Yellow Bush Lupine Invasion in Northern California Coastal Dunes I. Ecological Impacts and Manual Restoration Techniques

Andrea J. Pickart[1]
Linda M. Miller[2]
Thomas E. Duebendorfer[3]

Abstract

We studied the ecological effects of the invasion of coastal dunes by *Lupinus arboreus* (yellow bush lupine), an introduced species, and used the results to develop manual restoration techniques on the North Spit of Humboldt Bay. Vegetation and soil data were collected in five vegetation types representing points along a continuum of bush lupine's invasive influence. We collected data on the number and size of shrubs, vegetation cover, and soil nutrients. One set of plots was subjected to two restoration treatments: removal of lupine shrubs only, or removal of all nonnative vegetation and removal of litter and duff. Treatments were repeated annually for four years, and emerging lupine seedlings were monitored for three years. Prior to treatment, ammonium and nitrate were found to increase along the lupine continuum, but organic matter decreased at the extreme lupine end. Yellow bush lupine was not the most significant variable affecting variation in soil nutrients. After four years, nonnative grasses, including *Vulpia bromoides, Holcus lanatus* (velvet grass), *Bromus* spp. (brome), and *Aira* spp. (European hairgrass), were significantly reduced in those restoration plots from which litter and duff was removed. Native species increased significantly in vegetation types that were less influenced by lupine. By the third year, soil variables differed among vegetation types but not by treatment. Bush lupine seedling emergence was higher, however, in plots receiving the litter and duff removal treatment. Based on these results, we conclude that bush lupine invasion results in both direct soil enrichment and indirect enrichment as a result of the associated encroachment of other nonnative species, particularly grasses. Although treatment did not affect soil nutrients during the period of this study, it did reduce establishment of nonnative grasses and recruitment of new bush lupine seedlings. Restoration should therefore include litter and duff removal. In areas that are heavily influenced by lupine and contain few native propagules, revegetation is also required.

[1]The Nature Conservancy, Lanphere-Christensen Dunes Preserve, 6800 Lanphere Road, Arcata, CA 95521, U.S.A.
[2]Center for Natural Lands Management, 6800 Lanphere Road, Arcata, CA 95521, U.S.A.
[3]Humboldt State University, Department of Biology, Arcata, CA 95521, U.S.A.

Introduction

The coastal dunes of Humboldt County, California, have been extensively altered by invasive species. The two species most responsible are *Lupinus arboreus* Sims (yellow bush lupine) and *Ammophila arenaria* (L.) Link (European beachgrass). Since these two species were introduced in the early 1900s, they have come to dominate 83% of the 1077 ha of vegetated foredunes in Humboldt County (Pickart & Sawyer 1998).

Yellow bush lupine is a large shrub up to 2 m in height; it is generally restricted to sandy soils from Ventura County, California, northward to at least Vancouver Island, Washington (Hitchcock & Cronquist 1973; Horn 1993). It is native to dunes in the central and southern portion of its range, but the demarcation between native and naturalized populations in the north remains cloudy (Sholars 1993) despite Davy's (1902) observation that the species was not found north of Point Reyes. The introduction of yellow bush lupine to the Humboldt Bay region in 1908, and its subsequent spread on the North Spit, were documented by Miller (1988).

Changes in species composition as the result of yellow bush lupine invasion in Humboldt County have been inferred by vegetation classification (Parker 1974; Duebendorfer 1990; LaBanca 1993). The native foredune vegetation of northern California consists of low-growing, herbaceous to suffrutescent plants that form a mat-like layer of vegetation, classified as the Sand-verbena–beach bursage vegetation series (Sawyer & Keeler-Wolf 1995). Known colloquially as "dune mat" (Fig. 1), this

Figure 1. Dune mat vegetation type (*Artemisia* phase of the Sand-verbena–beach bursage vegetation series) at the study site. *Artemisia pycnocephala* (coastal sagewort) is the species most visible in the photograph, accompanied by *Solidago spathulata* (dune goldenrod) in the foreground.

vegetation type is variable in cover and frequently contains large amounts of open sand. Two associations of this vegetation type have been described (Pickart & Sawyer 1998). The *Artemisia* phase is distinguished by the presence of *Artemisia pycnocephala* DC. (coastal sagewort), whereas the *Lathyrus* phase is characterized by *Lathyrus littoralis* (Nutt.) Endl. (beach pea). The Yellow bush lupine vegetation series (Sawyer & Keeler-Wolf 1995), also referred to as "lupine scrub," is dominated by a near-continuous canopy of yellow bush lupine, with *Baccharis pilularis* DC. (coyote brush) locally abundant (Fig. 2).

