

INVASION OF FENNEL (*FOENICULUM VULGARE*) INTO SHRUB COMMUNITIES ON SANTA CRUZ ISLAND, CALIFORNIA

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ABSTRACT

Fennel (*Foeniculum vulgare* Mill.) was introduced to Santa Cruz Island in the 1850's, and is now present in 7.8% of the island grassland community. This study's goal was to determine the success of fennel invasion into chaparral and coastal sage communities bounding grassland infested by fennel, and whether fennel occurrence varied with physiognomic or disturbance parameters. Vegetation was sampled using line transects placed perpendicular to grassland/shrubland boundaries, in sites stratified by shrub community type, topographic position, and aspect. Results indicated that coastal sage was more susceptible than chaparral to invasion by fennel. Fennel cover in chaparral correlated positively with fennel cover in adjacent grassland, although fennel did not occur in chaparral past an average of 2–3 m. Where vegetation boundaries were most distinct, fennel was negatively correlated with shrub cover. Disturbance related to fennel occurrence only in grassland areas, and did not correspond to fennel invasion in shrub communities. With recent removal of grazers from the island, fennel expansion and natural vegetation recovery from grazing may be integrally related.

Baker (1965) listed fourteen attributes of the "ideal weed," but noted that probably no living plant has them all. The ideal weed is a competitive, self compatible, fast growing perennial adapted to growth in a wide range of environmental conditions. It may reproduce vegetatively or sexually, producing a large number of seeds with a wide range of dispersal, have long temporal viability, and no particular germination requirements. Newsome and Noble (1986) described fennel (*Foeniculum vulgare* Mill.; Apiaceae) as a mat-forming, shallow rooted, multistemmed perennial with "large leaves," and the ability to germinate in any season. Fennel is an introduced naturalized species from Old World Europe (Fernald 1950), and frequently occurs in roadside and waste places. Fennel populations commonly exhibit stem die-off after seed-set, with regeneration in the following year.

Typical of California grasslands, Santa Cruz Island's native grassland of perennial bunch grasses has been largely replaced by European annual grasses and their weedy associates, among them fennel which was introduced in the 1850's (Greene 1886; Dunkle 1950). Also introduced in the 1850's were sheep and pigs which formed substantial feral populations, and were the likely avenue of acci-

dental point introduction of fennel around Prisoner's Harbor. A cattle ranching operation also affected a part of the island, within which the largest fennel populations exist today. Cattle, and the few dirt roads traversing the ranching areas, were the most likely avenues of fennel dispersal over the past 100 years. However, with the exception of areas with cattle, fennel has not expanded very far along roads leading out of grasslands containing large fennel populations. The Nature Conservancy currently owns and manages the island, and is concerned about future fennel expansion.

In recent surveys Beatty (1991) found fennel occurring on about 6.4% of the island, in contrast to the 83% (calculated by author) occupied by grasslands and habitats which should be suitable sites for fennel colonization. With the removal of the feral sheep in 1985 and the cattle ranching operation in 1988, the continued expansion of fennel on Santa Cruz Island will largely depend on its ability to invade through natural dispersal mechanisms. Previous research has suggested that fennel may be successfully competing with established perennials in coastal sage communities, but not in the chaparral (Hobbs 1983; Beatty 1988). Fennel is found mainly in the eastern central parts of the island (Fig. 1), covering much of the central valley, slopes of the northern range (east of Prisoner's Harbor to Chinese Harbor), and on the north slope of the southern range to

