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Introduction History and Invasion Patterns of *Ammophila arenaria* on the North Coast of California

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Abstract: *European beachgrass (*Ammophila arenaria *[L.] Link), introduced to stabilize sand, is fully naturalized in central and northern California and has supplanted populations of native dune plants in many areas, including the North Spit of Humboldt Bay. We interpreted air photos of the North Spit for the presence of* Ammophila arenaria *at three points in time: 1939/1942, 1962, and 1989. To quantify the spread and to detect invasion patterns of* Ammophila, *we then compiled maps using a geographic information system. We documented introduction dates and locations to improve the accuracy of our photo interpretation. Interpretation of the three photo series revealed invasion and expansion of* Ammophila *in both foredunes and inland dunes. The most dramatic increase in cover was found in the foredunes, whereas documented and presumed plantings were found mostly on inland dunes. Adjusting for intentional eradication,* Ammophila *cover on the North Spit was found to have increased between 1939 and 1989 by 574%. The square root of the area occupied by* Ammophila *on the North Spit increased linearly with time, conforming to biological invasion theory.*

Historia de la introducción y patrones de invasión de *Ammophila arenaria* en la costa Norte de California

Resumen: Ammophila arenaria *(L.) Link, está plenamente establecida en el norte y centro de California, donde ha suplantado as poblaciones de vegetación autóctona de dunas en muchas áreas, incluyendo la de "North Spit" en la Bahía de Humboldt. Interpretamos fotografías aéreas del "North Spit" para detectar la presencia de* Ammophila arenaria *en tres momentos: 1939/42, 1962 y 1989. Los mapas fueron compilados utilizando sistemas de información geográfica para cuantificar la expansión de* Ammophila *en el "North Spit" y detectar patrones de invasión. Se documentaron fechas y lugares de introducción con la çinalidad del aumentar la presición en la interpretación de las fotografías aéreas. La interpretación de las tres series de fotografías revelaron la invasión y expansión de* Ammophila *tanto en las dunas costeras como en las interiores. El aumento de cobertura más pronunciado se detectó en las dunas costeras mientras que las plantaciones documentadas o supuestas fueron halladas principalmente en las dunas interiores. Ajustando para la erradicación intencional, la cobertura de* Ammophila *en el área se incrementó en un 574% entre 1939 y 1989. De acuerdo con la teoría de invasión biológica, la raíz cuadrada del área ocupada por* Ammophila *en el "North Spit" aumentó en forma lineal con respecto al tiempo.*

Introduction

European beachgrass (*Ammophila arenaria* [L.] Link) has long been recognized for its excellence as a sand stabilizer and has been used as such worldwide (Lamson-Scribner 1895; Kellogg 1915; Barbour & Johnson 1988). *Ammophila arenaria* has spread extensively on the west coast of the United States (Cooper 1967; Barbour & Johnson 1988) since its introduction at Golden Gate Park in San Francisco in the late 1800s (Lamson-Scribner 1895; Lamb 1898; Hitchcock & Chase 1951; Weintraub 1953). It has become fully naturalized north of San Francisco (Barbour & Johnson 1988), where it has altered

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dune topography (Cooper 1958; Wiedemann 1984; Wiedemann & Pickart in press), replaced native vegetation, and reduced species diversity (Breckon & Barbour 1974; Barbour et al. 1976; Pitts & Barbour 1979; Boyd 1992).

Ammophila arenaria is native to the sandy coastlines of the North Sea, the Atlantic Ocean, the Baltic Sea, the Mediterranean Sea, and the Black Sea, with a range from 30° to 63°N latitude (Huiskes 1979; Wiedemann 1987). Today it is found on the west coast of North America from southern California to the Queen Charlotte Islands, a range from 34° to 54°N latitude (Breckon & Barbour 1974; Wiedemann 1984).

Ammophila is a coarse, perennial, rhizomatous grass with stout culms in tufts up to 120 cm tall (Huiskes 1979). Natural establishment takes place through seedlings and vegetative reproduction, often in the form of regeneration from pieces of rhizome washed ashore at high tide (Gemmell et al. 1953; Huiskes 1977; Baye 1990).