Invading plant species, in addition to their direct, negative effects on native species and plant communities, can also alter ecosystem-level properties such as productivity, nutrient cycling, and soil characteristics (Vitousek 1986; Ramakrishnan & Vitousek 1989). Changes in productivity can occur as the result of both the introduction of a new life form or the addition of a new biological process, such as nitrogen fixation (Vitousek et al. 1987; Vitousek 1990). Prior to invasion by yellow bush lupine, northern California foredunes were both lacking in shrub species and deficient in nitrogen and other macronutrients (Barbour et al. 1985). A nitrogen-fixing species invading a nitrogen-limited community not only has a clear competitive advantage but may release nitrogen into the soil, making it available to other species. At Bodega Bay, California, yellow bush lupine has been shown to create nitrogen-rich resource patches that facilitate the invasion of exotic annual weeds by creating "points of entry" (Alpert & Mooney 1996; Maron & Connors 1996). Once ecosystem-level changes have occurred, the removal of an invading species may not be sufficient to return an ecosystem to its pre-invasion state (Hobbs & Humphries 1995).

The purpose of our study was two-fold. First, we wished to document the ecosystem effects of yellow bush lupine by measuring its contribution, relative to other vegetation variables, to available soil nitrogen and organic matter. Our second objective was to develop a restoration strategy designed to reverse observed ecosystem effects, thereby increasing the chance of long-term restoration success.

Methods

Study Site

The study site was located on the 16-ha Samoa Dunes Endangered Plant Protection Area owned by the U.S. Bureau of Land Management and located at the southern end of the North Spit of Humboldt Bay, northern California. The site contains a mosaic of vegetation types representing a continuum of yellow bush lupine invasion from undisturbed, semi-stable dunes (*Artemisia* phase of dune mat) to completely stabilized, lupine-

Figure 2. Lupine scrub vegetation type (Yellow bush lupine vegetation series) at the study site, characterized by a near-continuous canopy of yellow bush lupine shrubs.

dominated dunes (lupine scrub). Upland dune vegetation on the site was previously classified by means of TWINSPAN, a multivariate classification and ordination program, to describe vegetation (Duebendorfer 1990; Pickart et al. 1990). We selected five vegetation types representing points along the yellow bush lupine gradient ranging from dune mat (lupine absent) to lupine scrub (maximum lupine cover) (Figs. 1 & 2). Intermediate vegetation types were identified in the field with a key developed for this purpose (Appendix); they included mat-lupine, lupine-mat, and lupine-grass (Figs. 3–5). The lupine-grass type was characterized by the presence of abundant, annual, nonnative grasses, including *Bromus hordeaceus* L. (soft chess), *B. diandrus* Roth (ripgut grass), *Vulpia bromoides* (L.) S.F. Gray, *Aira praecox* L. (European hairgrass), and *Aira caryophyllea* L. (silver European hairgrass).

Experimental Design

Two separate samples of vegetation and soil variables were collected. The first sample consisted of 42 variable-sized plots randomly located in the mat-lupine, lupine-mat, lupine-grass, and lupine scrub vegetation types. Plot size ranged from 15 to 80 m^2 as a function of observed vegetation variability. In general, lupine-grass and lupine scrub plots were smaller due to greater homogeneity. Plots were delineated by placing wooden stakes around the perimeter at 1-m intervals.

In each plot we tallied the number of yellow bush lupine individuals by size class ($<$ 15 cm, 15–50 cm, $>$ 50 cm) in order to calculate the density of lupines per square meter. One soil core was collected form a random location in each plot. First, litter was cleared from the soil surface, and then the top 20 cm of soil were collected by means of an 8-cm auger. Soil was analyzed for ammonium by potassium chloride extraction plus steam distillation, for nitrate by potassium chloride extraction and nitrate electrodes, and for organic matter content by loss-on-ignition.

