littoralis.

Details of the methods are arranged by subheadings that refer to the questions they were used to answer.

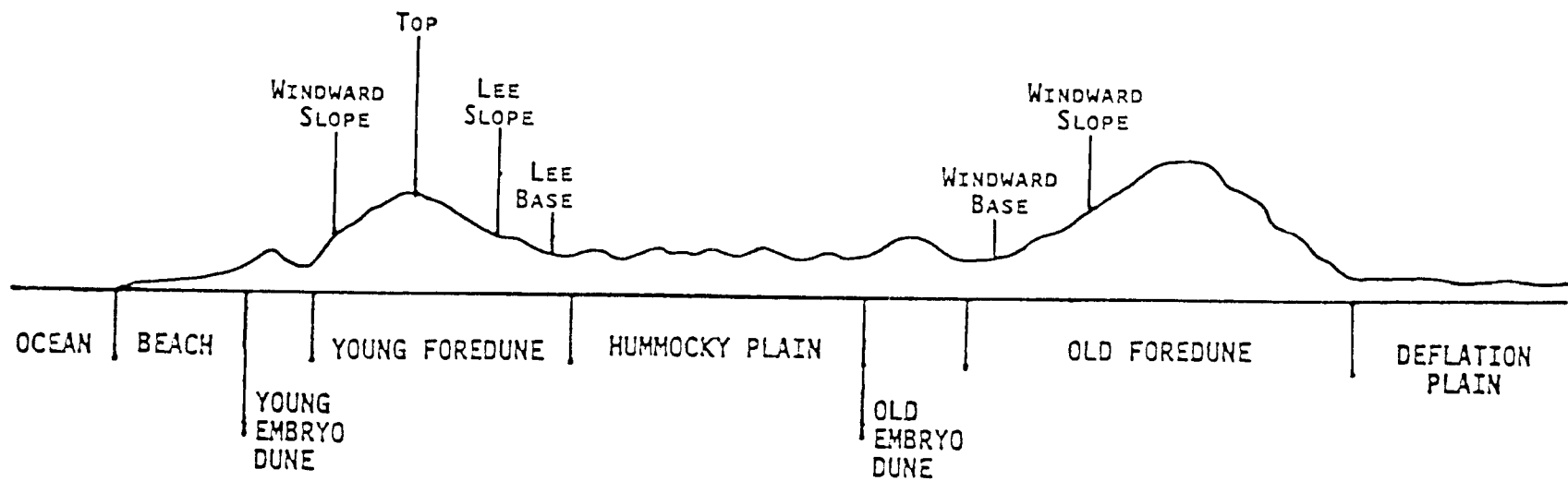


Figure 6. Topography of research site (view looking north; composite of Transects 6, 9, and 12) with landform types identified. Ratio of vertical scale to horizontal scale 2:1.

Relationship of Seashore Lupine to Topography and Soil

Relative elevations along Transects 6, 9, and 12 were determined using an engineer's level and stadia rod (Sherman et al. 1988). In May 1988, two holes were excavated to measure depth to water table on the hummocky plain near the old embryo dunes.

To measure indications of relative soil development across the research site at various landforms, the sand/soil in the research area was collected in July 1987 using a soil can along Transects 6, 9, and 12, running from shore inland across the hummocky plain (Fig. 7). Samples were collected at one depth (between the surface and 15 cm) at nine stations along each transect. At four of these stations, samples were collected at two depths (between the surface and 15 cm, and just below 15 cm). Station locations were subjectively chosen to measure the soil development gradient with distance from shoreline. Sand/soil samples were air dried after live roots, styrofoam, and chunks of wood were removed. In preparation for carbon determination, the samples were ground, sifted through a 0.25 mm mesh, oven dried at 105 C for 15 minutes, wrapped in pure tin (Sn) foil, and weighed. The Oregon State University Oceanography Lab measured total carbon by the dry combustion method using a LECO (Laboratory Equipment Company) carbon analyzer (Nelson and Sommers 1982).

Plants Associated With Seashore Lupine

Twenty transects were established west to east across the research site in June 1987 to document the relationship of L. littoralis and vegetation communities to the topography relative to

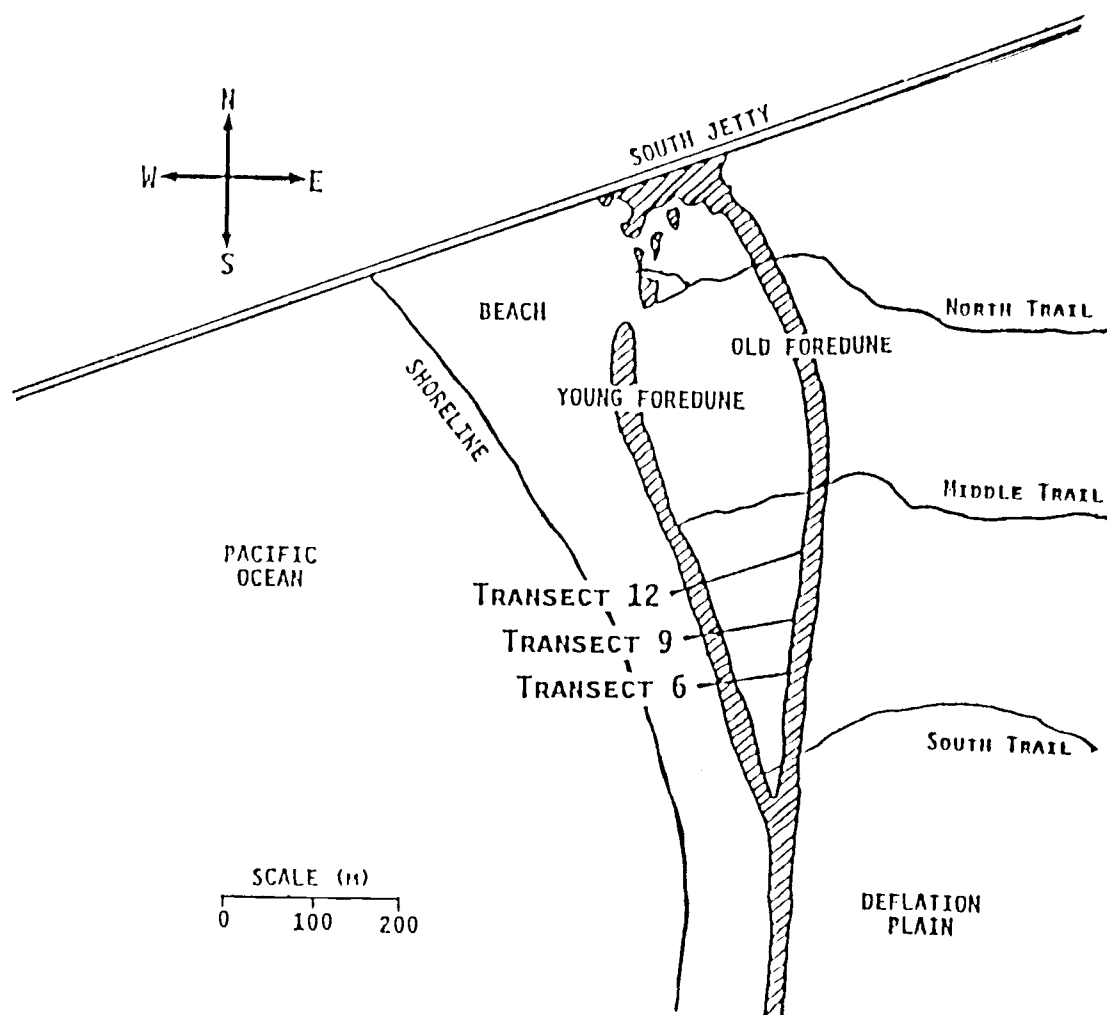


Figure 7. Map of research site showing Transects 6, 9, and 12 used for soil sampling and elevation measurements.

the shoreline (Fig. 8). Transects were 20 meters apart, and the southern ten (Transects 1 - 10) extended from the driftwood line on the beach, inland across the young foredune and hummocks, to the base of the old foredune. Transects 11 - 20 ran only half way across the hummocky plain. A 1-m² quadrat was placed every five meters along each transect. A total of 465 quadrats were sampled. For each quadrat, percent cover of each species, exposed sand/soil, leaf litter, and driftwood was estimated. Estimations were in actual percentages between 1% and 10%, and between 90% and 100%; whereas, estimations were made at intervals of 5% between 10% and 90% (e.g., 15%, 20%, 25%, ...). The landform type at each quadrat was identified.

Data from Transects 1 - 10 were summarized using direct gradient analysis, where percent cover of each species was averaged within each landform type (McCune, Oregon State University, pers. comm.). A portion of Transects 11 - 20 crossed an area of human disturbance, so data gathered from these transects were only used to validate trends seen in Transects 1 - 10, and to supplement the species list, which includes species found in transects as well as species observed casually on the site.

Gross Morphology of Seashore Lupine

During the course of this study, over 150 mature L. littoralis plants, and over 500 seedlings, were excavated from various areas on the research site (described in this section) to observe and describe their gross morphology. Mature plants were distinguished from seedlings by their multiple underground stems and lack of cotyledons.