Ammophila grows in substrates of low organic matter content and free drainage. It grows most vigorously on mobile and semi-stable dunes (Huiskes 1979) and thrives in the wind-blown foredune area just inland from the strand and above high-tide line. Highly adapted to sand accretion (Gemmell et al. 1953), *Ammophila* withstands sand burial of up to 1 m per year (Huiskes 1979). It appears to require the continued addition of fresh sand to grow vigorously and flower and to avoid senescence (Ranwell 1972; van der Putten et al. 1988). *Ammophila*'s nutrient and productivity relations are superior to those of American dunegrass (*Leymus mollis* [Trin.] Pilger) (Pavlik 1983*a*, 1983*b*, 1983*c*, 1984, 1985).

On the North Spit of Humboldt Bay in northern California, *Ammophila arenaria* has become a threat to the native "dune mat" community, a foredune community comprised of over 40 low-growing herbaceous and suffrutescent species (Pickart 1988*a*). This community, protected at The Nature Conservancy's 181-ha Lanphere-Christensen Dunes Preserve on the North Spit, is unique in that it is still dominated by native species, including *Leymus mollis*, and is the most pristine example of the community remaining in existence. The only other significant remnant of this once wide-ranging community (from Coos Bay, Oregon, to Monterey, California) occurs at Point Reyes National Seashore, just north of San Francisco (Barbour & Johnson 1988; Pickart 1988*b*).

This study provides a history of the introduction and spread of *Ammophila* on the North Spit and presents the results of research into the number, size, dates, and locations of plantings. The rate, extent, and patterns of spread of *Ammophila* on the North Spit are examined in the context of biological invasion theory. Results of this study may enhance management of *Ammophila* and therefore preservation of the remaining dune-mat community on the North Spit.

Study Area

The Samoa Peninsula in Humboldt County, California, is between 40°45′ and 41°N latitude and approximately 370 km north of San Francisco. This peninsula, known as the North Spit, separates Arcata Bay from the Pacific Ocean (Fig. 1). The mouth of the highly migratory Mad River (not pictured) provides its vague northern limit. The study area is 20.4 km long and 1 km wide, on average, and encompasses 2154 ha.

The geomorphology of the North Spit has been shaped by the interactions of northwestern winds, winter storms, and vegetation cover (Cooper 1967). Historic photos from the late 1800s show sparse vegetation at the south end of the spit, where storm surf periodically scoured and reshaped the strand and foredunes at the entrance to Humboldt Bay. Stereo air photos of the spit from the 1930s show small hummocks of vegetation sparsely populating the foredunes along the entire length of the spit. Inland southern dunes were mostly unvegetated. On the northern half of the spit, tongues of moving sand, oriented parallel with the prevailing northwestern winds, alternated with vegetated ridges. A forest comprised of beach pine (*Pinus contorta* ssp. *contorta* Dougl. ex Loud.) and Sitka spruce (*Picea sitchensis* [Bong.] Carr.) grew between the inland dunes and the Mad River Slough.

Many of these biophysical characteristics of the North Spit are still intact, but substantial degradation of the natural environment has occurred, especially from the town of Samoa south (Fig. 1). The southern end of the spit is now characterized by steep, *Ammophila*-dominated foredunes and stabilized inland dunes. Houses, roads, and industry border the Bay. Yellow bush lupine (*Lupinus arboreus* Sims.), introduced to Humboldt Bay in 1908, is common and is responsible for much of the inland dune stabilization (Miller 1988). Off-highway-vehicle paths lace through the foredunes.

North of the town of Samoa the spit has retained many of its historic characteristics, including the beach pine–Sitka spruce forest. Stretches of foredune are still dominated by dune mat species, such as beach bluegrass (*Poa douglasii* Nees.), beach pea (*Lathyrus littoralis* [Nutt. ex T. & G.]), sand verbena (*Abronia latifolia* Eschs.), beach strawberry (*Fragaria chiloensis* [L.] Duchn.), and—less commonly—*Leymus mollis*. *Ammophila* has come to dominate most of the unmanaged foredunes, however, and off-highway-vehicles have carved trails that have fragmented plant communities. Disturbance by housing and roads is mostly confined to the area around Manila.