A second sample was designed to permit a more accurate assessment of the correlation between soil and vegetation variables. We located 30 plots in three of the five vegetation types, representing the middle and endpoints of the vegetation continuum (dune mat, lupine-mat, and lupine scrub). Each plot was centered around a randomly placed soil core within the vegetation type and consisted of three nested quadrats of 0.06 m^2, 0.6 m^2 and 1.6 m^2. Cover within each nested subplot was visually estimated for the following vegetation variables: yellow bush lupine, native species, nonnative forbs, nonnative grasses, and litter and duff. The 0.6-m^2 plot size was later selected for use based on minimal variances. Soil cores were collected and analyzed as in the preceding sampling design.

Figure 3. Mat-lupine vegetation type, characterized by the presence of native dune mat species such as *Eriogonum latifolium* (beach buckwheat), right foreground, with relatively low yellow bush lupine influence (right background).

Restoration treatments were tested in the first sample of vegetation and soil plots described above. Prior to treatment, we estimated cover for the following vegetation classes: yellow bush lupine, native species, nonnative forbs, and nonnative grasses. Two treatments were used: (1) removal of yellow bush lupine only and (2) removal of all nonnative species in addition to the litter and duff layer. In the lupine-grass and lupine scrub types, characterized by high lupine cover, only the second treatment was applied, based on past observations that removal of lupine only from severely degraded areas does not result in vegetation changes. There were five replicates and three controls per treatment, resulting in 13 plots for dune mat and mat-lupine (two treatments plus controls) and eight plots for lupine-mat, lupine-grass, and lupine scrub (one treatment plus controls).

Treatments were applied in the spring, following soil and vegetation sampling. In lupine removal plots, yellow bush lupine shrubs were removed manually with hand tools. In litter and duff removal plots we also raked the surface clean of other herbaceous weeds, litter, and duff. A buffer area around all plots was cleared of yellow bush lupine, and dispersal barriers were erected where needed to prevent new dispersal of lupine seeds.

Treatments were repeated annually for four additional years. Vegetation was monitored prior to treatment and annually thereafter. Yellow bush lupine seedling emergence was monitored monthly for three years until emergence ceased, and lupine seedlings were removed as they emerged. Soil sampling was repeated three years after plots were established.

Results

Analysis of variance (ANOVA) revealed that all three soil variables—nitrate, ammonium, and organic matter—differed significantly among vegetation types in the first sample ($p = 0.0009$, 0.0031, and 0.0001, respectively). Data for the dune mat vegetation type were obtained from the second sample, because dune mat was not present in the first sample. Tukey multiple comparisons were used to locate significant differences (Table 1). Results differed for each soil variable, with organic matter exhibiting the greatest number of significant differences among types. Vegetation types at or near the ends of the continuum (dune mat, mat-lupine, and lupine scrub) were significantly different from one another for all three soil variables. In general, levels of all three soil variables increased with the increasing influence of yellow bush lupine, although not all differences were significant. One exception was organic matter, which was lower in lupine scrub than in lupine-grass.

As expected, the density of large lupine shrubs increased with the progression along the lupine-vegetation continuum (Table 2). The number of smaller individuals decreased at the lupine end of the continuum,

Figure 4. Lupine-mat vegetation type, with moderately high yellow bush lupine influence, retains native species such as *Abronia latifolia* (sand-verbena) and *Artemisia pycnocephala* (coastal sagewort), both visible in the right foreground.

however, presumably because mature lupine cover suppressed seed germination and/or emergence. Correlation analysis was used to explore the relationship between density of yellow bush lupine individuals and levels of ammonium ($r = 0.404$, $p = 0.008$), nitrate ($r = 0.304$, $p = 0.001$), and organic matter ($r = 0.398$, $p = 0.009$) in the first sample.

Data from the 0.6-m^2 plots in the second sample were used to perform multiple and step-wise regressions on each soil variable (Table 3). In the step-wise equation for organic matter, four vegetation variables exclusive of yellow bush described virtually 100% of the variation described in the multiple regression ($r = 0.905$, $p = 0.0004$). In the nitrate stepwise equation, only two variables, litter and duff and nonnative forbs, were required to explain all but 0.4% of the variation described by the regression ($r = 0.803$, $p = 0.0013$). Yellow bush lupine entered at the second step in the ammonium regression, accounting for an additional 21% (after nonnative grasses) of the total variation described by the multiple regression ($r = 0.769$, $p = 0.004$).

