SECONDARY SUCCESSION AND THE FATE OF NATIVE SPECIES IN A CALIFORNIA COASTAL PRAIRIE COMMUNITY

THEODORE C. FOIN
Division of Environmental Studies, University of California, Davis 95616

MARY M. HEKTNER
U.S. National Park, Service, Redwood National Park, Orick, CA 95555

ABSTRACT

Secondary succession in former sheep pastures in the northern California coastal prairie favors cover dominance by perennials, especially grasses. Studies of secondary succession at Sea Ranch, Sonoma County, show that the relative cover is dominated increasingly by *Anthoxanthum odoratum,* an introduced perennial grass. Native species are not successful at increasing their cover during succession and are unlikely to regain cover dominance in the coastal prairie.

Historically, large parts of the California coastal prairie were used for grazing by domestic animals. One of the main effects of grazing in this grassland is a change in species composition, accomplished by selection against grazing-intolerant species. Grazing has been implicated as a major factor in the change of vegetation in the Central Valley (Burcham 1957), and is likely to have been important in the coastal zone as well, although such changes have never been documented.

Secondary succession may be defined as the predictable sequence of species replacements occurring after a disturbance such as grazing defoliation. It differs from primary succession only in that the latter is assumed to start from a substrate that has not been occupied previously by any vegetation. Secondary succession is the key ecological process governing change in species composition once grazing pressure is reduced or eliminated, and thus successional studies may reveal whether or not the natural recovery process can ameliorate the effects of grazing (see McIntosh 1980).

The classic expectation of the effects of secondary succession are based on early work by Clements (1916), who argued that succession would favor native species, which are well adapted to each other and their physical environment. Invaders and weedy species, however, would be crowded out eventually and recovery to the original climax vegetation would be complete. More recently, Heady and others (1977) have predicted that "introduced plants will continue

MADROÑO, Vol. 33, No. 3, pp. 189–206, 1986

to be abundant on many hectares of coastal prairie, but succession will apparently move rapidly toward dominance of perennial grasses if land management practices are suitable." This is a modified Clementsian view, which recognizes that invading species may not be so easily displaced. Heady refers specifically to the replacement of introduced annuals by native perennial grasses in the coastal prairie. Although introduced Mediterranean annuals are commonly treated as the dominant vegetation of interior valleys, they have been as abundant in the coastal prairie flora, at least in range systems.

Studies in secondary succession would appear to be useful in California prairies for several basic and applied reasons. There are a number of succession models proposed (e.g., Connell and Slatyer 1977, Shugart 1984) that could be tested using California vegetation. On the other hand, range and reserve managers could use such information in management and restoration activities. Despite the obvious need, secondary succession in the coastal prairie is not well known at present. Those few studies that exist suggest that native species may dominate the vegetation as succession proceeds. Huffaker and Kennett (1959) showed that perennial grasses, especially one native species (*Danthonia californica*) replaced an introduced perennial (*Hypericum perforatum*) known as Klamath weed, following successful biological control by the Klamath weed beetle (*Chrysolina hyperici*) in the coastal prairie of Humboldt County.

Elliott and Wehausen (1974) analyzed cover in three plots with different grazing pressure in Point Reyes National Seashore. Their data predict that the coastal shrub *Baccharis pilularis* and the native perennial bunchgrass *Deschampsia holciformis* would increase during succession. Lathrop and Gogan (1985) surveyed the Tule Elk Range at Tomales Point, immediately to the north of the area studied by Elliott and Wehausen. They argued that shrubs would dominate secondary succession in wind-protected areas, but that perennial grasses would also increase (particularly the native perennial *Stipa pulchra* Hitchcock). The invasion of prairie by northern coastal scrub is indicated by their data, and is more strongly suggested by the work of McBride and Heady (1968) and McBride (1974). It is not clear, however, that the coastal prairie is a seral stage whose climax is ultimately shrub or forest dominated.

Despite the evidence suggesting the successional superiority of native species over introduced species, it is far from conclusive. A number of counter examples, demonstrating the tenacity of invading species, also exists; perhaps the best example is that of *Bromus tectorum* in the Great Basin (Harris 1967, Mack 1981). The literature pertaining to the emergence of natives during succession in California prairies also does not support the theory. White (1967) claimed that *Stipa pulchra* should be one of the climax dominants in the oak woodland at Hastings Reservation in Carmel Valley, and Burcham

(1957) hypothesized that the same species dominated the primeval Central Valley prairies. On the other hand, Wester (1981) has used historical records to argue that perennial grasses did not dominate the inland prairies now dominated by introduced annuals, except in wet places. Bartolome and Gemmill (1981) showed experimentally that *Stipa pulchra* was competitively inferior to *Bromus mollis* at high densities. Their evidence makes it clear that there may be great differences between species, and that being "native" does not necessarily confer a competitive advantage over introduced species.

Even the theoretical expectation is fragile because it was based on a number of assumptions that have been proven erroneous, the largest of which was the assumption of evolutionary advantage in a highly coevolved plant community (for a good discussion of the contribution of Clements to modern plant ecology see McMahon 1980). These arguments may be used to challenge the importance of the community in succession and to emphasize the importance of the population dynamics of "key" species in governing the outcome of succession (Foin and Jain 1977, Westoby 1979, McIntosh 1981).

To evaluate the dominance of native versus introduced plants in secondary succession of coastal prairie, we conducted chronosequential studies at Sea Ranch, Sonoma Co., California (38°40′N, 123°24′W) in 1974. An earlier paper (Hektner and Foin 1977) examined differences in the vegetation in different areas of the Sea Ranch coastal prairie using the data obtained in the summer of 1974. The present paper reports the results of succession based on the 1974 census and additional samples taken in 1975–1978. Detailed information on site conditions, species present, and land use history may be found in the 1977 paper.