Methods

To establish dates of introduction we reviewed records held at private and public agencies and institutions, examined local collections of historic ground photos, and

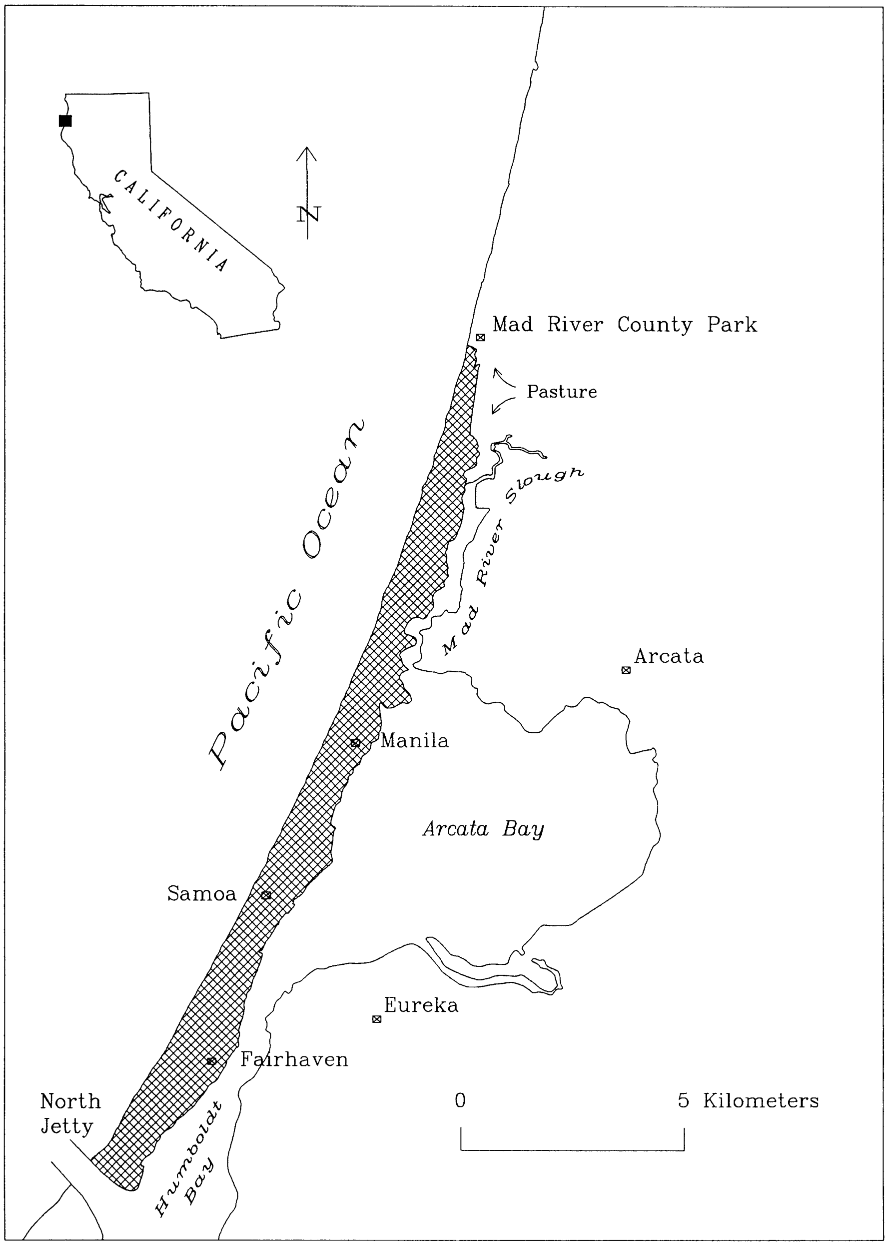

Figure 1. Map of study area: North Spit of Humboldt Bay, California.

interviewed local botanists, historians, and personnel from government agencies and private industry on the North Spit.

We interpreted high-quality stereo pairs of black-and-white air photos of the North Spit to determine past and present distributions of *Ammophila arenaria*. The air photos were taken in 1939 (20 photos, 1:10,200), 1942 (4 photos, 1:20,000), 1962 (25 photos, 1:12,000), and 1989 (26 photos, 1:9600). The 1942 photos supplemented the 1939 set, which did not cover the northern tip of the study area.

Although *Ammophila arenaria* has characteristic growth patterns, it is sometimes difficult to recognize in black-and-white air photos, especially at photo scales ranging from 1:9600 to 1:20,000. Its matted texture and light, mottled tone distinguish it from most herbaceous and woody species, but it is similar in appearance to *Leymus mollis* and *Poa douglasii*.