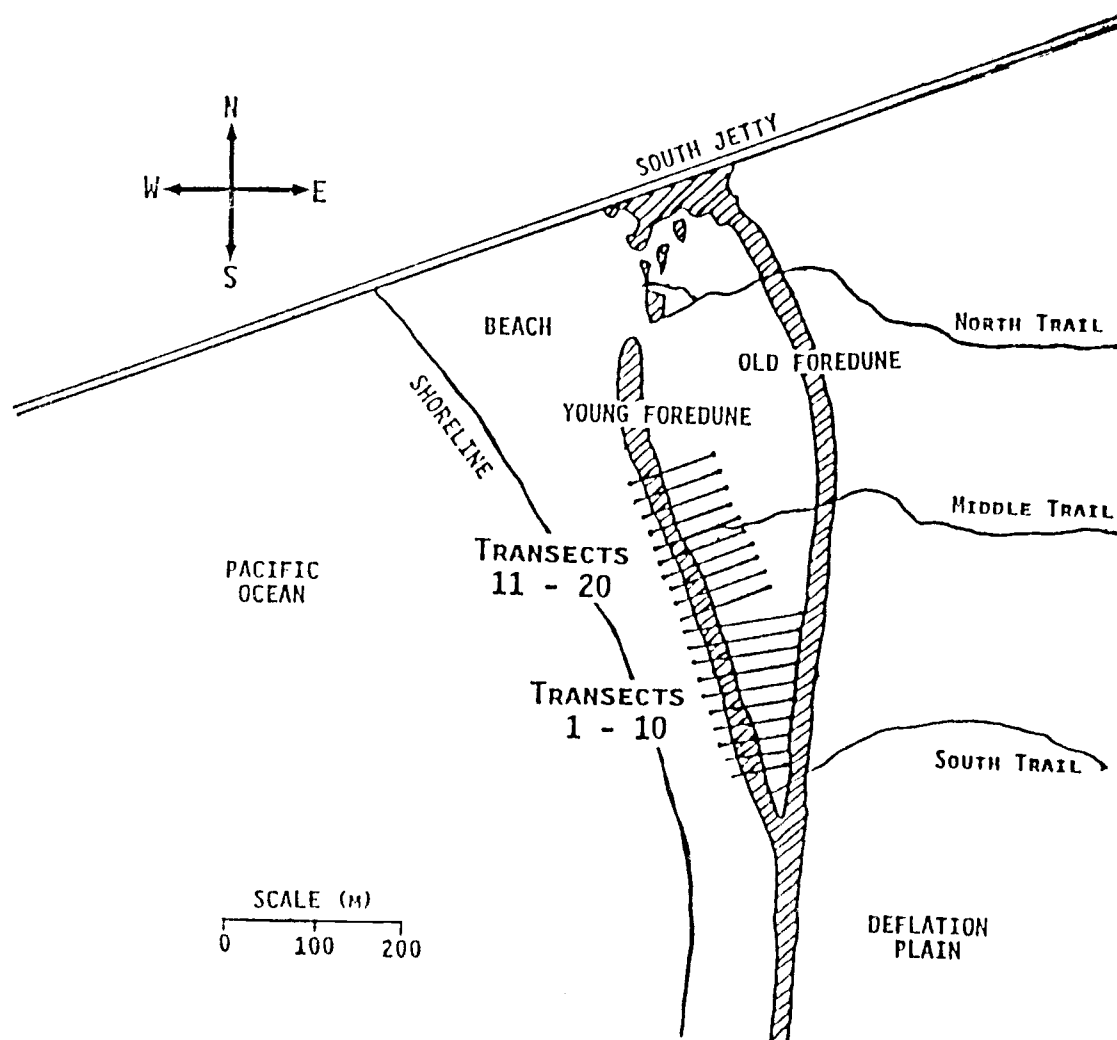


Figure 8. Map of research site showing Transects 1 - 20 used for community vegetation sampling.

L. littoralis seedlings were single stemmed and often had persistent cotyledons. Phenological observations were recorded at irregular intervals between June 1987 and June 1989 at the research site.

Mature L. littoralis plants were collected at six stations along each transect (corresponding to the soil sample stations along Transects 6, 9, and 12). Twenty-eight plants were measured for underground stem length and number, and for root crown diameter and depth. In August 1987, 12 additional mature plants were excavated; their subterranean stem morphology was measured, photographed, and described.

The underground stems of six plants were tagged just below the sand/soil surface in October 1987, and checked in April 1988, to test for subterranean winter dieback. Eight additional plants were excavated in the spring of 1988 to check for vegetative bud locations.

To avoid extensive destruction to the surrounding environment, roots of some mature plants were not excavated in their entirety, if their roots were not easily extracted. This decision was made due to the destruction involved in excavating a plant in July 1987. At that time, a large L. littoralis plant was partially excavated in an attempt to collect the entire root. At a depth of 1.3 m, final extraction was impeded by two buried logs. The excavated area (1.5 m in diameter) was easily observed 20 months after the hole was filled in.

Since clonal plant species form adventitious roots, and none were observed in the field, the ability of L. littoralis to produce adventitious roots was tested by severing the underground stems of 16 L. littoralis plants in April 1988, and placing the plant cuttings in

pots filled with vermiculite. Rooting hormone (synthetic auxin) was applied to the stemcut of half of the cuttings. The other cuttings were left untreated. All cuttings remained in a greenhouse for 1.5 months, and were checked periodically for adventitious root growth.

Differences in Subterranean Morphology of Seashore Lupine

To test a possible relationship between subterranean stem morphology and areas of sand deposition, two transects were laid south to north in June and July of 1988 (Fig. 9). Transect A (70 m) ran along the lee base of the young foredune where yearly sand deposition was still taking place. Transect B (50 m) ran 15 m west of the windward base of the old foredune where sand deposition was not evident. A 1-m² quadrat was placed every ten meters along each transect. If no L. littoralis was in the quadrat, a five meter sweep, starting east from the transect point, was made in order to find the closest individual. This plant then became the southwest corner of the new quadrat.

At each quadrat, all L. littoralis plants were excavated. A total of 62 mature plants with underground branches, and over 500 seedlings were sampled in this manner. Underground stems branching off the taproot of each mature plant were counted. Measurements were taken of depth to root crown, root crown diameter and underground stem lengths using a metric ruler. These morphometric data were averaged within each transect, and analyzed using independent sample t-tests. Correlations among morphology measurements were evaluated.

In case morphometric differences were due to plant ages, cross-sections were prepared from the taproots of three L. littoralis plants

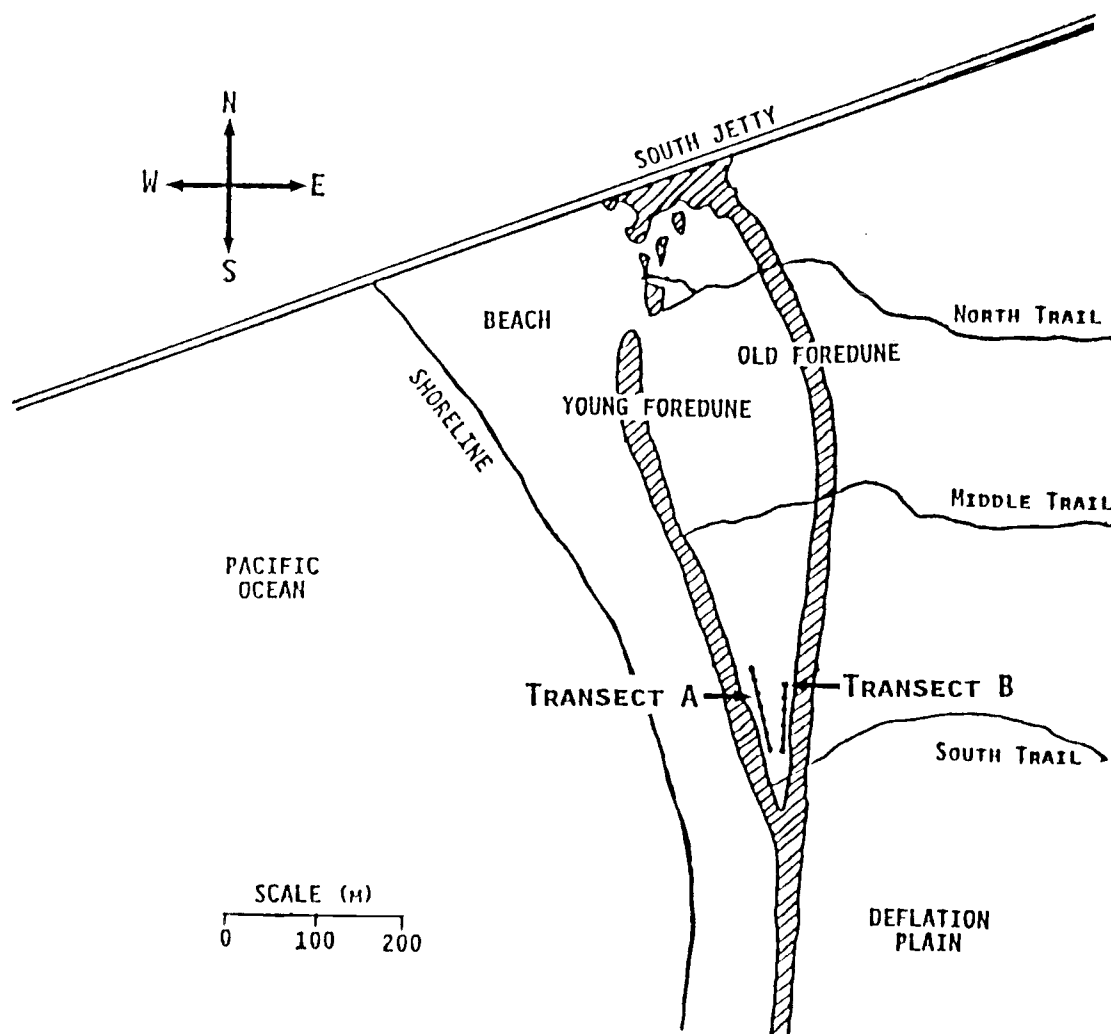


Figure 9. Map of research site showing Transects A and B used for morphology sampling of Lupinus littoralis Dougl.

collected in February 1988 with root diameters of: 4 mm, 7 mm, and 12 mm. Roots were used for aging since field observations indicated that individual underground stems did not survive the entire life of the plant. Root material was dehydrated in alcohol and embedded in paraffin (Jensen 1962). Tissue sections were mounted and stained using saffranin and fast green (Johansen 1940). Root anatomy and xylem patterns were observed and photographed under a microscope. Iodine was applied to freshly cut roots in the field to test for starch storage.

RESULTS

Results are arranged by subheadings that refer to the questions posed in the introduction concerning the ecology and morphology of Lupinus littoralis.

Relationship of Seashore Lupine to Topography and Soil

Elevations on the research site relative to the lowest point measured on the hummocky plain are shown in Figure 10. The young foredune was 4.8 m high, while the old foredune was estimated to be 8 m high. Hummocky plain elevations ranged from 0.0 m to 1.7 m. The hummocky plain was a jumble of hummocks with no particular pattern or slope. The old embryo dunes tended to be higher than the rest of the hummocky plain with an average elevation of 1.8 m. The lee base of the young foredune (average elevation of 1.0 m), as well as the windward base of the old foredune (average elevation of 1.0 m), tended to be higher than most of the hummocky plain. The water table was not reached, despite excavations to depths of 1.04 m in low areas of the hummocky plain.

The total carbon in the sand/soil increased from 0.040% to 0.350% with distance inland from the beach across the hummocky plain (Table 1).