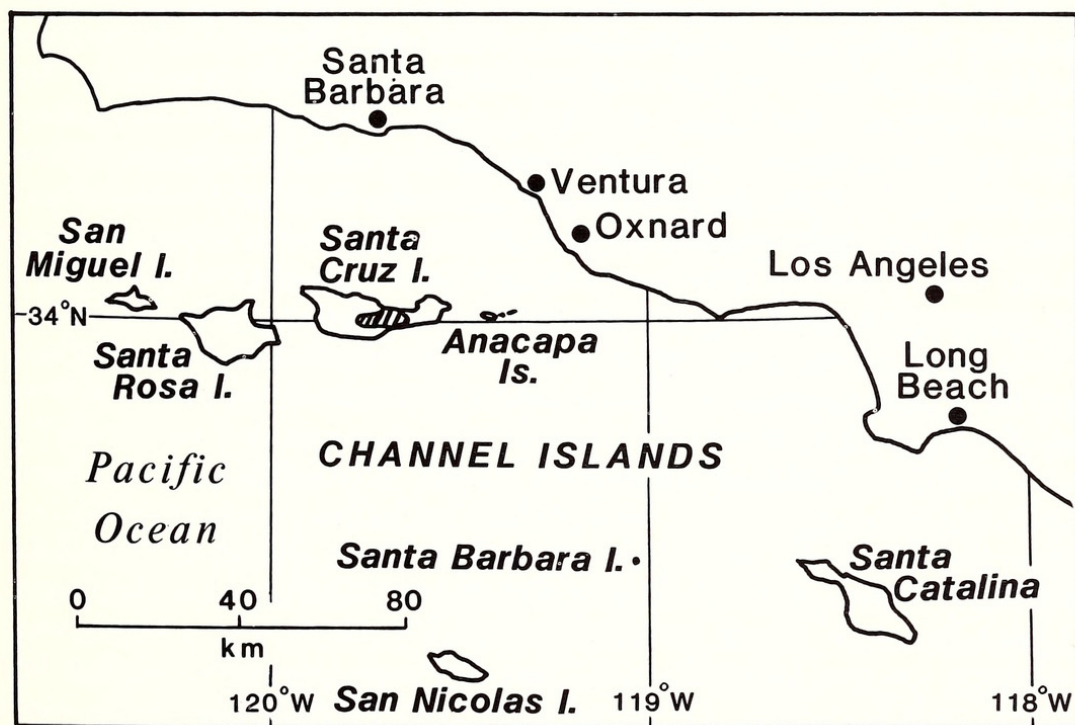


FIG. 1. Map showing location of Santa Cruz Island off the coast of southern California, USA. The shaded portion of the island indicates the area having the largest fennel populations, within which sample sites for the study were located.

the ridge. Throughout these areas, chaparral (mixed chamise, ceanothus, and manzanita) and coastal sage communities border grasslands such that fennel is located both upslope and downslope from shrub vegetation. The colonization potential of fennel could be related to whether dispersal was occurring upslope or downslope into the shrub communities because of variations in dispersal by overland flow, gravity, and/or wind associated with these topographic positions. Animal disturbances were of similar magnitude in all sites.

The hypotheses being tested in this study were: 1) chaparral and coastal shrub communities prevent fennel colonization and establishment, and 2) soil disturbance is associated with fennel colonization. If the first hypothesis is true, then such vegetation types may act as dispersal barriers for fennel. Potential for future fennel expansion could then be partially predicted in relation to vegetation patch sizes and distributions. Research on fennel seed dispersal dynamics and spatial components in dispersal is currently underway (Beatty 1991). The second hypothesis is relevant since feral pig disturbance is still widespread on the island, and such soil patches may serve to facilitate colonization, as has been found for other weedy aliens (Elton 1958; Platt 1975; Platt and Weis 1977; Grime 1979; Scorza 1983; Pickett and White 1985; Fox and Fox 1986).

STUDY AREA

Santa Cruz Island is situated 39 km S of the Santa Barbara coastline and is the largest of the eight California Channel Islands (Fig. 1). The island has two east-west trending mountain ranges (ca. 410–595 m elevation) with an intervening central valley. The island has been under continuous occupation since the early 1850's, primarily for grazing of sheep and cattle. Considerable landscape and vegetation change has taken place since the introduction of sheep (Brumbaugh 1983), mainly due to overstocking and consequent overgrazing along with other human clearing and cultivation (Hobbs 1978, 1983; Van Vuren and Coblenz 1987). The extent of grazing is reflected to some degree by the abundance of exotic species present (Hochberg et al. 1980; Minnich 1980).

Plant communities of Santa Cruz Island, at the physiognomic and floristic levels, are generally comparable with the community equivalents found on the mainland (Minnich 1980; Brumbaugh 1983; Westman 1983). However a distinct characteristic of the floristics of the California island communities is that many species are not restricted to any particular community, and are wide ranging in habitat (Philbrick and Haller 1977; Hobbs 1978). Structurally, the island chaparral is different from that of the mainland. It tends to have a more open overstory (Hochberg 1980; Minnich 1980), and more varied growth form (Philbrick and Haller 1977; Minnich 1980).

These differences in species habitat and community structure may influence the ability of fennel to invade these vegetation types.