To assess the accuracy of our photo interpretation we worked first with the 1989 photos, identifying the presence of *Ammophila* and outlining stand perimeters ("polygons") on acetate overlays. While ground-truthing these same photos, we kept a record of accuracy and subsequently corrected overlays. We distinguished photos depicting areas not previously visited by any of us (eight photos) from areas with which we were somewhat or very familiar (18 photos). A 1988 stereo set of large-scale color photos (1:2400) was used to assist interpretation. By looking for and recognizing patterns in the kinds of mistakes made in the 1989 interpretation, we were better prepared to interpret the earlier sets of photos.

We created four classes to describe *Ammophila* cover and to identify individual polygons on the photo overlays: pure stands (75 to 100%), mixed stands (50 to 74%), newly planted stands (recognizably planted in rows or documented as plantings with known introduction dates), and aggregations of clumps too small to be accurately drawn individually. All stands were classified according to their appearance in each photo set and were not necessarily carried through later time periods in their original class designation. Newly planted stands were considered new only once and were subsequently classified as pure, mixed, or clumped stands.

Our visual image of newly planted *Ammophila* was based on personal visits to planted sites and on photographic and descriptive documentation in McLaughlin and Brown (1942). Documented plantings of *Ammophila* that were identifiable in the air photos aided in the detection of nondocumented plantings by providing insight into the probable locations of *Ammophila* stabilization projects.

We made maps using pcARC/INFO software in a geographic information system (GIS). After digitizing the photo interpretation work off of acetate overlays (one per photo), we linked adjacent photos within each time period and obtained area calculations from the program's database. All time periods were treated identically.

Rate of Spread

We measured the rate of spread of *Ammophila* by following a model used in previous studies of biological invasion: regressing the square root of the area occupied (in our case, by *Ammophila*) over time (Skellam 1951; Roughgarden 1986; Hengeveld 1989). Points of time were 1901, 1939, 1962, and 1989. *Ammophila* cover totals in 1962 and 1989 were adjusted for eradication events.

Results

Ammophila arenaria was used to stabilize dunes on the North Spit in 1901 when seeds were imported from Golden Gate Park and planted over several acres (roughly 1 ha) of inland dunes adjacent to a timber mill in the town of Samoa (*Daily Humboldt Times* 1901). The detailed coverage of the *Daily Humboldt Times* article (1901) strongly implies that *Ammophila* was unknown on the spit prior to the "novel experiment" being carried out by mill management. Previous methods used to control shifting sands on the Samoa Peninsula had failed, and it was not known in 1901 whether *Ammophila* would grow well in the soil and climate of the peninsula (*Daily Humboldt Times* 1901).

Subsequent plantings of *Ammophila* were similarly positioned in proximity to property (*Arcata Union* 1914) and transportation routes (*Daily Humboldt Times* 1920*a*, 1920*b*, Chief of Engineers 1921, Humboldt County Department of Public Works 1970). These introductions were all detectable in the air photos. Although we were not able to find documentation for every planting, we found that all apparent plantings were strategically located near buildings, private property, or transportation corridors, such as railroad tracks.

The photo interpretation self-assessment procedure showed 75 to 80% accuracy in the identification of *Ammophila* in the 1989 photo set (75% in unfamiliar areas of the spit, 80% in familiar areas). The self-assessment data further revealed that polygons were correctly identified to class 61% of the time, with 96% of the errors being of one type: stands of pure *Ammophila* were identified as stands of mixed vegetation. This indicates that our interpretation was consistent and conservative and that we may have underestimated the total abundance of *Ammophila* in the 1939/1942 and 1962 sets of photos.

The distribution of *Ammophila* on the entire North Spit in 1932/1942, 1962, and 1989 is shown in Figure 2. The smallest polygon depicted is from the 1989 photo series and measures 40 m^2 (0.004 ha). The areas in which *Ammophila* cover appears to have decreased rather than increased are reflective of bridge and mill construction and industrial expansion on the south end of the spit near Samoa (Fig. 1). The large *Ammophila*-free expanse at the northern end of the spit roughly frames the location of The Nature Conservancy's Lanphere-Christensen Dunes Preserve, where managers began controlling the invasion of *Ammophila* in the 1980s (Wiedemann 1984, Fig. 2). In Table 1, cover by *Ammophila* is presented first by class for the entire study area and then

Table 1. *Ammophila arenaria* cover on the North Spit of Humboldt Bay, California, 1939/1942, 1962, and 1989.