Plants Associated With Seashore Lupine

Average percent cover for each plant species by landform type is presented in Table 2 and Appendix II. A complete species list is in Appendix III. Plant species appeared to separate into two distinct

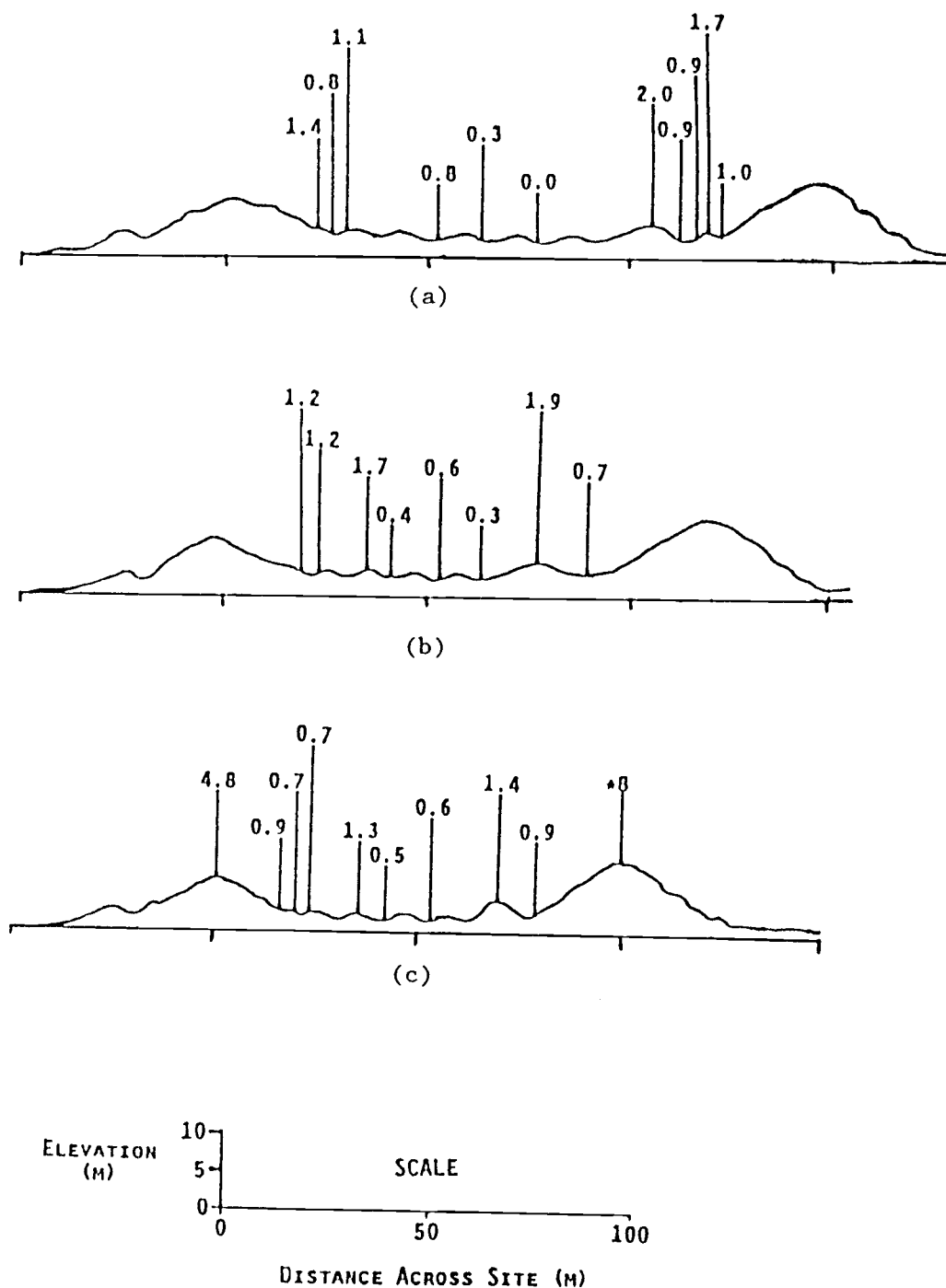
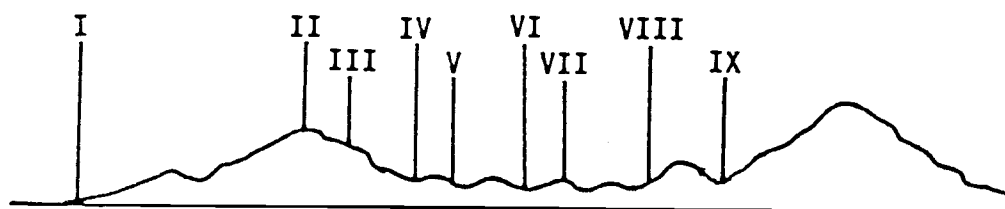


Figure 10. Elevations (m) in research site, relative to the lowest point measured. Measurements taken in feet and converted to meters by multiplying by 0.03.
 (a) Transect 12. (b) Transect 9. (c) Transect 6.
 * Estimated elevation of old foredune.

Table 1. Total carbon (%) in sand/soil as determined by LECO dry combustion method. Values are the mean of three transects ± 1 standard error. Relative positions of samples along transects described in table are illustrated in diagram below (composite of Transects 6, 9, and 12).



SAMPLE LOCATION AND DEPTH		TOTAL CARBON IN SAND/SOIL (%)
BEACH		
I.	0-15 cm	0.040 ± 0.003
YOUNG FOREDUNE		
Top		
II.	0-15 cm	0.036 ± 0.001
	>15 cm	0.037 ± 0.002
Lee Side		
III.	0-15 cm	0.041 ± 0.002
	>15 cm	0.045 ± 0.002
Lee Base		
IV.	0-15 cm	0.051 ± 0.013
	>15 cm	0.047 ± 0.008
HUMMOCKY PLAIN		
V.	0-15 cm	0.078 ± 0.034
VI.	0-15 cm	0.197 ± 0.033
VII.	0-15 cm	0.214 ± 0.062
VIII.	0-15 cm	0.350 ± 0.030
OLD FOREDUNE		
Windward Base		
IX.	0-15 cm	0.320 ± 0.087
	>15 cm	0.177 ± 0.018

Table 2. Means of percent cover values within m² quadrats by landform type for Transects 1-10. Plant species are organized as to strand and generalist species, or hummocky plain species. Dash indicates trace or not present. (Means with standard errors in Appendix II.)

Table 2.

			LANDFORM		TYPES				
	BEACH	EMBRYO DUNE	YOUNG FOREDUNE				HUMMOCKY PLAIN	OLD FOREDUNE	
			WINDWARD SLOPE	TOP	LEE SLOPE	LEE BASE		WINDWARD BASE	WINDWARD SLOPE
Exposed Sand/Soil	97.9	65.0	40.7	32.8	33.1	16.2	6.7	4.4	5.0
Driftwood	0.4	--	--	--	--	--	0.4	--	0.3
Leaf Litter	1.3	--	0.1	--	--	0.3	3.5	4.7	4.4
Strand and Generalist Species:									
<u>Ammophila arenaria</u>	0.1	33.3	56.6	62.8	45.0	50.5	60.6	64.7	57.7
<u>Cakile</u> spp.	0.4	0.2	0.1	--	--	--	--	--	--
<u>Elymus mollis</u>	--	2.5	5.4	7.1	10.2	20.9	19.4	5.1	4.7
<u>Lathyrus japonicus</u>	--	--	--	3.6	20.8	33.2	8.0	1.1	0.3
<u>Lathyrus littoralis</u>	--	--	--	--	0.4	--	0.1	--	--
Hummocky Plain Species:									
<u>Aira praecox</u>	--	--	--	--	--	0.7	10.9	15.6	27.1
<u>Anaphalis margaritacea</u>	--	--	--	--	--	1.7	5.1	7.9	3.2
<u>Anthoxanthum odoratum</u>	--	--	--	--	--	--	0.9	2.8	--
<u>Cerastium arvense</u>	--	--	--	--	--	--	0.2	0.4	1.3
<u>Ceratodon purpureus</u>	--	--	--	--	--	--	--	--	1.2
<u>Gladonia</u> sp.	--	--	--	--	--	--	--	--	0.1
<u>Convolvulus soldanella</u>	--	--	--	--	--	--	0.8	--	--
<u>Festuca</u> sp.	--	--	--	--	--	--	--	0.7	--
<u>Fragaria chiloensis</u>	--	--	--	--	--	1.2	7.6	16.7	14.0
<u>Glehnia leiocarpa</u>	--	--	--	--	--	--	0.2	--	--
<u>Gnaphalium purpureum</u>	--	--	--	--	--	--	0.5	0.1	--
<u>Hypochaeris radicata</u>	--	--	--	--	--	0.2	11.2	11.3	5.3
* <u>Lupinus littoralis</u>	--	--	--	--	--	7.6	14.8	25.5	8.7
<u>Poa</u> sp.	--	--	--	--	--	--	0.2	--	--
<u>Polypodium scolieri</u>	--	--	--	--	--	--	--	--	0.5
<u>Rumex</u> sp.	--	--	--	--	--	--	0.2	2.1	1.4
<u>Tanacetum camphoratum</u>	--	--	--	--	--	--	--	--	0.1
<u>Vicia gigantea</u>	--	--	--	--	--	--	1.6	0.8	0.3

groups: those able to live on the beach strand and young foredune, as well as inland (generalist species); and those only able to live inland from the young foredune (hummocky plain species). Cakile edentula (Bigel.) Hook, and C. maritima Scop. were strand species, restricted to the beach and windward side of the young foredune. Ammophila arenaria existed everywhere in relatively high amounts.

L. littoralis occurred at the lee base of the young foredune, as well as inland on the hummocky plain. This species was present where the average amount of exposed sand/soil ranged from 4% to 16%.

Gross Morphology of Seashore Lupine

✓ Inflorescences of L. littoralis were located at the terminuses of decumbent stems. Stems without flowers tended to remain erect. Flowering and fruiting in L. littoralis occurred throughout May, June, and July (Appendix IV). Seed dispersal took place in July and August. Immature fruitpods were green and covered with fine hairs. When dry and brown, the pods abruptly split open with a popping sound and tossed small (3 mm diameter), speckled, kidney-shaped seeds. After seed dispersal, the two halves of the fruit were coiled like two separate helices.

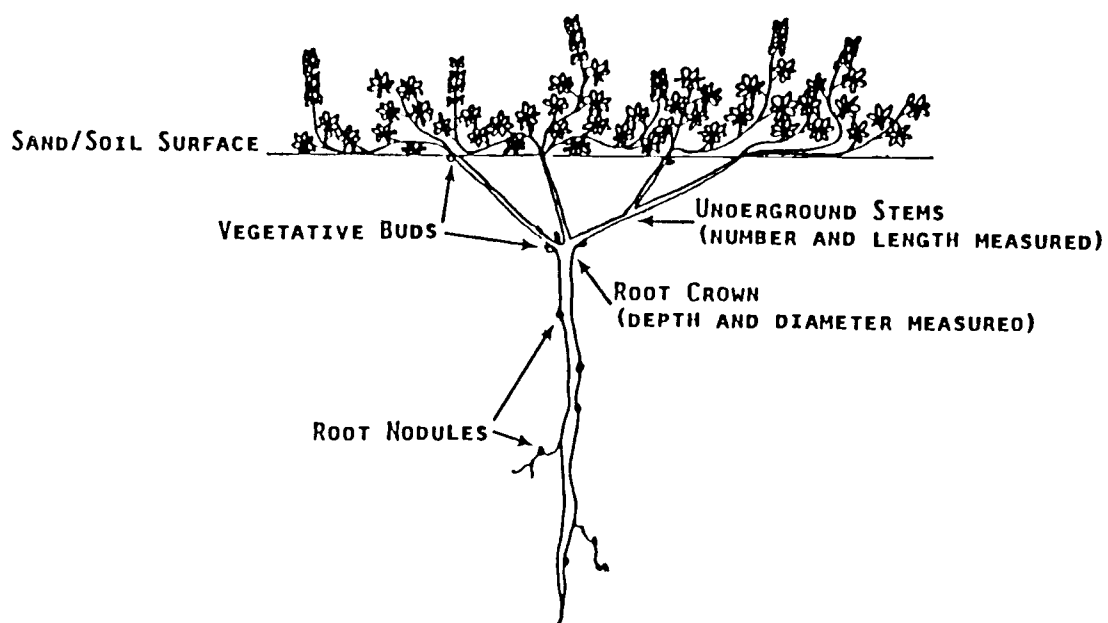
) In autumn and winter, the aboveground stems, foliage, and fruits died back to the sand/soil surface. Underground stems appeared to live one or more years, but tagging indicated that they did not usually persist for the entire life of the plant. Stems above the sand surface were distinguished from underground stems by their reddish-brown color and white appressed hairs. Underground stems were hairless and lighter brown. The yellowish taproot had a few branches

with clusters of root hairs, and tended to grow straight down into the sand/soil.)