Effects of Treatment on Species Composition

Changes in mean cover by year and treatment for the three response variables (native species, nonnative forbs, and nonnative grasses) are shown in Figures 6–8. Yellow bush lupine seedlings were removed from plots during recruitment monitoring, so cover values for yellow bush lupine were not analyzed. A repeated measures analysis, with year as the within-subject factor, was performed for each vegetation response variable to identify significant changes in cover over time. For the mat-lupine and lupine-mat vegetation types, the effect of treatment was analyzed as the between-subject factor. Results (Figs. 6–8) demonstrated a fairly continuous increase in native plants over time in the mat-lupine and lupine-mat types ($p < 0.0001$), a small but statistically significant reduction in nonnative forbs between the first and second years in the mat-lupine type ($p = 0.002$), and a decrease in nonnative grasses in all four vegetation types ($p \leq 0.001$). In the mat-lupine and lupine-mat types, nonnative grasses first increased and then decreased below pre-treatment levels. The duff removal treatment reduced nonnative forbs and grasses in both the mat-lupine and lupine-mat types ($p \leq 0.021$).

Because vegetation cover in control plots was not measured in 1992, controls were not included in the ANOVA, but t tests were used to compare mean cover in control plots by vegetation type for the three vegetation variables between 1988 and 1991. No significant differences were detected between years ($p > 0.05$), confirming that changes detected in treated plots were the result of treatments rather than regional vegetation changes over time.

Figure 5. Lupine-grass vegetation type, characterized by high yellow bush lupine influence and nonnative grasses (center foreground).

Effects of Treatment on Soil Variables

We used two-way ANOVA of the third-year soil data (Table 4) to determine whether treatment affected soil variables. A separate ANOVA was used for each soil variable, with vegetation type and treatment as factors. All three soil variables showed significant differences among vegetation type ($p < 0.05$), but there was no difference between treated and control plots, indicating that treatments did not change available nitrogen or organic matter.

Effects of Treatment on Yellow Bush Lupine Recruitment

Emergence of yellow bush lupine seedlings was extremely high in the year following treatment, then decreased dramatically (Fig. 9). Recruitment was higher in litter and duff removal treatments than those in which only lupine was removed. New emergence ceased by the fourth year.

Discussion

Ecological Impacts of Invasion

The initial ANOVAs and multiple comparisons performed on pre-treatment data demonstrated that the nitrate, ammonium, and organic matter varied with respect to vegetation type. Nitrate and ammonium were both highest in the lupine scrub type. Organic matter was unique in that lupine scrub, at the end of the lupine-vegetation continuum, was characterized by lower values than lupine-grass. As expected, the density of large yellow bush lupine shrubs increased with progression along the lupine-vegetation continuum. These results suggested a simple linear relationship. Despite the fact that both lupine density and soil nutrients increased along the lupine continuum, however, there was not a high correlation between them, implying that lupine abundance is not solely or primarily controlling nutrient levels.

Multiple and step-wise regression analysis of the second data set confirmed that vegetation variables other than yellow bush lupine may be influencing soil variables. Ammonium, the product of symbiotic bacteria in the root nodules of yellow bush lupine (Holton et al. 1991), was the only stepwise equation entered by lupine as a vegetation variable. Nearly all of the variation in nitrate was accounted for by litter and duff and nonnative forbs. The source of the litter and duff could not be determined, but it is probable that lupine contributed significantly because it is large, fast-growing, and short-lived (Davidson & Barbour 1997). Nonnative forbs and grasses accounted for 91% of the variation in organic matter. The influence of nonnative grasses on organic matter can be explained by their fibrous root systems, which provide organic matter that is easily incorpo-

Table 1. Means of soil variables (nitrate, ammonium, and organic matter) by vegetation type, and results of Tukey multiple comparisons showing differences among vegetation types.*

Mean	*Tukey Grouping*	*Vegetation Type*	*Position Along Lupine Continuum*
Nitrate (ppm)			
5.89	A	Dune mat	1
8.46	AB	Mat-lupine	2
9.00	ABC	Lupine-mat	3
11.25	B	Lupine-grass	4
13.00	C	Lupine scrub	5
Ammonium (ppm)			
4.62	A	Mat-lupine	2
4.89	A	Dune mat	1
6.31	AB	Lupine-mat	3
7.00	AB	Lupine-grass	4
9.25	B	Lupine scrub	5
Organic matter (%)			
5.88	A	Dune mat	1
8.46	A	Mat-lupine	2
9.00	B	Lupine-mat	3
11.25	C	Lupine scrub	5
13.00	D	Lupine-grass	4

*Significant differences ($p \leq 0.05$) are identified by different letters. The position of each vegetation type along the lupine influence continuum is indicated along a scale from 1, least influence, to 5, most influence.

rated into the soil at shallow depths (Hausenbuiller 1975). This would also explain why the lupine-grass vegetation type was higher in organic matter than lupine scrub.