*Cover (by class)**	*1939/1942 (ha)*	*1962 (ha)*	*1988 (ha)*
75%–100%	11.4	18.7	70.0
50%–74%	18.9	13.0	122.2
Planted stands	11.2	2.2	0.5
Scattered clumps	12.0	27.9	3.6
Total *Ammophila* cover	53.5	61.8	196.3
Cover in areas without *Ammophila* removal	27.2	48.1	183.1

**Cover is presented first by class for entire study area, then as a combined total of all classes from portions of the study area where no known removal of* Ammophila *took place. Newly planted stands were classified as such only during the time period in which they first appeared (from Buell 1992).*

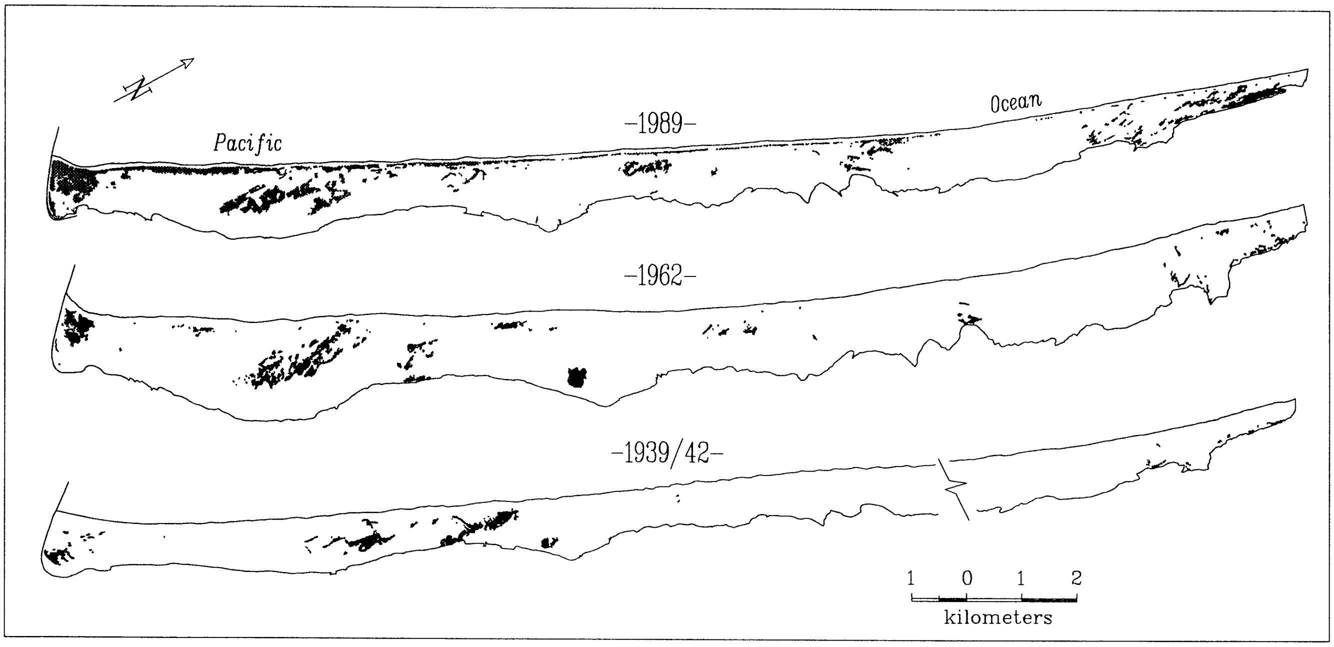

Figure 2. Distribution of Ammophila arenaria *on the North Spit of Humboldt Bay, California, 1939/1942, 1962, and 1989. Apparent differences in land mass are attributed to varying amounts of stereo overlap and tilt in air photos and to natural variance in coastlines over time.*

as the sum of all classes for those areas where no known removal took place.