All mature L. littoralis plants excavated at the research site had nitrogen-fixing nodules, as did the majority of the seedlings (as small as 3 cm tall). Nitrogen-fixing nodules were present on main and secondary roots, as well as on root hairs. When cut in half, smaller nodules (1-3 mm diameter) were full of red material, leghemoglobin. Large nodules (7-12 mm diameter) tended to have spots of red leghemoglobin interspersed throughout yellowish root tissue.)

Before excavation, L. littoralis appeared to be a clonal species where each genet (genetic individual) was composed of many ramets that could separate and root on their own. Each "ramet" had several trailing, leafy stems. Upon excavation, however, each "ramet" was found to be attached via an underground stem to a common taproot (Fig. 11). Because no buds or roots were present along the length of underground stems which originated from the taproot crown, each underground stem appeared to be comprised of a single internode with a node at the distal end. In early spring before leaf-out, perennating buds were found on plants, either at the root crown or just below the sand/soil surface at the distal ends of underground stems. New buds were not seen at both locations on any single individual. "Ramets" were never found separated from the main plant. No adventitious roots were seen in any of the hundreds ($n > 700$) of L. littoralis plants excavated. L. littoralis did not reproduce vegetatively in the field. It essentially was an "underground shrub" with the exposed leafy shoots being the apices of underground branches.

Although no adventitious roots were observed on L. littoralis in



TYPICAL SEASHORE LUPINE MORPHOMETRICS

NUMBER OF UNDERGROUND STEMS:	4
LENGTH OF EACH UNDERGROUND STEM:	10 CM
DEPTH OF ROOT CROWN:	8 CM
DIAMETER OF ROOT CROWN:	8 MM

Figure 11. Typical morphology of mature *Lupinus littoralis* Dougl. summarized from over 100 samples of mature plants at research site. Height of crown and length of root is estimated average, as measurements were not always possible.

the field, this species had limited ability to develop adventitious roots from cuttings. Of 16 plant cuttings placed in the greenhouse, only three cuttings produced adventitious roots in vermiculite. These three cuttings were not treated with rooting hormone.

Mature L. littoralis plants (n = 62) had 2 to 15 underground stems per taproot. Lengths of underground stems ranged from < 1 cm to 40 cm. Depth to root crown ranged from 1 cm to 25 cm. Diameter of root crowns ranged from 3 mm to 25 mm.

Differences in Subterranean Morphology of Seashore Lupine

The morphology of L. littoralis varied with respect to proximity to the young foredune. The subterranean morphologies of plants growing near the young foredune differed significantly ($p \leq 0.025$) from plants growing further inland (Table 3). Plants growing at the lee base of the young foredune had more and longer underground stems, as well as thicker and deeper root crowns, than plants growing at the windward base of the old foredune.

The length of underground stems was correlated positively with depth to root crown ($r^2 = 66\%$; Fig. 12). Number of underground stems and diameter of root crown were also positively correlated ($r^2 = 42\%$; Fig. 12). There were weak positive correlations between the following morphometrics:

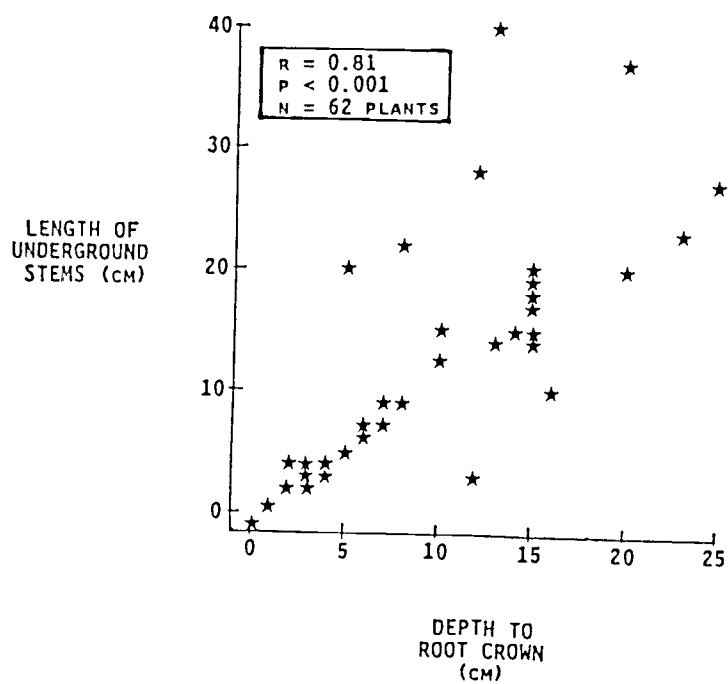
diameter of root crown and depth to root crown
($r^2 = 25\%$; $p < 0.001$),

diameter of root crown and length of underground stems
($r^2 = 16\%$; $p = 0.001$),

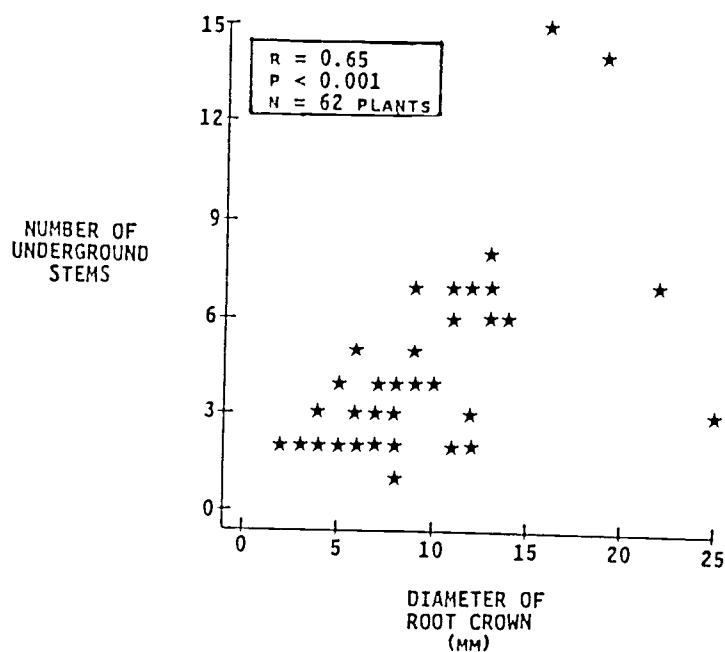
number of underground stems and depth to root crown
($r^2 = 21\%$; $p < 0.001$), and

Table 3. Morphometrics and comparisons of Lupinus littoralis Dougl. at two locations on research site. Values are averages of measures made on mature plants \pm 1 standard error.

MORPHOLOGICAL MEASUREMENTS	LEE BASE OF YOUNG FOREDUNE (n = 27)	BASE OF OLD FOREDUNE (n = 35)	P FROM T-TEST
Length of Underground Stems (cm)	17.8 \pm 1.7	3.6 \pm 0.3	< 0.0005
Depth to Root Crown from Soil Surface (cm)	12.8 \pm 1.1	3.6 \pm 0.3	< 0.0005
Diameter of Root Crown (mm)	9.6 \pm 0.9	7.1 \pm 0.7	= 0.025
Number of Underground Stems per Taproot	4.9 \pm 0.7	3.2 \pm 0.3	= 0.010



(a)

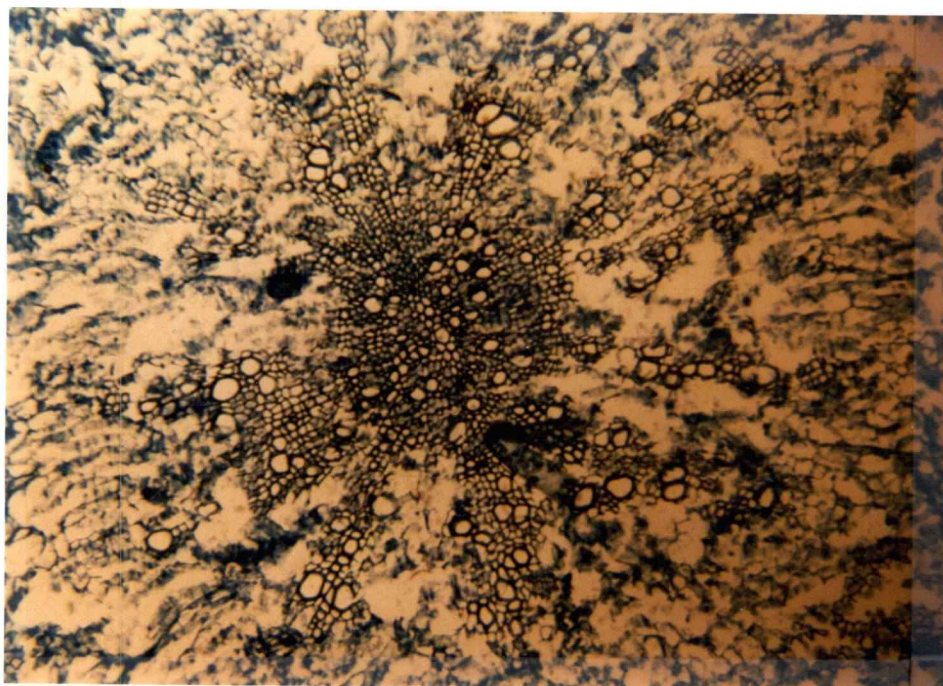


(b)

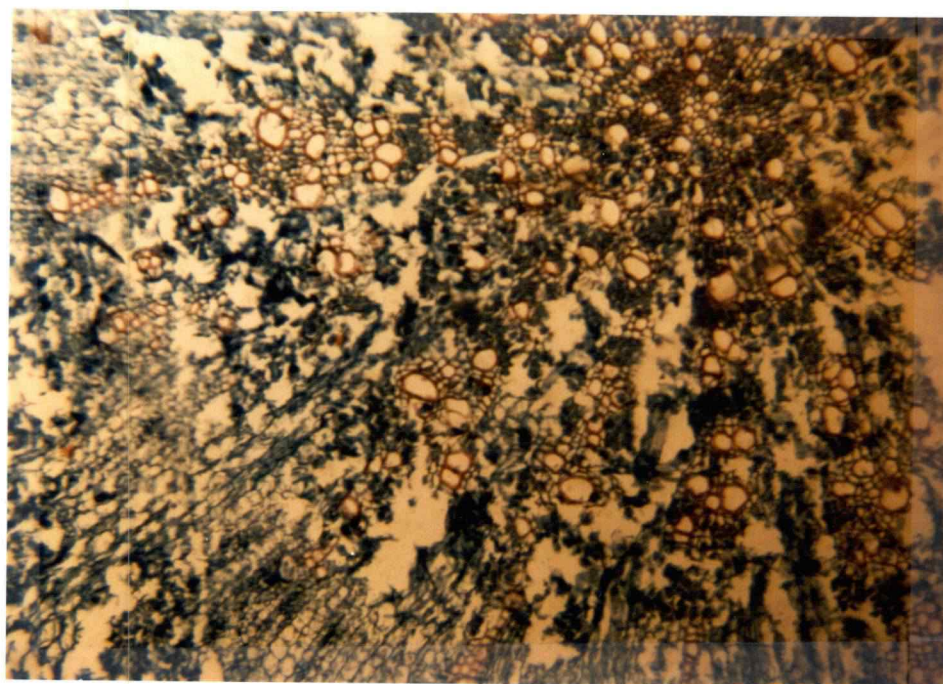
Figure 12. Correlations and scatterplots between morphological measurements of *Lupinus littoralis* Dougl. (a) Length of underground stem and depth to root crown. (b) Number of underground stems and diameter of root crown.

number of underground stems and length of underground stems
($r^2 = 15\%$; $p = 0.002$).