Study Areas

Sea Ranch is a recreational subdivision 180 km north of San Francisco. It occupies 16 km of the coastal terrace from Stewarts Point northward to the Mendocino Co. line. Homesites have been developed such that large areas of meadow and forest have been preserved as permanent open space. Sea Ranch includes two uplifted marine terraces with sandy loams (Baywood and Rohnerville series: U.S. Dept. Agr. 1972) overlying sandstone and basalt. All study areas reported in this paper are located in the commons areas of the first terrace (that terrace adjacent to the coast) and were protected from grazing, fire, mowing, and other overt management for the duration of the study. Disturbance of the vegetation was not excluded completely because soil disturbance by gophers and moles, grazing by insects, rabbits, deer, and mice, and limited trampling by hikers were all present. Three study areas were sampled, the names of which

FIG. 1a. Photograph of Lone Tree Meadow taken in June 1984. The photograph was taken from the top of the slope looking to the northwest. The white stakes mark the location of soil moisture monitoring stations. The light-colored vegetation in the foreground is an annual-*Rytidosperma* patch. The vegetation behind it is the wet-type (*Deschampsia-Holcus-Anthoxanthum*). The vegetation to the left side is mostly *Anthoxanthum odoratum*.

FIG. 1b. Aerial photograph of Buck Meadow looking east-northeast, 8 Jul 1975. There is a prominent hedgerow (composed of Monterey cypress) to the right. The light dots are scattered *Lupinus arboreus* Sims. One set of vehicle tracks and several trails made during the 1974 vegetation survey are evident in the photograph.

are traditional ones used by the previous owner of the ranch (the late E. J. Ohlson).

Lone Tree Meadow. This study area is a 160 × 80 m rectangular grid located on a northwest-facing slope, approximately 300 m from the ocean to its western boundary (Fig. 1a). The site is unprotected from the prevailing northwesterly winds. It was the one area of the former sheep ranch that was used most intensively, particularly for year-round herds of ewes and their lambs. Estimates of stocking rates are not available.

Buck Meadow. This study area is a 200 × 300 m rectangle with the seaward edge 100 m from the coast bluff (Fig. 1b). This site is flat, with no pronounced slope. It was named for its grazing history: it was used as the ram (buck) pasture. Ohlson noted that ram densities were always low, particularly in later years when stock densities were falling rapidly.

Stable Meadow. This site is the only study area available on Sea Ranch that is still grazed. The area is fenced-off and used as a pasture and paddock for horses. Use rates are low but continuous, on the order of 2 animals per ha. Vegetative biomass is low, making the site visually distinctive, and there appears to be at least as much damage from hooves breaking the soil surface as from defoliation. The area sampled (50 × 50 m) is approximately 120 m from the coastal bluff, in the center of the pasture, with a gentle west-facing slope towards the ocean. Other than its present use, Stable Meadow is very similar in slope and aspect to Buck Meadow.

The Sea Ranch lands were used for grazing purposes from the late 19th century to 1968. Small parts were used experimentally for agriculture, but those experiments were unsuccessful. In 1965, when the ranch was sold for development, sheep were removed progressively from south to north, until the last sheep were sold in 1968. Lone Tree and Buck meadows remained under grazing until 1968.

METHODS

Sampling procedure. The sampling methodology followed in this study used line transects established for the initial survey in 1974. Complete details of the methodology are found in Hektner and Foin (1977). In brief, line transects were established randomly, one transect each 10 m, and sample locations were taken randomly, one for each 10 m of transect length. Cover estimations were made using the Domin index, as modified by Major from Evans and Dahl (1955), using 0.25 m^2 circular quadrats.

Stable Meadow was sampled using 30 quadrats in 1978 to establish a frame of reference for the other two sites. Lone Tree Meadow was sampled three times (1974, 1976, 1978) at 143 quadrat locations.

Buck Meadow was sampled twice (1975, 1978) at 242 quadrat locations.

Two possible problems exist in the methodology used. First, placement of the quadrat sampling ring was not centered on the permanent marking stake (which was on the transect line), but was offset to avoid sampling pathways. This procedure did not permit precise relocation of the quadrat in subsequent censuses. Second, all sites were sampled late in the summer (August and September). This is an artifact of the first census (1974) because all later censuses were made at the same time to maximize year-to-year comparability. Sampling earlier in the summer, when the grass species were clearly identifiable, but annuals were more evident in the field, would have been preferable. Although annuals, especially forbs, were undoubtedly underrepresented in our results, it is the comparative aspect and trend in time that we required. These two aspects of the data are least sensitive to absolute bias in cover estimates.

Treatment of cover data. The Domin value of each species in each quadrat was converted first from its index value, each of which covers a range of percent cover, to the midpoint of the range for that value. This follows the procedure used by Hektner and Foin (1977). The converted Domin values were then calculated to yield four indices: *absolute cover,* the sum of converted Domin values for each species over all quadrats; *relative cover,* the percent representation of a given species over all quadrats as a fraction of the cover attributable to all species; *mean cover,* the mean absolute cover per quadrat; and *adjusted mean cover,* the mean absolute cover calculated only for those quadrats in which the species occurred.

Error bars were taken as $\pm$ 2 s.e. (standard errors) on mean cover. Nonoverlapping error bars were used as tests of significant differences between means with $\alpha = 0.05$. This procedure is more conservative, i.e., it has smaller Type I error, than standard parametric confidence limits unless df $\leq$ 5 (see Steele and Torrie 1960). None of the comparisons was based on so few degrees of freedom.