To adjust for known removal we divided the spit into seven areas according to management or disturbance themes and excluded all data from the two areas in which eradication had occurred (31 ha total were eradicated). Based on these adjusted data there was a 77% increase in *Ammophila* cover between 1939/1942 and 1962, a 281% increase between 1962 and 1989, and a 574% increase over the 50-year period between 1939/1942 and 1989. Between the earliest and the middle time periods analyzed, representing approximately 22 years, *Ammophila* cover almost doubled. Between the middle and most recent time periods, spanning 27 years, *Ammophila* cover nearly quadrupled. The regression of the square root of the area occupied by *Ammophila* (where no eradication occurred) as a function of time was significant at $p = 0.03$ ($y = 0.336 + 0.136x$; $R^2 = 0.940$).

Discussion

Ammophila arenaria has been planted at numerous locations along the west coast of North America since its introduction at Golden Gate Park in San Francisco in the late 1800s. Our study presents new information on introduction sites by documenting the initial planting at Humboldt Bay in 1901. The next-earliest documented planting of *Ammophila* on the Pacific coast was at Coos Bay, Oregon around 1910 (McLaughlin & Brown 1942; Cooper 1958).

Patterns of *Ammophila* invasion on the North Spit are difficult to interpret because of the localized eradication and repeated introduction events that are known to have taken place and because of the complex processes at work in biological invasions (Mack 1985; Hengeveld 1989). Despite these complicating variables, it is hard to dismiss three salient patterns: (1) *Ammophila* spread rapidly through the foredunes, in spite of its not having been planted there; (2) *Ammophila* cover increased substantially after 1962 (Table 1), especially in the foredunes; and (3) *Ammophila* cover on the North Spit increased exponentially over time.

The rapid and successful spread of *Ammophila* through the foredunes probably resulted from the interaction of a number of processes and conditions: optimal habitat, multiple introductions to the surrounding area, natural and human disturbance, and proximity to the strand where rhizome fragments are washed ashore by storm surf (Gemmel et al. 1953; Huiskes 1977, 1979; Mack 1985; Mooney et al. 1986; Hengeveld 1989). The steady advance through the linear habitat of the foredunes resembles the "wave front" invasion pattern described by Baker (1986) and Hengeveld (1989). Originating in population-genetics (Fisher 1937) and brought into an ecological context by Skellam (1951), wave fronts describe the steady spatial advance of a species (Baker 1986; Hengeveld 1989) and are characterized by exponential growth

(Mack 1985; Roughgarden 1986; Hengeveld 1989) until, presumably, suboptimal conditions or lack of available space force a period of slower spread.

In contrast to the pattern observed in the foredunes, the spread of *Ammophila* on inland dunes, where it was introduced, resembles invasion patterns of "satellite" populations, which emanate from a point of origin and fill in the space around them (Baker 1986). Satellite populations or "broken-up fronts" (Hengeveld 1989) are accelerated by each additional focus and enhanced by foci that are far apart (Mack 1985). The successful establishment of *Ammophila* in inland areas and expansion from planted or clumped stands into dense and well-established populations are consistent with this pattern.

The marked increase in the rate of spread of *Ammophila* after 1962, averaging 5 ha per year between 1962 and 1989, compared with 1 ha per year between 1939/1942 and 1962, was apparently due to factors other than new plantings (Table 1). Natural and human disturbance are often cited as probable agents increasing the vulnerability of an environment to invasion, but their respective roles are not fully understood (Mooney et al. 1986; Ramakrishnan & Vitousek 1989; Rejmánek 1989; Simberloff 1989). Regardless of the cause, this accelerated rate of spread detected in the second time period fits the pattern of exponential growth expected in a biological invasion.

Given the dynamic nature and ecological complexities of the North Spit dune system and the series of disturbances that have affected it since the turn of the century, it is almost surprising to have found discernible patterns in the invasion of *Ammophila*. The successful application of biological invasion theory to the spread of *Ammophila* on the North Spit substantiates not only the applicability of the theory to highly complex systems, but also the appropriateness of applying the theory to invasions with a history of multiple introductions at multiple foci (Mack 1985).

Based on the life history of *Ammophila* and on biological invasion theory, we would expect *Ammophila* to continue to invade unpopulated and *Leymus*-dominated foredunes elsewhere on the spit. Without active management of the *Ammophila* in the foredunes at the northern end of the study area near Mad River County Park (Figs. 1 and 2), for example, we would expect the dunemat community to eventually be displaced. Inland dunes may continue to support slow *Ammophila* growth in some areas, with greater growth expected in areas open to onshore winds and lesser growth in areas already populated by stabilizing plants such as *Lupinus arboreus*.

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