Cross-sections of roots of mature L. littoralis revealed the anatomy of a root with well developed storage capabilities, instead of a root that acted mainly as a support structure (Fig. 13). Iodine placed on freshly cut roots in the field turned blue-black, indicating that starch was present in the roots. Even with cell breakage during sectioning, parenchyma tissue was evident in between the arms of xylem. Annual growth increments were unclear since the xylem did not form contiguous growth rings. Various sizes of vessels formed patterns that suggested early and late wood; however, the patterns were not consistent among the xylem arms. Because vessel patterns were not easily discernable, plant ages were not determined.



(a)



(b)

Figure 13. Cross-sections of roots of Lupinus littoralis Dougl. Parenchyma tissue (green) is located in between the arms of xylem (red) radiating out from the center of the root. (a) Young root, 4 mm diameter. (b) Mature root, 7 mm diameter. Scale approximately 1 : 0.0125.

DISCUSSION

Relationship of Seashore Lupine to Topography and Soil

Wet sand was observed on top of the leaves of foredune beach grasses after winter storms, indicating that the young foredune was continuing to accumulate sand. A large portion of the windward side was unvegetated. On the lee side of the young foredune there was a reduction in sand burial, indicated by a lower percentage of exposed sand. This reduction in burial is due to the ability of beach grass canopies to reduce wind and sand turbulence and, therefore, to accumulate blown sand (Barbour et al. 1985). Lupinus littoralis grew at the lee base of the young foredune where less sand burial took place than on the top of the foredune. L. littoralis also grew on the stable sand of the hummocky plain and at the windward base of the old foredune, both places where sand deposition was not observed and the percent of exposed sand estimated at the quadrats was minimal.

Percent organic matter in soil can be calculated from total carbon values by multiplying total percent carbon by 2.0 (Nelson and Sommers 1982). Organic matter in surface sand/soil on the site was low (0.1% - 0.7%) in comparison to typical forest soils, which tend to be 2% - 5% organic matter (Brady 1984). Small amounts of organic matter indicated that the site had relatively undeveloped soils, which was expected in a young sand dune ecosystem. The amount of soil organic matter increased across the site to the base of the old foredune. In northern California, Rose (1988) also found that "organic carbon levels were low in the littoral zone and increased across the dune ecosystem".

Relatively low soil organic content on the foredune, where active sand burial took place, may have been due to additional sand diluting the organic matter already present. In addition, fewer plants were able to live in the dynamic sand conditions, so fewer decayed plant parts were available to increase soil organic matter. Relatively high organic content where sand was stable (hummocky plain, inland to base of the old foredune), may have been due to less dilution of organic material by additional sand and to the higher cover of plants. The even higher soil organic content in the older sand/soil of the windward base of the old foredune could have been caused by leaf litter blowing and collecting inland, as well as by more time for vegetation to develop the soil.

Soil water from precipitation (including fog drip) and possibly from internal dew (condensation of atmospheric moisture on sand grains at shallow depths) (Barbour et al. 1985) were probably the major sources of water for L. littoralis, because the water table appeared to be below the reach of many L. littoralis taproots during at least part of the growing season. The amount of water held in the soil (water-holding capacity) is related to percent organic matter of the soil (Brady 1984). Less water is held in coarse sand low in organic matter than in coarse sand higher in organic matter (Barbour et al 1985). Therefore, severe seasonal water stress in sand/soil low in organic matter (lee base of the young foredune) must have been common. L. littoralis grew in this xeric environment, as well as inland where the seasonal water stress was reduced by larger amounts of organic matter in the sand/soil.

In summary, L. littoralis was a pioneer species that colonized

the lee base of the foredune, but did not create the foredune in the manner of Ammophila arenaria and Elymus mollis. L. littoralis tolerated some sand burial and water stress at the lee base of the young foredune (due to low percent organic matter), but it did not encounter as much sand burial, wind, sandblast, and saltspray as species living on the windward face of the young foredune. L. littoralis also grew inland on the hummocky plain where there was little or no sand deposition and slightly more organic matter in the sand/soil, creating a less xeric environment.

Plants Associated With Seashore Lupine

L. littoralis was found in two plant communities on the research site (Fig. 14). Direct gradient analysis by landform type (Table 2) clearly displays differences between the two communities as far as species composition and relative percent cover for each species. A. arenaria was dominant in both communities. One community inhabited the lee side of the active foredune, where sand deposition was evident and exposed sand averaged 16% of the surface area. This community was called the foredune community. The generalist species (A. arenaria, E. mollis, and Lathyrus japonicus) had the highest percent cover. L. littoralis occurred in small amounts (average cover of 8%). The foredune community differed from Kumler's (1969) "pioneer community" of active sand dunes, where exposed sand occupied 90% of the surface area. L. littoralis occurred in Kumler's "pioneer community", but A. arenaria, E. mollis, and L. japonicus did not. The foredune community was more like Wiedemann's (1966) "dry meadow community" which inhabited areas of dry shifting sand on deflation plains, and also

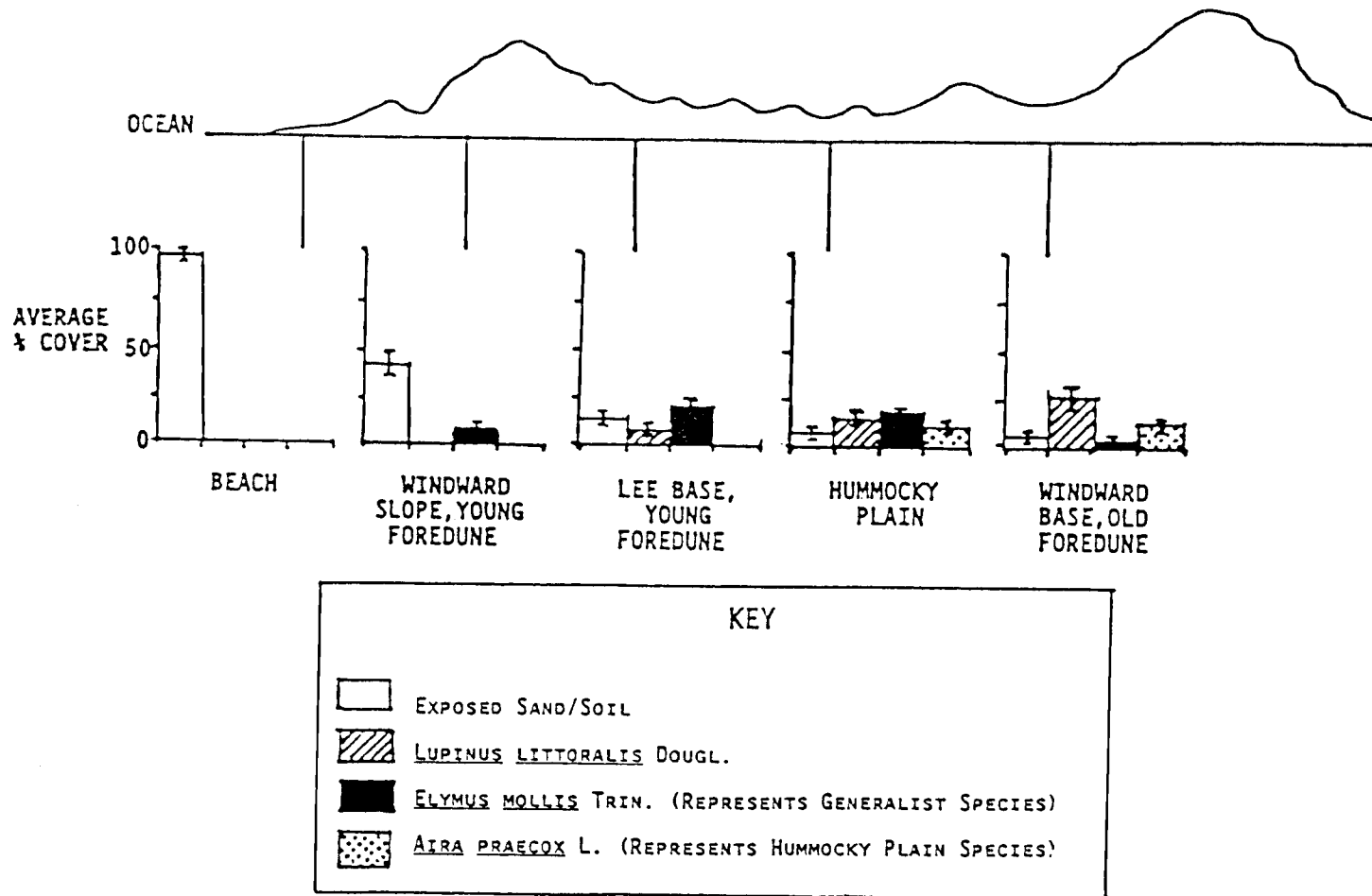


Figure 14. Relationship of species composition to topography along Transects 1-10. Error bars represent ± 1 standard error. (Based on Table 2.)

included A. arenaria, L. japonicus and L. littoralis.