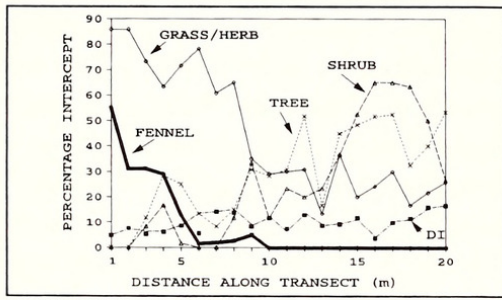
The most prominent communities are grassland, coastal sage, chaparral, oak woodland, riparian woodland, and closed-cone pine forest (Minnich 1980; Brumbaugh 1983). Coastal sage communities however, are often restricted to areas which had largely been free of feral sheep (Minnich 1980) owing to difficulty of access. Coastal sage dominants are *Artemisia californica* Less., *Eriogonum arborescens* E. Greene., *E. grande* (E. Greene) S. Stokes., *Rhus integrifolia* (Nutt.) Benth. & Hook., and *Lupinus* spp., but includes *Baccharis pilularis* DC. subsp. *consanguinea* (DC.) C. Wolf. *Opuntia littoralis* (Engelm.) Ckll., *O. oricola* Philbr. and hybrids of these two also occur (Philbrick and Haller 1977). *Quercus dumosa* Nutt., *Heteromeles arbutifolia* M. Roem. and *Rhus integrifolia* dominate the west end chaparral, with *Arctostaphylos subcordata* Eastw., *A. insularis* E. Greene., *A. tomentosa* (Pursh) Lindl. (manzanitas) dominating the upper areas of the southern ridge, grading into a more varied chaparral dominated by *Quercus dumosa* Nutt., *Q. macdonaldii* E. Greene., *Ceanothus megacarpus* Nutt. var. *insularis* Munz, *C. arboreus* E. Greene., *Cercocarpus betuloides* Nutt. ex Torrey & A. Gray, *Adenostoma fasciculatum* Hook. & Arn. (chamise), and *Rhus integrifolia* on the lower slopes of the central valley (Minnich 1980).

METHODS

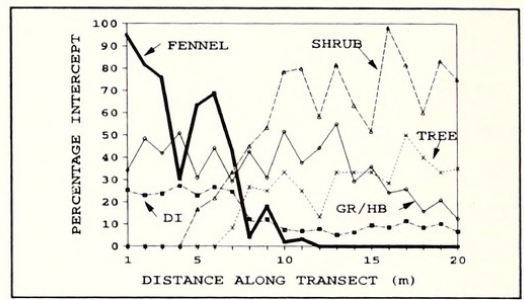
Sample sites were chosen from aerial photographs and ground reconnaissance, using a stratified random design. Sites were stratified by shrub community (chaparral, coastal sage), aspect (north facing, south facing), and slope position of the vegetation boundary between grassland and shrub community (fennel upslope = upper sites, fennel downslope = lower sites). We had eight sample sites, with six replicate transects placed in each site.

Vegetation was sampled using 20 m line transects placed perpendicular to the grassland/shrub community boundary, and centered on the boundary (extending 10 m into each community). The location of the line transects were randomly determined on a 100 m baseline running parallel to the boundary. Each line transect was divided into 1 m contiguous samples, with the following observations made for each: 1) vegetative characteristics of percent intercept of previous year's fennel stems, the percent intercept of the current year's fennel growth (leaf fronds, flowering stems, and seedlings), the density of fennel canes intercepted (per meter and per plant on the transect), height of intercepted vegetation (fennel, woody vegetation), and the percent intercept of forb/herb, shrub (≤ 5 m), and "tree" (over 5 m) growth form categories; 2) physical characters of soil disturbance area and depth (including animal trails and pig