Assignments of life form were made using Reed et al. (1963). Five classes were used: annual forbs, perennial forbs, annual grasses, perennial grasses, and "other life forms". The last category is composed primarily of three species: *Pteridium aquilinum* var. *pubescens, Rubus ursinus,* and *Linum bienne.* All nomenclature follows Munz (1973), except for *Deschampsia holciformis* (Crampton 1974) and *Rytidospermum pilosum* (=*Danthonia pilosa*).

RESULTS

Successional Changes in Life Form Composition

Species data from the three censuses of Lone Tree Meadow are aggregated into life form groups and plotted in Fig. 2. This plot

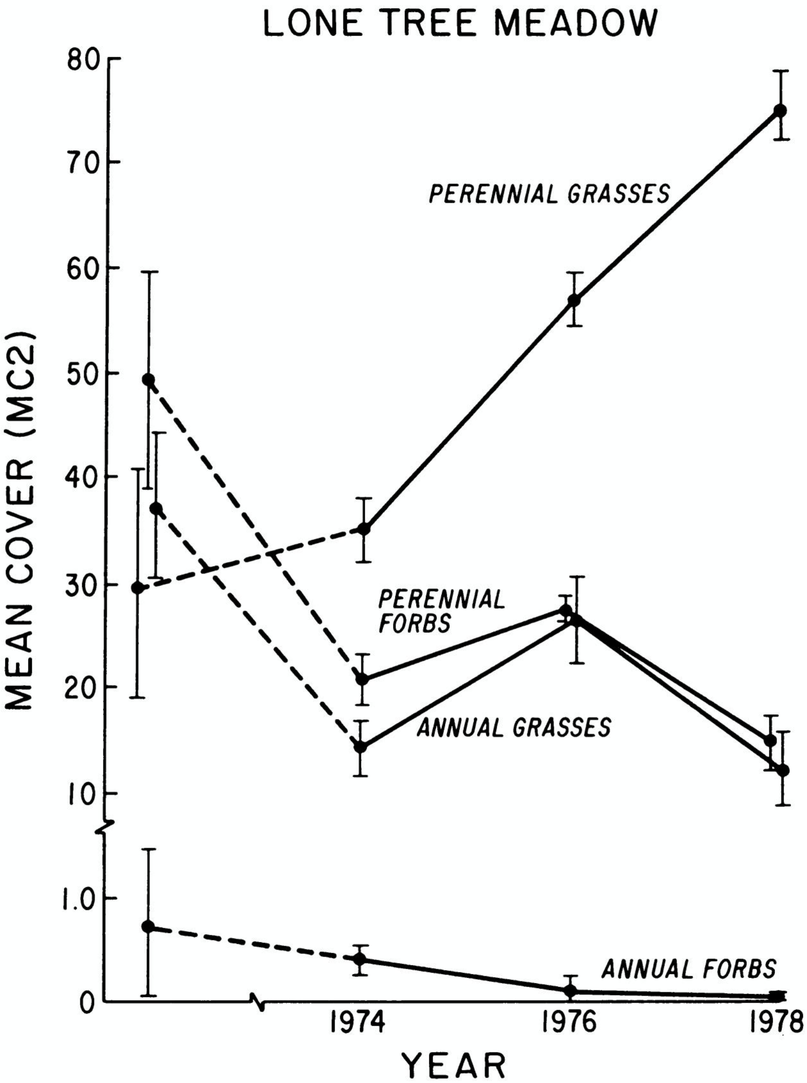

FIG. 2. Mean cover trends (MC2) for life forms in Stable Meadow (leftward points) and Lone Tree Meadow, 1974–1978. Error bars are ±2 standard errors.

shows mean cover for each of the major life forms except "other life forms". The three censuses in Lone Tree Meadow are plotted with the data from Stable Meadow displayed at the extreme left. The Stable Meadow data are included to provide an indication of the structure of the presuccessional coastal prairie vegetation. Because these data are only an indication of life form mean cover values for Lone Tree Meadow, these points are connected to the 1974 data with dashed lines. In any case, the extrapolations must be viewed cautiously, because environmental differences between sites and differences between sheep and horse grazing could be very important (Harper 1977). Note that annual forbs comprise so little of the total cover that the ordinate in Fig. 2 must be broken in order to include them. Two s.e. confidence intervals do not overlap in the following comparisons: 1) the mean cover of annual forbs decreased from 1974–1978; 2) annual grasses increased from 1974 to 1976 and decreased from 1976–1978; 3) perennial forbs increased from 1974 to 1976, and decreased from 1976–1978 and from 1974–1978; and 4) perennial grasses increased in cover at each sampling period. Lone Tree Meadow had less cover for annual grasses and perennial forbs than Stable Meadow for all three sampling periods, and had greater cover in perennial grasses for 1976 and 1978.

Figure 3 shows the cover data for Buck Meadow arranged in the same fashion as the data in Fig. 2. Using the same comparisons, annual grasses showed a decrease in cover, whereas perennial grasses showed an increase over the period 1975 to 1978. Neither forb group showed a significant change over this period. Comparison to Stable Meadow data shows (1) no significant differences for annual forbs; (2) significantly higher cover for annual grasses in Buck Meadow in 1978; (3) significantly lower cover in perennial forbs for both years; and (4) a significant difference for perennial grasses by 1978.

Comparison of Figs. 2 and 3 illustrates that trends in life forms in each site were similar. Annual forbs were not common in either site and did not have significantly higher cover in Stable Meadow. This situation, however, is likely to be an artifact of the timing of sampling, because adjacent sheep meadows can support a variety of annual forbs, especially when heavily grazed. Both annual grasses and perennial forbs decreased during succession, which is particularly evident in the Lone Tree Meadow data. Perennial grasses increased significantly to similar cover values in both sites. Lone Tree and Buck Meadows showed decreasing cover in perennial forbs and, with time, more perennial grasses than Stable Meadow.