The dominant species of the foredune community (generalist species) also lived on the hummocky plain together with species restricted to the hummocky plain and windward base of the old foredune (hummocky plain species) forming the hummocky plain community. Active sand deposition was not evident, and only 4% to 7% of the surface area was exposed sand. In addition to the generalist species, Aira praecox L. was present in the greatest amount. Hypochaeris radicata L., Fragaria chiloensis (L.) Duch., and Anaphalis margaritacea (L.) B. and H. were also important. L. littoralis occurred in great amounts (average cover ranged from 15% to 26%) in the hummocky plain community. This community was similar to Kumler's "herbaceous community" of stabilized sands to the lee of sand dunes which had 6% of the surface area occupied by exposed sand. All dominant species of the hummocky plain community, except E. mollis and L. japonicus, occurred in Kumler's "herbaceous community". The hummocky plain community was also similar to Wiedemann's "meadow community" of deflation plains, which had slightly wetter soil and less sand deposition than the "dry meadow community". L. littoralis, A. praecox, H. radicata, and F. chiloensis dominated Wiedemann's "meadow community".

Fragaria chiloensis (beach strawberry) had the most similar distribution to L. littoralis of the endemic species growing on the research site. Whenever F. chiloensis was observed, L. littoralis was nearby; however, L. littoralis sometimes occurred where F. chiloensis did not. L. littoralis was found more often than F. chiloensis at the lee base of the active foredune. Inland, on the hummocky plain, both

species increased in percent cover; however, L. littoralis was always found in greater amounts (percent cover there averaged 15% and 8%, respectively, for L. littoralis and F. chiloensis). Though F. chiloensis was clonal and L. littoralis was not, these two species appeared to have similar ecological tolerances, as expressed by their similar distributions on the research site.

The two plant communities faced different abiotic pressures. The foredune community existed in an area of active sand deposition, where organic material in the sand/soil was minimal, creating a xeric environment. Soil development was hindered by seasonal sand deposition and sparse plant cover. The hummocky plain community existed in an area of minimal sand accumulation, where organic material in the sand/soil was the highest found on the site, creating a slightly mesic environment. Soil development was favored by the lack of sand deposition and almost total plant cover.

The foredune and hummocky plain communities did not appear to represent different successional stages. The differences between these communities appeared to be caused more by differences in abiotic site factors than by age. They had been established for the same length of time, except for the older portion of the hummocky plain community near the old embryo dunes (Figs. 2, 3, and 4). Differences in vegetation were most likely shaped by abiotic factors, such as saltspray and sand movement (Wiedemann 1966, Barbour et al. 1985). Unless the shoreline prograded again, succession from herbaceous vegetation to shrubs and trees would probably take place only on the hummocky plain where sand was relatively stable and soil could develop. The young foredune would need to stop accumulating sand

before soil could develop and shrubs would be able to survive on it. However, as long as sand was deposited and Ammophila arenaria survived, the young foredune would continue to grow higher, maintaining a dynamic sand environment (Wiedemann et al. 1969).

If the shoreline prograded again, due to jetty extension or geologic uplift, new sand would be deposited in front of the young foredune. A. arenaria would pioneer this area, collect sand, and, thus, establish a new active foredune. The new foredune would collect the windblown sand, allowing the foredune behind it to stabilize. Herbaceous vegetation on the newly stabilized foredune would be able to contribute to the development of the soil. Eventually, the herbaceous plants would probably be replaced by trees and shrubs (Wiedemann et al. 1969).

Even without shoreline accretion, succession on the hummocky plain would probably proceed to trees, and L. littoralis would be shaded out by dense shrub and tree cover. However, even while the hummocky plain was forested, L. littoralis would probably still survive at the lee base of the young foredune, because sand deposition there would most likely prevent the establishment and survival of trees.

The results of this study suggest that L. littoralis exemplified a response of vegetation to the particular combinations of abiotic factors present in the two communities in which it was observed. The ability of L. littoralis to survive in both of these environments was related to its gross morphology.

Gross Morphology of Seashore Lupine

Results from this research indicate that L. littoralis was not clonal, although Kumler (1969) described L. littoralis as clonal (and a literature search found no further discussions on the issue). Although L. littoralis produced adventitious roots from cuttings placed in vermiculite, this response did not necessarily indicate it had the ability to clone in a natural setting, since many woody plants (whether clonal or not) can be propagated vegetatively via human manipulation. In addition, no asexual reproduction of L. littoralis was observed on the site. Lack of vegetative reproduction was unexpected since sand dune pioneers tend to reproduce extensively by vegetative means (Kumler 1969). The morphology of L. littoralis was like an "underground shrub" with foliage above the sand/soil surface and branches below the sand/soil surface.

The "underground shrub" morphology is evident in prostrate alpine plants. Chujo (1983) studied alpine mat plants in Japan. Some species had morphologies similar to L. littoralis, where the foliage was in discrete clumps attached via underground stems to a taproot. Erosion and downhill movement of slope materials play a selective role in the development of alpine slope communities. Alpine species live in a situation where pieces of the mat can easily be broken and carried downhill by the movement of slope materials. Therefore, the ability to reproduce vegetatively is strongly selected for on alpine slopes, and the subterranean structure is very important. In response to downslope movement, the alpine slope plants of the study often had underground stems with adventitious roots and taproots that pointed uphill (Chujo 1983).

The subterranean morphology of L. littoralis appeared to be a response to burial, rather than the response to erosion and downslope movement found in alpine slope communities. This was evident by the fact that the taproot of L. littoralis did not point uphill. Also, lack of vegetative reproduction in L. littoralis may explain why this species had, as Wiedemann (1966) pointed out, a limited tolerance to burial. The next two paragraphs describe a possible scenario of growth in L. littoralis.

Large amounts of sand deposition in the winter bury the crown of the taproot. In spring, underground stems grow from perennating buds on the root crown. Once these underground stems reach the sand surface, they branch into leaf and flower-bearing shoots. If no burial takes place the next year, then perennating buds just below the sand surface at the tips of the underground stems, or perennating buds at the root crown, can produce a new growth of stems. If burial does take place again (or some of the underground stems die that year), then perennating buds grow only from the root crown.

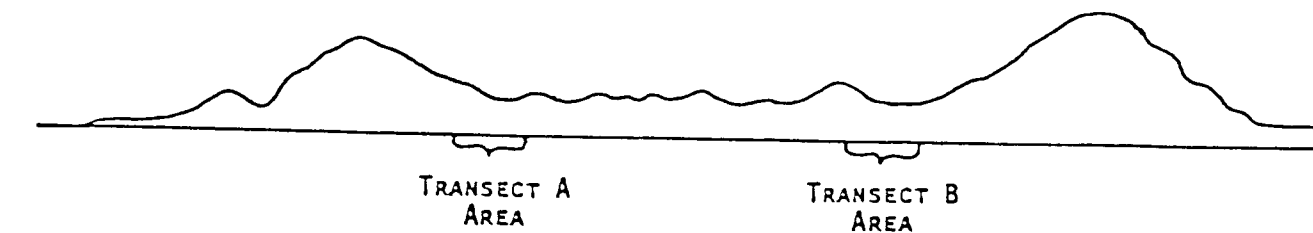
The buds of L. littoralis do not remain at the sand/soil surface for more than a few years since underground stems die periodically. Therefore, new shoots must occasionally come from buds on the root crown. If the root crown is buried deeply by accumulating sand (e.g., deeper than 25 cm, the deepest root crown measured), the root may not have enough energy to send an underground shoot all the way up to the surface. Hence, L. littoralis tolerates some sand burial, yet has limits as to the depth of burial it can tolerate.

Differences in Subterranean Morphology of Seashore Lupine

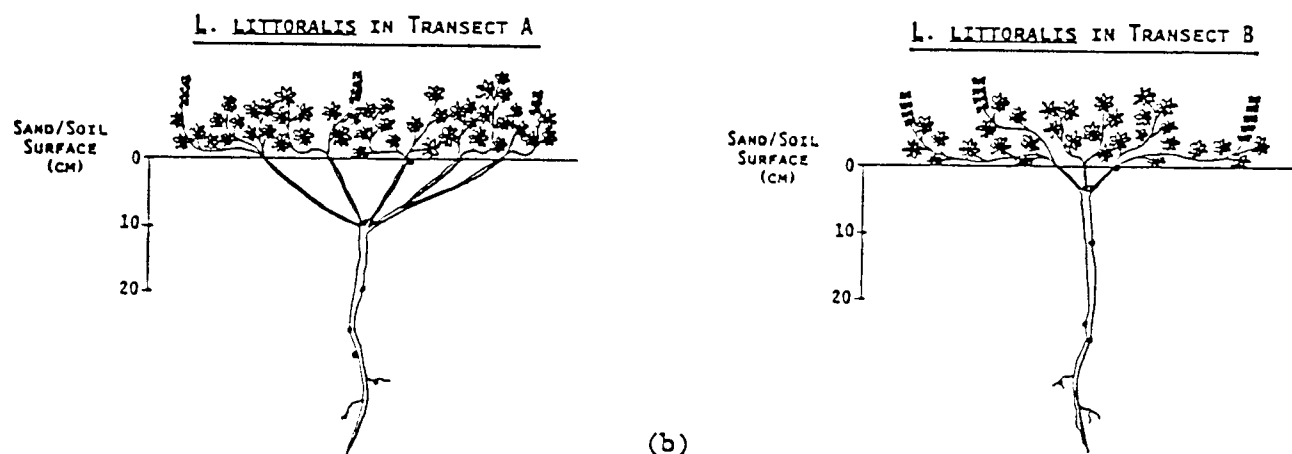
The subterranean morphology of L. littoralis was different between the two communities described on the site (Fig. 15, Table 4). In the foredune community, where active sand deposition occurred, individuals had long underground stems and deep root crowns. In the hummocky plain community, where sand was stable, individuals had shorter underground stems and shallower root crowns. The two subterranean morphologies of L. littoralis might have been responses to different environments. Morphologic plasticity gives a species a broad range of ecological tolerances (Seliskar 1985).

A burial experiment would test the morphological response of L. littoralis to sand deposition. L. littoralis plants in both communities could be buried under various amounts of sand in autumn, and checked in spring for underground stem growth. Results would show the response of underground stems to burial at different depths. Results would also show whether the two morphologies represented ecotypes or plasticity within individuals.

In the absence of a burial experiment, circumstances imply a relationship between the morphology of L. littoralis and its environment (Table 4). Some sand deposition took place at the lee base of the young foredune, as indicated by the large percentage of exposed sand/soil. Soil was less developed at the lee base of the young foredune, as indicated by the small amount of organic matter. At the lee base of the young foredune, where sand burial took place, the root crown was significantly ($p = 0.0005$) deeper, and the underground stems were significantly ($p = 0.0005$) longer than they were on the hummocky plain. The strong positive correlation between



(a)



(b)

Figure 15. Comparison of subterranean morphology of Lupinus littoralis Dougl. relative to proximity of plants to foredune. (a) Relative position of Transects A and B. Transects run parallel to sand dunes. (b) Underground stem morphologies averaged for Transects A and B. Height of crown and length of root are estimated averages, as measurements were not always possible. (Based on Table 3.)

Table 4. Characteristics of environment and Lupinus littoralis Dougl. in two locations on research site. Data are means \pm 1 standard error. (Based on Tables 2 and 3.)