These findings suggest that the invasion of yellow bush lupine into a nitrogen-deficient dune environment creates complex changes in soil and vegetation. Lupine directly results in soil enrichment, particularly of ammonium, during both growth and decay. A similar phenomenon was described by Vitousek (1986, 1990), who studied ecosystem changes resulting from the invasion of *Myrica faya* Ait., a nitrogen-fixing tree, into young volcanic substrates in Hawaii. Nitrogen fixation by *Myrica* was found to alter both the quantity and availability of nitrogen. In addition to the direct affects of yellow bush lupine invasion on soils, changes may occur indirectly by the facilitation of colonization by nonnative grasses and forbs that further enrich the soil.

The role of soil fertility in plant invasions has been examined in several recent studies. Burke and Grime

Table 2. Mean density of nonseedling yellow bush lupine individuals by size class and vegetation type.*

Vegetation Type	*Position Along Lupine Continuum*	*Mean Lupines/m² (SD) 15–50 cm*	*Mean Lupines/m² (SD) > 50 cm*	n
Mat-lupine	1	0.19 (0.11)	0.09 (0.04)	13
Lupine-mat	2	0.25 (0.25)	0.28 (0.12)	13
Lupine-grass	3	0.16 (0.16)	0.43 (0.20)	8
Lupine scrub	4	0.03 (0.05)	0.52 (0.39)	8

*The position of each vegetation type along the lupine continuum is indicated along a scale from 1, least abundant, to 4, most abundant.

Table 3. Results of multiple (total *r*) and step-wise regressions ($p < 0.005$) of vegetation variables (as independent variables) on soil variables (as dependent variables).

Variable	r
Organic matter	
Nonnative forbs	0.581
Nonnative grasses	0.821
Litter and duff	0.843
Native species	0.904
Total *r*	0.905
Nitrate	
Litter and duff	0.769
Nonnative forbs	0.800
Total *r*	0.803
Ammonium	
Nonnative grasses	0.620
Bush lupine	0.767
Total *r*	0.769

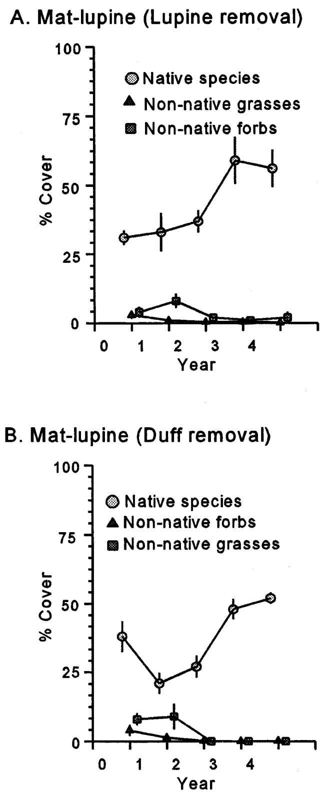

Figure 6. Changes in mean cover (±SE) of native species, nonnative forbs, and nonnative grasses in the mat-lupine vegetation type, lupine removal treatment (a) and litter and duff removal treatment (b) over the four years of the study.

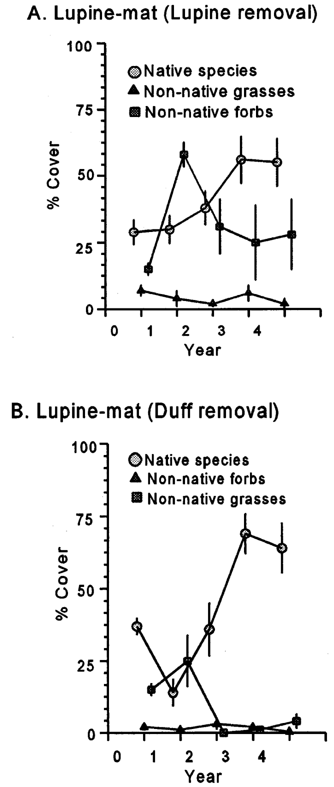

Figure 7. Changes in mean cover (± SE) of native species, nonnative forbs, and nonnative grasses in the lupine-mat vegetation type, lupine removal treatment (a) and litter and duff removal treatment (b) over the four years of the study.