This trend can be seen more easily in a plot of relative cover (Fig. 4). These data are separate estimates for Lone Tree and Buck Meadows, except for 1978, which is the arithmetic average for both sites. The figure shows a decrease in relative cover for all categories and for bare ground, except for perennial grasses and "other life forms". Bare ground never exceeded 5% relative cover at Sea Ranch, and decreased to less than 1% of the relative cover in the 1978 censuses.

Successional Changes in Species Composition

Principal seral dominants during succession. The majority of the species encountered in the quadrats were infrequent and low in

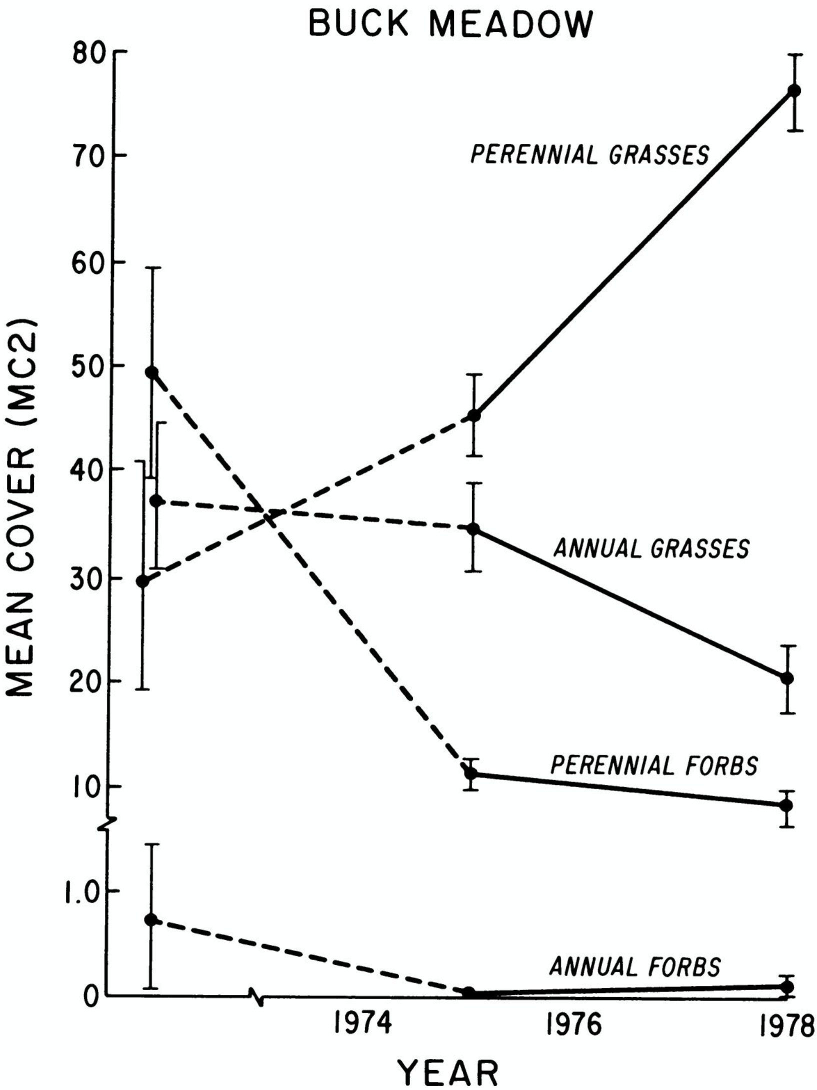

FIG. 3. Mean cover trends for Stable Meadow compared to Buck Meadow, 1975–1978. Arrangement of this figure corresponds to that of Fig. 2.

cover. We used two criteria to single out those species that had high cover values at one census or another: 1) any species that occurred in five or more quadrats at any one of the three sites in one or more census periods, and 2) that also had 1% relative cover in the site for which criterion (1) was met. Application of these criteria excludes all annual forbs and reduces the list to 19 species (Table 1).

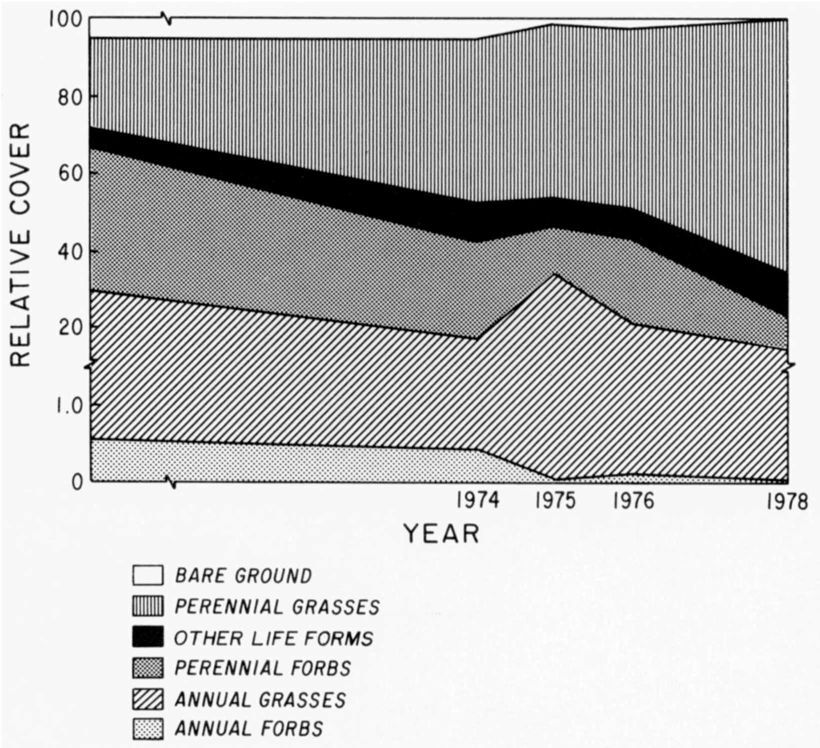

FIG. 4. Relative cover assigned to all life forms and to bare ground for Lone Tree and Buck Meadows; 1978 is the average for both sites. Relative cover for Stable Meadow is given at the left end of the abscissa, as done in Figs. 2 and 3.