CHARACTERISTICS	YOUNG FOREDUNE LEE BASE	OLD FOREDUNE WINDWARD BASE	P FROM T-TEST
Average Percent Cover of Exposed Sand/Soil (quadrats)	16.2 % \pm 3.5 (n=30)	4.4 % \pm 3.5 (n=30)	= 0.0015
Average Percent Carbon in Sand/Soil (samples)	0.051 % \pm 0.013 (n=3)	0.350 % \pm 0.030 (n=3)	< 0.0005
Average Percent Cover of Seashore Lupine (quadrats)	7.6 % \pm 2.8 (n=30)	25.5 % \pm 5.0 (n=30)	= 0.0015
Average Length of Underground Stems of Seashore Lupine (plants)	17.8 cm \pm 1.7 (n=27)	3.6 cm \pm 0.3 (n=35)	< 0.0005
Average Depth to Root Crown of Seashore Lupine (plants)	12.8 cm \pm 1.1 (n=27)	3.6 cm \pm 0.3 (n=35)	< 0.0005
Average Diameter of Root Crown of Seashore Lupine (plants)	9.6 mm \pm 0.9 (n=27)	7.1 mm \pm 0.7 (n=35)	= 0.025
Average Number of Underground Stems per Seashore Lupine (plants)	4.9 \pm 0.7 (n=27)	3.2 \pm 0.3 (n=35)	= 0.010

length of underground stems and depth to root crown ($r = 0.65$, Fig. 12) implies that root crowns were being buried, and underground stems were growing directly up to the sand surface, rather than travelling horizontally (at various distances) from the root crown before growing to the surface.

Lupinus latifolius, subalpine lupine, is a perennial, nonclonal herb that grows in mesic meadows near Mount St. Helens, Washington. Like L. littoralis, L. latifolius has underground stems that attach to a taproot (Zobel, Oregon State University, pers. comm.). Antos and Zobel (1984) reported that the underground stems of L. latifolius grew to the surface when buried by volcanic tephra. Maximum burial depth tolerated by L. latifolius was 18 cm. At the end of the growing season, underground stems died back to original soil surface (previous to burial by tephra). Unlike L. littoralis, where perennating buds can be found either at the sand surface or at the root crown, the perennating buds of L. latifolius do not move up into the tephra but remain on the root crown; consequently, much energy must be expended each year for stems to grow from the root crown to the tephra surface. L. littoralis probably expends less energy for vegetative growth, because it does not grow new shoots from the root crown every year, but sometimes grows shoots from the tips of the underground stems instead. Therefore, L. littoralis may be more adapted to burial than L. latifolius.

L. littoralis plants growing at the lee base of the young foredune appeared to undergo water stress earlier than L. littoralis plants growing inland on the hummocky plain. When root nodules senesce (due to water stress or other seasonal factors), leghemoglobin

breaks down, changing from a bright red to a dull green inside the nodule (Quispel 1974). Sections of the nodules, and observations of the roots, indicated that the root nodules and root hairs of L. littoralis senesced earlier at the lee base of the young foredune (late July 1987 vs. late August and September 1987). In addition, the above ground foliage and stems of L. littoralis plants at the lee base of the young foredune died back earlier than L. littoralis plants at the windward base of the old foredune (late August vs. primarily in January).

The root crown diameter of L. littoralis was significantly ($p = 0.025$) larger at the lee base of the young foredune, where the sand/soil environment was xeric, than inland on the hummocky plain. Since the taproot had the anatomy of a storage organ, the root (and root crown) diameter might have been related to amount of storage taking place. Extra starch reserves would be useful, since the dormant period was long at the base of the young foredune (at least four months, Appendix IV), and underground stems needed to grow far to reach the sand surface before they could sprout photosynthetic shoots.

Root crown diameter strongly correlated with number of underground stems per plant ($r = 0.81$, Fig. 12). Root crown diameter was also related to proximity to foredune (Table 4). Perhaps, the number of underground stems were more abundant on plants at the lee base of the young foredune, because there was more exposed sand to occupy. This exploitation of available space could have created a large foliar crown which would capture and fix more carbon. The extra photosynthate could then be stored in the taproot, increasing the root crown diameter.

The results of this study suggest that root crown diameters may have been related to age of L. littoralis individuals, i.e., the larger the root crown the older the plant. If root crown diameter increased with age, then the correlation between root crown diameter and number of underground stems ($r = 0.81$, Fig. 12) indicates that the number of underground stems also generally increased with age; however, the death of some underground stems occasionally created individuals with a thick root and only one attached underground stem, thus complicating the use of the number of underground stems as an indication of age. If age and root crown diameter were positively related, then older plants would be found at the lee base of the young foredune (Table 4); however, since vegetation at the windward base of the old foredune was probably six years older than at the young foredune, L. littoralis plants were not likely to be older at the base of the young foredune.

Weak correlations existed between diameter of root crown and depth to root crown, as well as to length of underground stems, ($r = 0.50$ and $r = 0.40$, respectively). Since root crown depth and underground stem length were greatest at the base of the young foredune (Table 4), the correlations with root crown diameter support the idea that food storage increased in the xeric site where sand burial took place. In addition, these correlations do not refute the idea that root crown diameter could increase with age.

Accurate age determination of L. littoralis would have assisted in interpreting morphometric data. Since anatomical sections did not clearly reveal annual growth rings in the taproot, several years of detailed observation of plants of known ages would be required to

age the plants. Until the ages of individual plants L. littoralis are established, the relationship of the root crown diameter to age or to food storage cannot be determined.

Weak correlations existed between number of underground stems and depth to root crown, as well as to length of underground stems, ($r = 0.45$ and $r = 0.39$, respectively). These correlations support the idea that burial could have stimulated sprouting, as well as the idea that the number of underground stems per plant could increase at the base of the young foredune because xeric conditions and sand burial could reduce competition for space.

Apparently, a plastic morphology allowed L. littoralis to inhabit two communities in the non-deflated sand dune ecosystem. L. littoralis plants growing in the xeric environment with sand deposition and burial on the active foredune had many and long underground stems, as well as thick and deep root crowns. L. littoralis plants growing in the more mesic environment, with the stable sand on the hummocky plain, had fewer and shorter underground stems, as well as thinner and shallower root crowns.

CONCLUSIONS

This study documented the distribution and morphology of Lupinus littoralis in the early successional communities of a recently prograded shoreline, where sand burial was a dominant factor, and sand deflation had not taken place. The following questions were answered:

Relationship to Environment of Active Sand Burial

- * Where does L. littoralis occur in the pattern of topography and soil organic matter accumulation relative to a recently prograded shoreline?

L. littoralis occurred at the lee base of the active foredune, on the hummocky plain, and at the windward base of the old foredune. The lee base of the young foredune had minimal sand deposition relative to the top of the foredune; low soil organic content indicated a xeric soil environment. The hummocky plain and old foredune appeared relatively stable in that sand deposition was not evident; higher soil organic content indicated an environment less xeric than the young foredune.

- * What plants are found in association with L. littoralis?

L. littoralis grew in two communities on the research site. The foredune community occurred at the top and lee side of the active foredune. Ammophila arenaria, Elymus mollis, and Lathyrus japonicus dominated the community. L. littoralis was present in small amounts. The hummocky plain community occurred at the windward base of the inactive foredune and on the hummocky plain. A. arenaria, E. mollis,

L. japonicus, L. littoralis, Aira praecox, Hypochaeris radicata and Fragaria chiloensis dominated the community. L. littoralis was present in moderate amounts. The endemic sand dune species with the closest distribution to L. littoralis was F. chiloensis.

Morphology

- * What is the gross morphology of L. littoralis?

L. littoralis was discovered to be a nonclonal, perennial herb. A single taproot connected multiple underground stems. Each underground stem supported a cluster of leafy trailing stems at the sand/soil surface.

- * Does the subterranean morphology of L. littoralis change with distance from shore?

Two different subterranean morphologies of L. littoralis were evident on the research site. These morphologies were related to the amount of burial by sand. Plants growing in the area of active sand deposition, at the lee base of the young foredune, had more and longer underground stems, as well as thicker and deeper root crowns, than plants growing in the stable sand/soil at the windward base of the old foredune.

LITERATURE CITED

- Antos, J.A. and D.B. Zobel. 1984. Plant form, developmental plasticity, and survival following burial by volcanic tephra. *Canadian Journal of Botany* 63: 2083-2090.
- Barbour, M.G., J.H. Burk, and W.D. Pitts. 1980. *Terrestrial Plant Ecology*. The Benjamin/Cummings Publishing Company, Inc. Menlo Park, California.
- Barbour, M.G., T.M. DeJong, and B.M. Pavlik. 1985. Marine beach and dune plant communities, 296-322. *In* Chabot, B.F., and H.A. Mooney, Eds. *Physiological Ecology of North American Plant Communities*. Chapman and Hall, New York, New York.
- Boyce, S.G. 1954. The salt spray community. *Ecological Monographs* 24 (1): 29-64.
- Brady, N.C. 1984. *The Nature and Properties of Soils*, Ninth Ed. Macmillan Publishing Company, New York, New York.
- Byrd, N.L. 1950. Vegetation zones of coastal dunes near Waldport, Oregon. Thesis. Oregon State University, Corvallis, Oregon.
- Chujo, H. 1983. Alpine vegetation and periglacial movement on Mt. Ontake, Central Japan: factors controlling the Cardamine nipponica community. *Japanese Journal of Ecology* 33: 461-472.
- Cooper, W.S. 1958. *Coastal Sand Dunes of Oregon and Washington*. Memoir 72. Geological Society of America, New York, New York.
- Hanson, M. 1989. Personal communication. U.S. Army Corps of Engineers, Portland District, Oregon.
- Hitchcock, C.L., A. Cronquist, M. Ownbey, and J.W. Thompson. 1984. *Vascular Plants of the Pacific Northwest*. Vols. 1-5. University of Washington Press, Seattle, Washington.
- Jensen, W.A. 1962. *Botanical Histochemistry*. W.H. Freeman and Company, San Francisco.
- Johansen, D.A. 1940. *Plant Microtechnique*. McGraw-Hill, New York.
- Kentula, M.E. 1973. A study of the relationship between nitrogen, phosphorus, and water table depth, and the plant communities of the Lily Lake deflation plain. Thesis. Oregon State University, Corvallis, Oregon.
- Kumler, M.L. 1963. Succession and certain adaptive features of plants native to the sand dunes of the Oregon coast. Thesis. Oregon State University, Corvallis, Oregon.