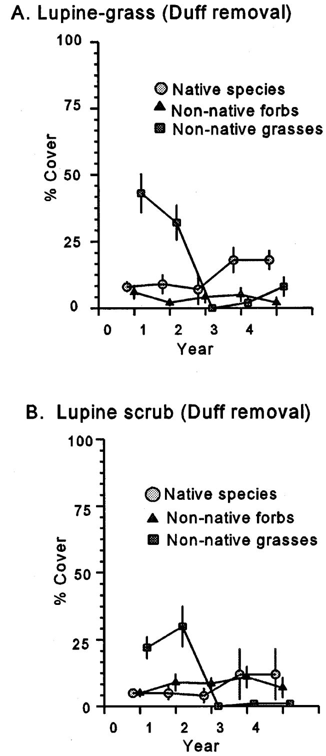

Figure 8. Changes in mean cover (± SE) of native species, nonnative forbs, and nonnative grasses in the lupine-grass vegetation type (litter and duff removal treatment) (a) and the lupine scrub vegetation type (litter and duff removal treatment) (b) over the four years of the study.

(1996) demonstrated the importance of fertility changes in predicting plant invasions in a nutrient-limited ecosystem in the United Kingdom. In the dune system at Bodega Bay, California, yellow bush lupine, a putative native, was responsible for the invasion of nonnative grasses through enhanced soil productivity (Maron & Connors 1996). Zink et al. (1996) found that disturbance caused by a pipeline placed through several intact southern California plant communities resulted in the proliferation of exotic annual plants, which in turn

Table 4. Mean and standard deviation of soil variables (ammonium, nitrate, and organic matter) by vegetation type and treatment in the third year of the study ($n = 5$ per treatment type; $n = 3$ per control).

	Vegetation Type							
	Mat-lupine		*Lupine-mat*		*Lupine-grass*		*Lupine Scrub*	
Treatment	*Mean*	*(s)*	*Mean*	*(s)*	*Mean*	*(s)*	*Mean*	*(s)*
Ammonium (ppm)								
Lupine removal only	2.26	(1.72)	2.40	(0.73)	—	—	—	—
Lupine plus duff removal	1.94	(0.65)	2.86	(1.84)	2.96	(1.31)	3.62	(1.19)
Control	1.70	(0.18)	2.52	(1.07)	2.19	(0.83)	3.96	(2.41)
Nitrate (ppm)								
Lupine removal only	4.07	(1.16)	4.46	(1.01)	—	—	—	—
Lupine plus duff removal	3.74	(0.58)	3.66	(0.54)	4.70	(0.83)	5.89	(1.38)
Control	3.43	(0.25)	6.38	(0.46)	3.84	(1.86)	5.90	(1.65)
Organic matter (%)								
Lupine removal only	0.54	(0.13)	0.89	(0.56)	—	—	—	—
Lupine plus duff removal	0.56	(0.22)	0.63	(0.30)	1.17	(0.33)	1.05	(0.38)
Control	0.45	(0.17)	0.60	(0.10)	1.24	(0.20)	1.36	(0.13)

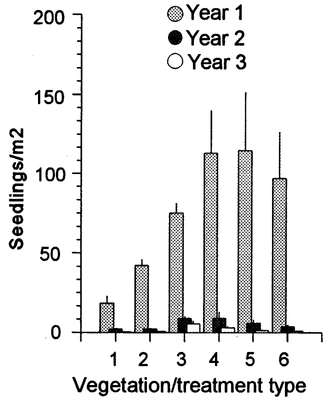

Figure 9. Yellow bush lupine seedling emergence (mean seedlings/m^2) by vegetation per treatment type (error bar denotes SE). 1, mat-lupine, lupine removal; 2, mat-lupine, duff removal; 3, lupine-mat, lupine removal; 4, lupine-mat, duff removal; 5, lupine-grass; 6, lupine scrub.

caused unstable litter and increased mineralization, favoring the persistence of weedy over indigenous species.