The species in Table 1 are arranged by life form. Absolute cover (AC) and frequency in sample quadrats are tabulated for all 19 species meeting the criteria outlined above for each survey of the three sites sampled. There is sufficient consistency among the results shown in Table 1 to suggest successional patterns in the species as well as the life forms. The species that had high frequency also had high absolute cover. The dominants of early and later stages in succession are readily identified from this table, assuming Stable Meadow represents the starting point. *Cynosurus echinatus* is an example of an annual that showed high cover and frequency in Stable Meadow and in early surveys of the other two sites. Other examples of characteristic species of earlier successional stages, which followed the termination of grazing, include *Plantago lanceolata, Linum bienne, Lolium perenne,* and *Rytidosperma pilosum.*

Changes in species composition may be identified by considering significant changes in mean cover (Table 2). All but one of the early

TABLE 1. IMPORTANT SPECIES IN THE SUCCESSIONAL SEQUENCE IN THE COASTAL PRAIRIE AT SEA RANCH. N = native species; I = introduced species. Frequency is in quadrats and absolute cover is the sum of mean Domin values for each species.

	Lone Tree Meadow						Buck Meadow				Stable Meadow	
	Frequency			Absolute cover			Frequency		Absolute cover		Fre-quency	Abso-lute cover
Species	1974	1976	1978	1974	1976	1978	1975	1978	1975	1978	1978	1978
Annual grasses												
Aira caryophyllea (I)	90	51	31	345	179	368	104	21	422	128	5	47
Bromus mollis (I)	66	54	18	58	1399	118	171	101	6722	2458	25	254
Cynosurus echinatus (I)	94	83	44	1538	1144	124	62	9	127	49	20	494
Hordeum leporinum (I)	0	0	0	0	0	0	0	0	0	0	5	188
Vulpia bromoides (I)	43	25	31	26	382	1182	169	69	1128	2064	20	114
Perennial forbs												
Corethrogyne californica (N)	1	0	0	2	0	0	18	4	564	204	0	0
Hypochoeris radicata (I)	42	42	7	102	398	78	53	12	62	46	4	18
Iris douglasiana (N)	26	31	33	375	450	709	0	1	0	42	2	50
Plantago lanceolata (I)	106	100	76	2284	2415	1048	195	92	1530	566	27	1402
Rumex acetosella (I)	16	12	3	16	29	6	102	69	454	472	0	0
Perennial grasses												
Anthoxanthum odoratum (I)	102	111	131	2062	4514	7540	170	192	6298	10,038	0	0
Rytidosperma pilosum (I)	91	60	46	1210	936	638	184	159	3272	5598	9	118
Deschampsia holciformis (N)	34	34	29	1547	1888	1761	4	9	251	396	0	0
Holcus lanatus (I)	31	23	37	174	352	758	87	85	939	1986	0	0
Lolium perenne (I)	22	28	7	12	202	6	0	0	0	0	19	779
Other life forms												
Juncus bufonius (N)	4	0	0	16	0	0	0	0	0	0	9	69
Linum bienne (I)	67	51	34	62	68	56	67	40	34	92	19	130
Pteridium aquilinum (I)	13	15	13	158	266	210	50	82	1200	2482	0	0
Rubus ursinus (N)	62	62	83	774	905	1412	39	53	335	652	0	0
Total actual cover				11,976	17,884	16,798			23,962	28,490		3965
Total quadrat	143	143	143				242	242			30	

TABLE 2. MEAN COVER ESTIMATES AND STANDARD ERRORS FOR THE NINETEEN SPECIES LISTED IN TABLE 1. * = occurred in one sample only; no variance estimate possible.