- Kumler, M.L. 1969. Plant succession on the sand dunes of the Oregon coast. *Ecology* 50(4): 695-704.
- McCune, B. 1989. Personal communication. General Science Department. Oregon State University, Corvallis, Oregon.
- Nelson, D.W. and L.E. Sommers. 1982. Total carbon, organic carbon, and organic matter, 539-580. *In* A.L. Page, Ed. *Methods of Soil Analysis, Part 2. Chemical and Microbiological Properties*. Soil Science Society of America, Madison, Wisconsin.
- Quispel, A. 1974. *The Biology of Nitrogen Fixation*. North-Holland Publishing Company, Amsterdam, Netherlands.
- Rose, S.L. 1988. Above and below ground development in a marine sand dune ecosystem. *Plant and Soil* 109: 215-226.
- Sator, C. 1983. *In vitro* breeding of lupins, 79-86. *In* Thompson, R., and R. Casey, Eds., *Perspectives for Peas and Lupins as Protein Crops*. Martinus Nijhoff Publishers, The Hague, Netherlands.
- Schwendiman, J.L. 1977. Coastal sand dune stabilization in the Pacific Northwest. *International Journal of Biometeorology* 21 (3): 281-289.
- Seliskar, D.M. 1985. Morphometric variations of five tidal marsh halophytes along environmental gradients. *American Journal of Botany* 72 (9): 1340-1352.
- Sherman, A.D., S.E. Gwin, and M.E. Kentula, in conjunction with M. Brown. 1988. Quality Assurance Project Plan: Florida Wetlands Study. Internal Report, U.S. Environmental Protection Agency, Environmental Research Laboratory, Corvallis, Oregon.
- U.S. Army Corps of Engineers. 1985. Yaquina Bay Interim Ocean Dredged Material Disposal Site Evaluation Study. U.S. Army Corps of Engineers, Portland District, Oregon.
- Vitt, D.H., J.E. Marsh, and R.B. Bovey. 1988. *Mosses, Lichens and Ferns of Northwest North America*. Lone Pine Publishing, Edmonton, Alberta, Canada.
- Wiedemann, A.M. 1966. Contributions to the plant ecology of the Oregon coastal sand dunes. Thesis. Oregon State University, Corvallis, Oregon.
- Wiedemann, A.M., L.R.J. Dennis, and F.H. Smith. 1969. *Plants of the Coastal Dunes*. O.S.U. Book Stores, Inc., Corvallis, Oregon.
- Zobel, D.B. 1988. Personal communication. Botany and Plant Pathology Department, Oregon State University, Corvallis, Oregon.

APPENDICES

Appendix Table I. Record of Construction of North and South Jetties at Yaquina Bay, Newport, Oregon (Hanson, U.S. Army Corps of Engineers, pers. comm.).

1880-1895	North and South Jetties first built
1921	South Jetty extended
1930	North Jetty extended
1939-1940	North Jetty extended
1965-1966	North Jetty extended
1970-1972	South Jetty extended

Appendix Table II. Means of percent cover values (one standard error in parentheses) within m² quadrats by landform type for Transects 1-10. Plant species are organized as to strand and generalist species, or hummocky plain species. Dash indicates trace or not present.

	LANDFORM TYPES				
	BEACH	EMBRYO DUNE	YOUNG FOREDUNE		
	(n-38)	(n-24)	WINDWARD SLOPE (n-20)	TOP (n-20)	LEE SLOPE (n-13)
Exposed Sand/Soil	97.9 (1.3)	65.0 (6.9)	40.7 (7.6)	32.8 (5.9)	33.1 (7.9)
Driftwood	0.4 (0.3)	--	--	--	--
Leaf Litter	1.3 (1.3)	--	0.1 (0.1)	--	--
Strand and Generalist Species:					
<u>Amnophila arenaria</u>	0.1 (0.0)	33.3 (7.0)	56.6 (7.9)	62.8 (5.6)	45.0 (6.8)
<u>Cakile</u> spp.	0.4 (0.3)	0.2 (0.2)	0.1 (0.0)	--	--
<u>Elymus mollis</u>	--	2.5 (1.3)	5.4 (1.8)	7.1 (2.1)	10.2 (2.7)
<u>Lathyrus japonicus</u>	--	--	--	3.6 (2.5)	20.8 (7.0)
<u>Lathyrus littoralis</u>	--	--	--	--	0.4 (0.4)
Hummocky Plain Species:					
<u>Alra praecox</u>	--	--	--	--	--
<u>Anaphalis margaritacea</u>	--	--	--	--	--
<u>Anthoxanthum odoratum</u>	--	--	--	--	--
<u>Cerastium arvense</u>	--	--	--	--	--
<u>Ceratodon purpureus</u>	--	--	--	--	--
<u>Cladonia</u> sp.	--	--	--	--	--
<u>Convolvulus soldanella</u>	--	--	--	--	--
<u>Festuca</u> sp.	--	--	--	--	--
<u>Fragaria chiloensis</u>	--	--	--	--	--
<u>Glehnia leioarpa</u>	--	--	--	--	--
<u>Gnaphalium purpureum</u>	--	--	--	--	--
<u>Hypochaeris radicata</u>	--	--	--	--	--
<u>Lupinus littoralis</u>	--	--	--	--	--
<u>Poa</u> sp.	--	--	--	--	--
<u>Polypodium scolieri</u>	--	--	--	--	--
<u>Rumex</u> sp.	--	--	--	--	--
<u>Tanacetum camphoratum</u>	--	--	--	--	--
<u>Vicia gigantea</u>	--	--	--	--	--

Appendix Table II. (continued)

	LANDFORM TYPES			
	YOUNG FOREDUNE	HUMMOCKY PLAIN	OLD FOREDUNE	
	LEE BASE (n=30)	(n=66)	WINDWARD BASE (n=30)	WINDWARD SLOPE (n=15)
Exposed Sand/Soil	16.2 (3.5)	6.7 (1.6)	4.4 (3.5)	5.0 (2.3)
Driftwood	--	0.4 (0.3)	--	0.3 (0.3)
Leaf Litter	0.3 (0.3)	3.5 (1.3)	4.7 (1.4)	4.4 (1.7)
Strand and Generalist Species:				
<u>Ammophila arenaria</u>	50.5 (3.3)	60.6 (3.1)	64.7 (4.1)	57.7 (7.7)
<u>Cakile</u> spp.	--	--	--	--
<u>Elymus mollis</u>	20.9 (3.2)	19.4 (3.0)	5.1 (1.3)	4.7 (1.4)
<u>Lathyrus japonicus</u>	33.2 (5.4)	8.0 (1.7)	1.1 (0.6)	0.3 (0.2)
<u>Lathyrus littoralis</u>	--	0.1 (0.1)	--	--
Hummocky Plain Species:				
<u>Aira praecox</u>	0.7 (0.7)	10.9 (2.2)	15.6 (3.1)	27.1 (6.4)
<u>Anaphalis margaritacea</u>	1.7 (1.7)	5.1 (1.6)	7.9 (2.6)	3.2 (1.5)
<u>Anthoxanthum odoratum</u>	--	0.9 (0.8)	2.8 (2.7)	--
<u>Cerastium arvense</u>	--	0.2 (0.1)	0.4 (0.2)	1.3 (1.0)
<u>Ceratodon purpureus</u>	--	--	--	1.2 (0.7)
<u>Cladonia</u> sp.	--	--	--	0.1 (0.1)
<u>Convolvulus soldanella</u>	--	0.8 (0.5)	--	--
<u>Festuca</u> sp.	--	--	0.7 (0.7)	--
<u>Fragaria chiloensis</u>	1.2 (0.9)	7.6 (1.5)	16.7 (2.8)	14.0 (1.5)
<u>Glehnia leiocarpa</u>	--	0.2 (0.1)	--	--
<u>Gnaphalium purpureum</u>	--	0.5 (0.3)	0.1 (0.1)	--
<u>Hypochaeris radicata</u>	0.2 (0.2)	11.2 (1.9)	11.3 (2.1)	5.3 (1.7)
<u>Lupinus littoralis</u>	7.6 (2.8)	14.8 (2.6)	25.5 (5.0)	8.7 (2.8)
<u>Poa</u> sp.	--	0.2 (0.1)	--	--
<u>Polypodium scolieri</u>	--	--	--	0.5 (0.4)
<u>Rumex</u> sp.	--	0.2 (0.1)	2.1 (0.7)	1.4 (0.8)
<u>Tanacetum camphoratum</u>	--	--	--	0.1 (0.1)
<u>Vicia gigantea</u>	--	1.6 (0.8)	0.8 (0.5)	0.3 (0.3)

Appendix Table III. List of plant species at research site.
Nomenclature follows Hitchcock et al. (1984), and
Vitt et al. (1988).

MOSSES AND LICHENS

Ceratodon purpureus (Hedw.) Brid.
Dicranum fuscescens Turn.
Cladonia sp. Hill ex Browne

FERNS

Polypodiaceae:

Polypodium scouleri Hook. and Grev.

CONIFERS

Pinaceae:

Pinus contorta Loud.

FLOWERING PLANTS

MONOCOTYLEDONAE

Poaceae (Gramineae):

Aira praecox L.
Ammophila arenaria (L.) Link
Anthoxanthum odoratum L.
Elymus mollis Trin.
Festuca sp. L.
Poa sp. L.

Cyperaceae:

Carex sp. L.

DICOTYLEDONAE

Polygonaceae:

Rumex sp. L.

Myricaceae:

Myrica californica C. and S.

Nyctaginaceae:

Abronia latifolia Esch.

Caryophyllaceae:

Cerastium arvense L.
Stellaria media (L.) Vill.

Appendix Table III. (continued)

Brassicaceae (Cruciferae):

- Cakile edentula (Bigel.) Hook var. california (Hel.) Fern.
C. maritima Scop.

Rosaceae:

- Fragaria chiloensis (L.) Duch.

Fabaceae (Leguminosae):

- Lathyrus japonicus Willd. var. glaber (Ser.) Fern.
L. littoralis (Nutt. ex Torr. and Gray) Endl.
Lupinus littoralis Dougl.
Vicia gigantea Hook.

Apiaceae (Umbelliferae):

- Angelica hendersonii C. and R.
Glehnia leiocarpa Math.

Ericaceae:

- Gaultheria shallon Pursh
Vaccinium ovatum Pursh

Plumbaginaceae:

- Armeria maritima (Mill.) Willd.

Convolvulaceae:

- Convolvulus soldanella L.

Plantaginaceae:

- Plantago maritima L.

Rubiaceae:

- Galium sp. L.

Caprifoliaceae:

- Lonicera involucrata (Rich.) Banks.

Asteraceae (Compositae):

- Achillea millefolium L.
Anaphalis margaritacea (L.) B. and H.
Gnaphalium purpureum L.
Hypochaeris radicata L.
Tanacetum camphoratum Less.
-

Appendix Table IV. Estimated phenology of Lupinus littoralis Dougl. at research site; based on observations from June 1987 to June 1989 (not observed at regular intervals nor in every month).

<u>PHENOLOGY</u>	<u>MONTHS</u>
Seeds germinate	February - March
Mature plants leaf-out	February
Mature plants flower and set fruit	May - July
Seed dispersal	July - August
Root hair and root nodule senescence begins	* late July 1987 ** late August - September 1987
Dieback of above-ground stems and foliage	* late August - September ** January ? (after November and before February, in individuals that dieback that year)

* At lee base of young foredune
 ** At windward base of old foredune