A. UPPER CHAPARRAL TRANSECTS

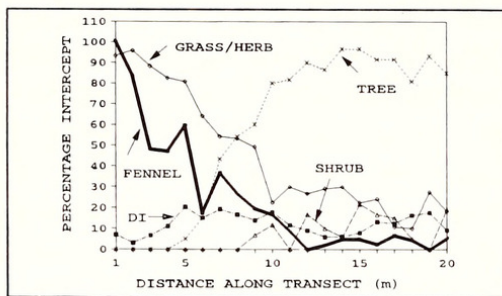


SOUTH-FACING ASPECT

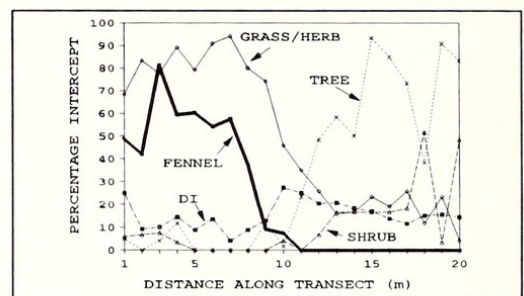


NORTH-FACING ASPECT

B. LOWER CHAPARRAL TRANSECTS



SOUTH-FACING ASPECT



NORTH-FACING ASPECT

FIG. 2. Composite profile across (A) upper topographic positions (fennel/grassland upslope from shrub community) and (B) lower topographic positions (fennel/grassland downslope from shrub community) for boundaries between chaparral and grassland vegetation. Meter 1 was in grassland, meter 20 was in chaparral, and meter 10 was centered visually on the boundary. North-facing and south-facing aspects are shown for each topographic position, giving a total of 4 sites. Average (6 transects/site) percent intercept values per meter on 20 m line transects are given for fennel, grass/herb growth form, shrub growth form, and tree (> 5 m tall) growth form. Disturbance index (DI) reflects the degree of bare and excavated soil per meter on the transects.

digging), litter depth, and rocks. Transect slope profiles were measured using an inclinometer and a telescopic surveying rod at subjectively identified breaks in slope.

Vegetation was sampled in growth form categories of forb/herb, shrub, and tree because characterization of community structure was considered an important factor in fennel colonization potential. Species composition among sites of like vegetation had previously been found to be similar in this study area (Sholes and Beatty 1987; Beatty 1988). Intercept values were averaged for corresponding meter length segments on the six transects, and a vegetation profile was constructed for each site (see also Hobbs 1986). The percent intercept of old-growth and new-growth fennel was combined to give a comprehensive view of fennel abundance and distribution. Separate analyses of fennel seedlings showed the same trends as those reported

for total fennel abundance. Nomenclature of the plants follows Munz (1974).

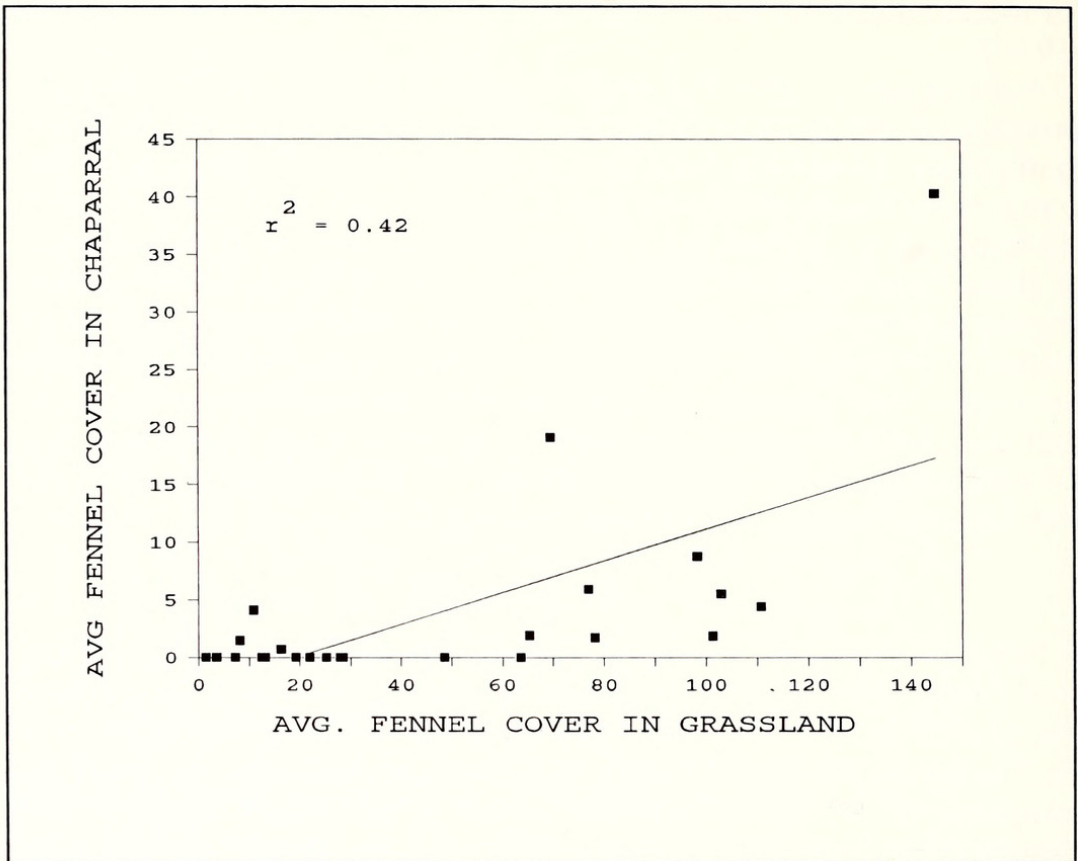
A disturbance index (DI) was calculated as the square root of the product of the percent intercept of disturbance and the depth of disturbance in each meter segment. The purpose of the calculation was to provide an integrated index for the availability of open sites for fennel colonization, such that a site with very little bare ground or disturbance would have a very low DI, a site with much bare ground but no broken soil would be intermediate, and a site with disturbance would have a high DI. For the purposes of constructing the index, bare ground was designated to have a depth of 1 cm, so that only area cover contributed to the value for bare ground. The DI was averaged for each meter along the six transects in a site, and was included as part of the composite profiles.