Species	Lone Tree Meadow 1974	Lone Tree Meadow 1976	Lone Tree Meadow 1978	Buck Meadow 1975	Buck Meadow 1978	Stable Meadow 1978
Annual grasses						
Aira caryophyllea	3.8 ± 1.5	13.0 ± 5.2	11.9 ± 5.1	4.1 ± 2.05	6.1 ± 6.1	9.4
Bromus mollis	0.9 ± 0.2	25.9 ± 7.5	6.6 ± 6.1	39.3 ± 5.4	24.3 ± 5.3	10.2
Cynosurus echinatus	16.4 ± 4.8	13.8 ± 1.9	2.8 ± 1.9	2.0 ± 2.1	5.4 ± 8.6	24.7
Hordeum leporinum	0	0	0	0	0	37.7
Vulpia bromoides	0.6 ± 0.1	15.3 ± 8.2	38.1 ± 10.0	6.7 ± 2.2	27.9 ± 6.5	5.7
Perennial forbs						
Corythrogyne californica	2.0—*	0	0	31.3 ± 9.9	50.9 ± 8.6	0
Hypochoeris radicata	2.4 ± 1.0	9.5 ± 2.7	11.1 ± 11.1	1.2 ± 0.4	3.8 ± 2.4	4.4
Iris douglasiana	14.4 ± 6.4	14.5 ± 7.4	21.5 ± 5.8	0	42.0—*	24.8
Plantago lanceolata	21.5 ± 3.4	24.1 ± 3.5	13.8 ± 3.7	7.8 ± 4.5	6.1 ± 3.5	51.9
Rumex acetosella	1.0 ± 0.9	2.4 ± 1.4	2.0 ± 0.0	4.5 ± 2.9	6.8 ± 1.1	0
Perennial grasses						
Anthoxanthum odoratum	20.2 ± 4.1	40.7 ± 6.2	57.6 ± 5.6	37.0 ± 5.1	52.0 ± 4.5	0
Rytidosperma pilosum	13.2 ± 4.2	15.6 ± 5.4	13.9 ± 5.0	17.8 ± 4.7	35.2 ± 4.9	13.1
Deschampsia holciformis	45.5 ± 8.6	55.5 ± 10.1	60.7 ± 10.8	62.8 ± 14.5	44.1 ± 14.3	0
Holcus lanatus	5.6 ± 3.1	15.3 ± 0.8	20.5 ± 7.9	10.8 ± 3.4	23.4 ± 5.1	0
Lolium perenne	0.6 ± 0.5	7.2 ± 3.7	0.9 ± 0.5	0	0	41.0
Other life forms						
Juncus bufonius	0	0	0	0	0	7.7
Linum bienne	0.9 ± 0.5	1.3 ± 1.0	1.7 ± 0.6	0.5 ± 0.0	2.3 ± 0.8	6.8
Pteridium aquilinum	12.2 ± 5.3	17.7 ± 5.7	16.2 ± 4.6	24.0 ± 4.5	30.3 ± 3.7	0
Rubus ursinus	12.5 ± 2.4	14.6 ± 3.2	17.0 ± 2.7	0	12.3 ± 1.1	0

dominants (the exception being *Rytidosperma pilosum*) decreased significantly ($p < 0.05$) in Buck and Lone Tree Meadows by 1978.

The dominant species in the latest surveys were mostly perennial grasses. *Anthoxanthum odoratum* and *Holcus lanatus* were two introduced species absent from Stable Meadow that showed significant increases in mean cover in the other sites. *Anthoxanthum odoratum* had higher cover values, greater dispersion over the successional sites, and higher rates of increase than most other species. In Lone Tree Meadow, *Anthoxanthum odoratum* reached 69% of the relative cover (Fig. 5a) of the perennial grasses in 1978, occupied 91% of the sample quadrats, and had increased 266% in actual cover. In Buck Meadow, the corresponding figures were 54% (Fig. 5b), 80%, and 59%. *Holcus lanatus* increased significantly in both meadows and showed higher percent rates of increase than did *A. odoratum.* Its frequency values were lower, reflecting high patchiness and locally high cover. *Rytidosperma pilosum* was the only perennial grass to show differences between sites. In Lone Tree Meadow, *R. pilosum* disappeared from half the quadrats in which it occurred and lost 47% of its cover. In Buck Meadow, *R. pilosum* increased significantly (71%), despite a reduction in frequency, because its mean cover increased in those plots occupied at the beginning of the study in 1975. *Deschampsia holciformis,* a large native bunchgrass characteristic of wetter sites, did not show significant change in time and may represent a relict species that survives grazing rather than a later successional dominant. Other species that showed significant increases in cover include *Vulpia bromoides* (=*Festuca dertonensis*) and *Rubus ursinus. Rubus ursinus* is characteristic of heavy stands of perennial grass, especially in wetter areas. *Vulpia bromoides* was unique in that its frequency decreased, whereas cover increased in the remaining quadrats. This pattern of locally patchy occurrence in perennial stands persists to the present time.

Representation of native species in secondary succession. Table 3 shows that native species are present at all stages of succession, but at low cover values. There is no significant temporal increase in the representation of native species, with the exception of *Rubus ursinus.* We see little evidence suggesting that a major increase in native species, at least in the herbaceous vegetation, is to be expected in the future. *Deschampsia holciformis,* however, is one native species that could be a successional dominant, but it has a static population at Sea Ranch with no evidence suggesting dominance at climax, contrary to what Elliott and Wehausen (1974) suggest for Point Reyes.

Two other well-known natives are relatively rare and likely to remain so. *Stipa pulchra* is uncommon at Sea Ranch. It tends to be concentrated along roadsides and in relict annual-dominated patches. Our observations on this species at Sea Ranch support the conclu-