Restoration

Restoration treatments resulted in a decrease in nonnative grasses and sometimes forbs, and/or an increase in native species cover over a 4-year period. Only those vegetation types less strongly influenced by yellow bush lupine (mat-lupine and lupine-mat) experienced significant increases in native cover. The increase in native cover observed in mat-lupine and lupine-mat may have been caused by the release of nutrients associated with dead lupine roots in addition to competitive release. The lack of change in native species cover in vegetation types more heavily influenced by lupine was most likely due to the absence of remnant native plants or nearby sources for dispersal.

Annual, nonnative grasses decreased in all four vegetation types. It has been previously observed that grasses are frequently the species to respond and dominate—to the detriment of broad-leaved plants—under nutrient enhancement (Hobbs & Huenneke 1992). The decline of grasses in the more lupine-influenced vegetation types (lupine-grass and lupine scrub) was the most dramatic. In the lupine-mat type, grasses initially increased following treatment, probably due to competitive release. In the litter and duff removal treatments grasses eventually declined, but in the lupine-only treatment grasses never returned to pre-treatment levels. Removal of the litter and duff layer has similarly been shown to be effective in preventing recolonization of sand dunes by weedy grasses on the Great Lakes (Choi & Pavlovic 1994).

Nonnative forbs underwent little change during the 4-year period of the study, although even the minor changes that occurred as a result of the litter and duff removal treatment in the mat-lupine type were statistically significant. Nonnative forb-cover values were initially low, and reductions may not have been essential to restoration.

After three years, treated plots did not differ significantly from controls in levels of available nitrogen and organic matter. The lack of effect of treatment on soil variables implies that a reduction in nitrogen and/or organic matter is not a prerequisite for the restoration of lupine-influenced dunes, despite the fact that soils underlying native vegetation are deficient in nitrogen. But there are several caveats to this conclusion. First, because this sample represents a single slice in time, it is possible that soil variables initially increased after removal of vegetation from plots. A subsequent decline would then be masked, and the net result would be indistinguishable from control plots. It is also possible that soil changes are lagging behind vegetation changes and may be more noticeable in the future.

Monitoring of yellow bush lupine recruitment demonstrated that seedling emergence is stimulated by removal of the litter and duff layer. But if treatment is continued for at least three years this can be considered a benefit, because the seedbank is presumably being depleted. Lupine seeds are characterized by a hard seed coat (Murdoch & Ellis 1992) and, without the disturbance or temperature fluctuations associated with removal of litter and duff, may remain in the soil and continue to emerge for a longer period.

These results have led to a restoration protocol for dunes invaded by yellow bush lupine. In addition to the removal of lupine, other nonnatives (especially nonnative grasses) and litter and duff should be cleared from the site, even in newly invaded areas, to discourage recolonization of lupine and other weeds. Treatment must be repeated for at least three years in order to deplete the weedy and lupine seedbanks. In areas where yellow bush lupine has become heavily established, revegetation with natives will be necessary if a source of propagules is lacking.

Acknowledgments

Funding for this study was provided by Louisiana-Pacific Corporation, Simpson Timber Company, The Nature Conservancy, the U.S. Bureau of Land Management, and the California Department of Fish and Game Endangered Plant Program. We thank J. Sawyer for his contributions to the study, M. Barbour for facilitating soils testing, and A. Buell for her review. Comments by Associate Editor Edith Allen and two anonymous reviewers were very helpful.

LITERATURE CITED

Alpert, P., and H. A. Mooney. 1996. Resource heterogeneity by shrubs and topography on coastal sand dunes. Vegetatio **122:**83–93.

Barbour, M. G., T. M. DeJong, and B. M. Pavlik. 1985. Marine beach and dune plant communities. Pages 296–322 in B. F. Chabot and H. A. Mooney, editors. Physiological ecology of North American plant communities. Chapman and Hall, New York.

Burke, M. J., and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology **77:**776–790.

Choi, Y. D., and N. D. Pavlovic. 1994. Comparison of fire, herbicide, and sod removal to control exotic vegetation. Natural Areas Journal **14:**217–218.

Davidson, E. D., and M. G. Barbour. 1997. Germination, establishment, and demography of coastal bush lupine (*Lupinus arboreus*) at Bodega Head, California. Ecology **58:**592–600.