RESULTS

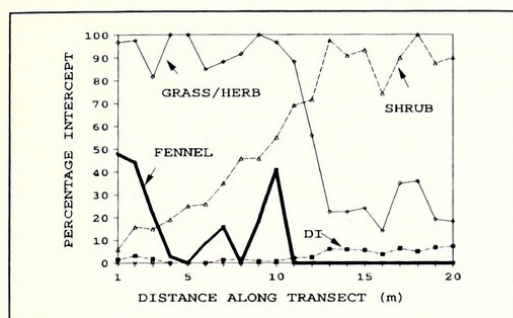
Vegetation profiles. Chaparral-grassland boundaries were distinct, characterized by an abrupt increase in coverage of shrubs and "trees" (shrubs > 5 m tall) and a decrease in grass-herb growth forms (Fig. 2). The latter persisted, however, throughout the entire length of the transects. In the upper transects where fennel could disperse into chaparral from upslope positions, fennel only penetrated an average of 1 m (Fig. 2A). Lower transects, where fennel dispersed from a downslope position into chaparral, showed fennel penetrating further into shrub canopies (Fig. 2B). There was a significant positive relationship between the average cover of fennel in the grassland portion of a transect, and the average cover of fennel established in the chaparral community (Fig. 3). Regressions of fennel cover on other vegetative cover for each chaparral site (Table 1), often showed

TABLE 1. LINEAR REGRESSION COEFFICIENTS (r^2) FOR ANALYSES PERFORMED ON AVERAGE FENNEL COVER m^{-1} TRANSECT (20 m LENGTH) (DEPENDENT VARIABLE) VERSUS AVERAGE COVER OF OTHER VEGETATION GROWTH FORM CATEGORIES (INDEPENDENT VARIABLE) IN THE FOUR CHAPARRAL SITES. Averages for each meter segment along the transect are from the six replicate transects per site. For each site and each analysis, $n = 20$, $df = 18$. Significance is indicated by * $P < 0.05$, ** $P < 0.01$. Trends are indicated as positive (+) or negative (−) even when relationships are not statistically significant.

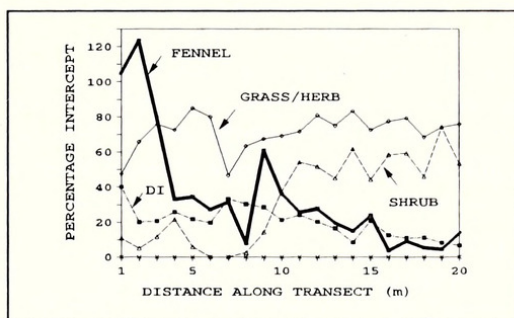
Independent variable	Regression coefficients			
	Upper, S	Upper, N	Lower, S	Lower, N
Grass/herb cover	*0.48+	0.04+	**0.63+	**0.59+
Shrub cover	0.23−	**0.63−	0.25−	0.17−
Tree cover	0.42−	**0.63−	**0.56−	*0.48−
Shrub + tree cover	0.35−	**0.67−	*0.55−	*0.46−