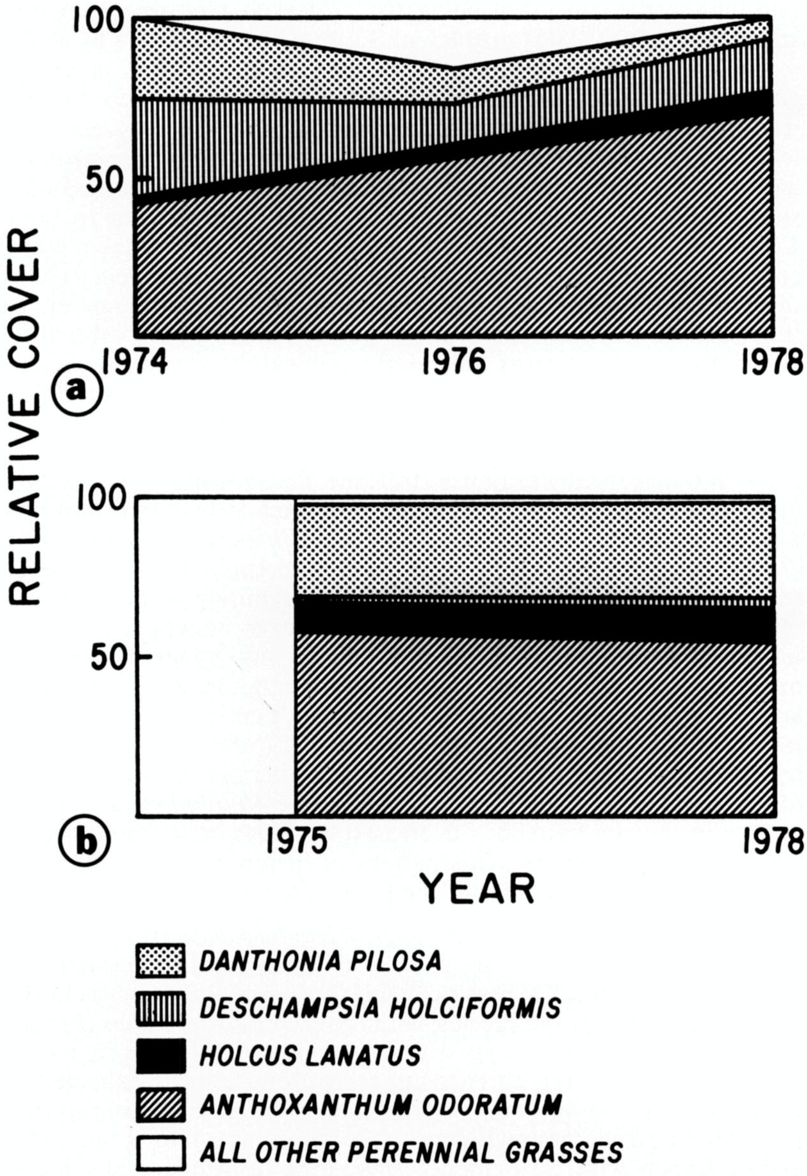

FIG. 5. Relative cover for perennial grasses in Lone Tree Meadow (Fig. 5a) and Buck Meadow (Fig. 5b).

TABLE 3. REPRESENTATION OF NATIVE SPECIES IN SECONDARY SUCCESSION IN THE SEA RANCH COASTAL PRAIRIE. Statistics are absolute cover (AC) assigned to the 19 native and introduced species of Table 1.

Site and year	AC native species	AC all species	Proportion of natives
Stable Meadow			
1978	119	3663	0.032
Lone Tree Meadow			
1974	2714	10,761	0.252
1976	3243	15,527	0.209
1978	3882	16,014	0.242
Buck Meadow			
1975	1150	12,338	0.093
1978	1294	27,273	0.047

sions drawn by Bartolome and Gemmill (1981). *Danthonia californica* is a low-growing, native, perennial that is restricted to the low vegetation found on exposed bluffs (see Hektner and Foin 1977). It has never been found inland in the taller vegetation.

DISCUSSION

Secondary succession in the California coastal prairie. Our data show that secondary succession in the Sea Ranch coastal prairie is characterized by rapid replacement of annuals by perennials and subsequently the concentration of dominance within a small number of mostly introduced species of perennial grasses. The replacement of annuals by perennials is most easily explained as a decline in yearly establishment by annuals because perennials utilize most of the soil surface. Peart and Foin (1985) have shown that establishment is strongly retarded by biomass at Sea Ranch. As succession has progressed, biomass has accumulated (much of it standing dead material and litter). The cause of the replacement of annuals and perennial forbs by perennial grasses is more speculative at this time, but may be a function of competition for light and soil moisture. Peart (1982) measured light levels beneath the grass canopy using a light meter measuring only the photosynthetically active spectrum. He found that light values beneath the grass canopy were typically much less than at the floor of nearby redwood forests. Because most of the forbs at Sea Ranch are low-growing, it is easy to imagine that they would be readily overtopped and shaded out.

The replacement of some perennial grasses by others at Sea Ranch is exemplified most strikingly by the increase in *Anthoxanthum odoratum.* This species has continued to increase; at present, it has even larger cover values than those presented in this paper (the informal estimate for 1985 in Lone Tree Meadow is greater than 70%). Explanation of the success of this species is still incomplete, although there are suggestions in some of our current work that soil moisture is an important, perhaps the most important, explanation. Peart and Foin (1985) showed in experimental invasion studies that *Anthoxanthum odoratum* was the best at colonizing the stands of annual-perennial forb-*Rytidosperma* that were present with the sheep. Differences in colonizing ability are adequate to explain the changes in secondary succession reported in this paper, but newer data (Foin, unpublished) strengthen the argument by showing the role of soil moisture in the dynamics of the dominant perennial species.

Succession and the native vegetation. Our research at Sea Ranch demonstrates that native species cannot be expected to recover in the coastal prairie in the face of competition from a small number of well-adapted introduced species. Even with intensive management, species like *Anthoxanthum odoratum* and *Holcus lanatus* probably cannot be eliminated from the prairie community. This is because the coastal climate is mild enough in the summer to permit the survival of perennials, and because these two introduced species are opportunistic and adapted to a wide variety of environmental conditions. The research reported here suggests that, under mesic conditions on the northern coast, these two introduced species are the prairie dominants and likely to remain so. Barry and Schlinger (1977) have shown that introduced perennial grasses dominate at Inglenook fen, and recently Saenz and Sawyer (1986) have drawn a similar conclusion about introduced species in Humboldt County. The Sea Ranch data also are in harmony with the replacement of natives by introduced annuals in the interior valleys. Thus, Heady and others (1977) were correct in their prediction that introduced species would continue to persist in the coastal prairie, but they did not foresee that persistence also would mean even greater dominance.