Davy, J. B. 1902. Stock ranges of northwestern California: notes on the grasses and forage plants and range conditions. Bulletin no. 12 of the Bureau of Plant Industry, U.S. Department of Agriculture. Government Printing Office, Washington, D.C.

Duebendorfer, T. E. 1990. An integrated approach to enhancing rare plant populations through habitat restoration. II. Habitat characterization through classification of dune vegetation. Pages 478–487 in T. M. Bonnicksen and H. G. Hughes, editors. Restoration '89: the new management challenge. Society of Ecological Restoration, Madison, Wisconsin.

Hausenbuiller, R. L. 1975. Soil science, principles and practices. William C. Brown, Dubuque, Iowa.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest: an illustrated manual. University of Washington Press, Seattle.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology **6:**324–337.

Hobbs, R. J., and S. E. Humphries. 1995. An integrated approach to the ecology and management of plant invasions. Conservation Biology **9:**761–770.

Holton, B., M. G. Barbour, and S. N. Martens. 1991. Some aspects of the nitrogen cycle in a California strand ecosystem. Madroño **38:**170–184.

Horn, E. L. 1993. Coastal wildflowers of the Pacific Northwest. Mountain Press Publishing Company, Missoula, Montana.

LaBanca, T. 1993. Vegetation changes at Clam Beach coastal dunes, Humboldt County, California. M.A. thesis. Department of Biology, Humboldt State University, Arcata, California.

Maron, J. L., and P. G. Connors. 1996. A native nitrogen-fixing shrub facilitates weed invasion. Oecologia **105:**302–312.

Miller, L. M. 1988. How yellow bush lupine came to Humboldt Bay. Fremontia **16:**6–7.

Murdoch, A. J., and R. H. Ellis. 1992. Longevity, viability and dormancy. Pages 193–230 in M. Fenner, editor. Seeds: the ecology of regeneration in plant communities. CAB International, Wallingford, United Kingdom.

Parker, J. 1974. Coastal dune systems between Mad River and Little River, Humboldt County, California. M.A. thesis. Department of Biology, Humboldt State University, Arcata, California.

Pickart, A. J., and J. O. Sawyer. 1998. Ecology and restoration of northern California coastal dunes. California Native Plant Society. Sacramento, California.

Pickart, A. J., T. E. Duebendorfer, and L. M. Miller. 1990. An integrated approach to enhancing rare plant populations through habitat restoration. III. Restoration of altered coastal dunes. Pages 488–500 in H. G. Hughes and T. M. Bonnicksen, editors. Restoration '89: the new management challenge. Society for Ecological Restoration, Madison, Wisconsin.

Ramakrishnan, P. S., and P. M. Vitousek. 1989. Ecosystem-level processes and the consequences of biological invasions. Pages 281–300 in J. A. Drake, H. A. Mooney, F. Di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. Wiley, New York.

Sawyer, J. O., and T. Keeler-Wolf. 1995. A manual of California vegetation. California Native Plant Society, Sacramento, California.

Sholars, T. 1993. Lupines. Pages 622–636 in J. C. Hickman, editor. The Jepson manual: higher plants of California. University of California Press, Berkeley.

Vitousek, P. M. 1986. Biological invasions and ecosystem properties: can species make a difference? Pages 163–176 in H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York.

Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos **57:**7–13.

Vitousek, P. M., L. R. Walker, L. D. Whiteaker, D. Mueller-Dombois, and P. A. Matson. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science **238:** 802–804.

Zink, T. A., M. F. Allen, B. Heindl-Tenhunen, and E. B. Allen. 1996. The effect of a disturbance corridor on an ecological reserve. Restoration Ecology **3:**304–310.

Appendix. Vegetation types studied.

A. Lupine absent	Dune mat (Fig. 1)
A. Lupine present	B
B. Total plant cover < 80%; yellow bush lupine cover < 25%; dune mat species present	Mat-lupine (Fig. 2)
B. Total plant cover > 80%; yellow bush lupine cover > 25%; dune mat species present or absent	C
C. Dune mat species (except *Solidago*) > 25%	Lupine-mat (Fig. 3)
C. Dune mat species (except *Solidago*) < 25%	D
D. Yellow bush lupine cover < 75%; nonnative grasses > 25%	Lupine-grass (Fig. 4)
D. Yellow bush lupine cover > 75%	Lupine scrub (Fig. 5)