Acknowledgments

Support for this work was provided by the National Science Foundation (DEB 76-82503), the Rockefeller Foundation, and the Opportunity Program for Ecological Research, University of California. We are grateful to the members and staff of The Sea Ranch Association, particularly George Wickstead, the late Larry Marshall, Robert Kirkwood, and Ruth Riordan, for their generous assistance over the years. We also thank Harold Heady and Carla Scheidlinger for their extensive comments on the manuscript.

Literature Cited

Barry, W. J. and E. I. Schlinger. 1977. Inglenook Fen. Dept. Parks and Recreation, State of California.

BARTOLOME, J. W. and B. GEMMILL. 1981. The ecological status of *Stipa pulchra* (Poaceae) in California. Madroño 28:172–184.

BURCHAM, L. T. 1957. California rangeland. Calif. Div. Forestry, Sacramento.

CLEMENTS, F. E. 1916. Plant succession. Publ. Carnegie Inst. Wash., no. 242.

CONNELL, J. H. and R. O. SLATYER. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Amer. Naturalist 111:1119–1144.

CRAMPTON, B. 1974. Grasses of California. Univ. California Press, Berkeley.

ELLIOTT, H. W. and J. D. WEHAUSEN. 1974. Vegetational succession on coastal rangeland of Point Reyes Peninsula. Madroño 22:231–238.

EVANS, F. C. and E. DAHL. 1955. The vegetational structure of an abandoned field in southeastern Michigan and its relation to environmental factors. Ecology 36: 635–706.

FOIN, T. C. and S. K. JAIN. 1977. Population biology and ecosystem analysis: lessons for the development of community ecology. BioScience 27:532–538.

HARPER, J. L. 1977. Population biology of plants. Academic Press, New York.

HARRIS, G. A. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum.* Ecol. Monogr. 37:89–111.

HEADY, H. F. 1975. Rangeland management. McGraw-Hill, New York.

———, T. C. FOIN, M. M. HEKTNER, D. W. TAYLOR, M. G. BARBOUR, and W. J. BARRY. 1977. Coastal prairie and northern coastal scrub. *In* M. G. Barbour and J. Major, eds., Terrestrial vegetation of California, p. 733–759. Wiley-Interscience, New York.

HEKTNER, M. M. and T. C. FOIN. 1977. Vegetation analysis of a northern California coastal prairie: Sea Ranch, Sonoma County, California. Madroño 24:83–103.

HUFFAKER, C. B. and C. E. KENNETT. 1959. A ten-year study of vegetational changes associated with biological control of Klamath weed. J. Range Managem. 12: 69–82.

LATHROP, K. T. and P. J. P. GOGAN. 1985. Plant communities of the Tule Elk Range, Point Reyes National Seashore. Tech. Report 18, Cooperative National Park Resources Studies Unit, Univ. California, Davis.

MCBRIDE, J. 1974. Plant succession in the Berkeley Hills, California. Madroño 22: 317–329.

——— and H. F. HEADY. 1968. Invasion of grassland by *Baccharis pilularis* DC. J. Range Managem. 21:106–108.

MCINTOSH, R. P. 1980. The relationship between succession and the recovery process in ecosystems. *In* J. Cairns, Jr., ed., The recovery process in damaged ecosystems. Ann Arbor Science Press, Ann Arbor, MI.

———. 1981. Succession and ecological theory. *In* D. C. West, H. H. Shugart, and D. B. Botkin, eds., Forest succession. Springer-Verlag, New York.

MACK, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America: an ecological chronicle. Agroecosystems 7:145–165.

MCMAHON, J. A. 1980. Ecosystems over time: succession and other types of change. *In* R. H. Waring, ed., Forests: perspectives from ecosystem analysis. Oregon State Univ. Press, Corvallis.

MUNZ, P. A. 1973. A California flora and supplement. Univ. California Press, Berkeley.

PEART, D. R. 1982. Experimental analysis of succession in a grassland at Sea Ranch, California. Ph.D. dissertation, Univ. California, Davis.

——— and T. C. FOIN. 1985. Analysis and prediction of population and community change: a grassland case study. *In* J. White, ed., The population structure of vegetation. W. Junk, The Hague.

REED, M. J., W. R. POWELL, and B. S. BAL. 1963. Electronic data processing codes for California wildland plants. U.S. Forest Service Research Note PSW-N20.

SAENZ, L. and J. O. SAWYER, JR. 1986. Grasslands as compared to adjacent *Quercus* *garryana* woodland understories exposed to different grazing regimes. Madroño 33:40–46.

SHUGART, H. H. 1974. A theory of forest succession. Springer-Verlag, New York.

STEELE, R. G. D. and J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill, New York.

UNITED STATES DEPT. OF AGRICULTURE. 1972. Soil survey of Sonoma County, California. United States Government Printing Office, Washington, DC.

WESTER, L. 1981. Composition of native grasslands in the San Joaquin Valley, California. Madroño 28:231–241.

WESTOBY, M. 1979. Elements of a theory of vegetation dynamics in arid rangelands. Israel J. Bot. 28:169–194.

WHITE, K. L. 1967. Native bunchgrass (*Stipa pulchra*) on Hastings Reservation. Ecology 48:949–955.

(Received 6 Sep 1985; revision accepted 20 Apr 1986.)

ANNOUNCEMENT

SYMPOSIUM TO HONOR G. LEDYARD STEBBINS

An International Symposium will be held in Davis, California, on 12–14 September 1986, to honor Professor G. Ledyard Stebbins in the year of his 80th birthday. Invited talks by leading plant biologists will include topics in population and ecological genetics, organelle and nuclear molecular genetics, morphogenesis and plant development, and evolution and systematics. For further information please contact: Dr. L. D. Gottlieb, Department of Genetics, or Dr. S. K. Jain, Department of Agronomy and Range Science, University of California, Davis, CA 95616.