A. UPPER COASTAL SAGE TRANSECTS

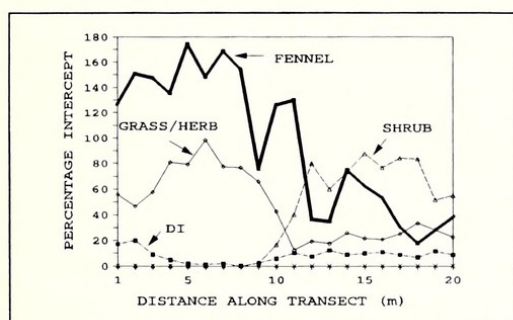


SOUTH-FACING ASPECT

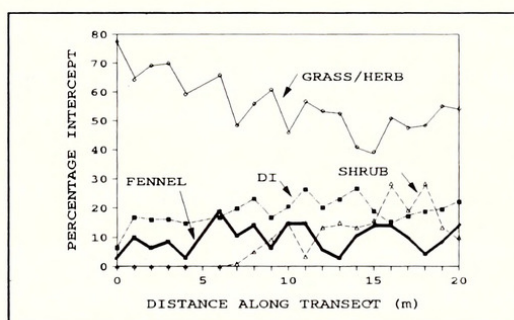


NORTH-FACING ASPECT

B. LOWER COASTAL SAGE TRANSECTS



SOUTH-FACING ASPECT



NORTH-FACING ASPECT

FIG. 4. Composite profile across (A) upper topographic positions (fennel/grassland upslope from shrub community) and (B) lower topographic positions (fennel/grassland downslope from shrub community) for boundaries between coastal sage and grassland vegetation. Meter segment 1 was in grassland, meter segment 20 was in coastal sage shrubland, and meter 10 was centered visually on the boundary. North-facing and south-facing aspects are shown for each topographic position, giving a total of 4 sites. Average (6 transects/site) percent intercept values per meter on 20 m line transects are given for fennel, grass/herb growth form, and shrub growth form. Tree growth form was absent in coastal sage. Disturbance index (DI) reflects the degree of bare and excavated soil per meter on the transects.

length (Table 3). However, shrub/tree cover was negatively correlated with disturbance as well as with fennel in these sites. Other sites showed both positive and negative correlation trends between shrub/tree cover and disturbance (Table 3). In the two upper coastal sage sites, grass/herb cover was negatively related to disturbance, but both sites maintained substantial fennel populations (Fig. 4).

Disturbance may be associated with colonization by fennel in some grassland areas. The average cover of fennel was regressed against average disturbance index for grassland halves (10 m averages for six transects/site and four sites/community type; $df = 22$) and for shrubland halves of transects in chaparral and coastal sage communities. No significant correlations were found for coastal sage sites, either in grassland ($r^2 = 0.05$) or shrub ($r^2 = 0.00$) portions.

TABLE 2. LINEAR REGRESSION COEFFICIENTS (r^2) FOR ANALYSES PERFORMED ON AVERAGE FENNEL COVER m^{-1} TRANSECT (20 m LENGTH) (DEPENDENT VARIABLE) VERSUS AVERAGE COVER OF OTHER VEGETATION GROWTH FORM CATEGORIES (INDEPENDENT VARIABLE) IN THE FOUR COASTAL SAGE SITES. Averages for each meter segment along the transect are from the six replicate transects per site. For each site and each analysis, $n = 20$, $df = 18$. Significance is indicated by $*P < 0.05$. Trends are indicated as positive (+) or negative (–) even when relationships are not statistically significant.

Independent variable	Regression coefficients			
	Upper, S	Upper, N	Lower, S	Lower, N
Grass/herb cover	0.39+	0.17–	0.29+	0.04–
Shrub cover	*0.48–	0.29–	*0.49–	0.00

However, fennel cover was significantly correlated with disturbance index in grassland portions of chaparral sites (Fig. 5), although not under chaparral shrub cover ($r^2 = 0.00$).

DISCUSSION AND CONCLUSIONS

Other studies have shown the success of alien species in displacing native species of communities they invade. A study of site susceptibility to invasion by *Melaleuca quinquenervia* in southern Florida (Meyers 1983) suggested that in this island-like peninsula the invader may displace the native vegetation in some sites. Weiss and Noble (1984) conducted a study on the invasion of *Chrysanthemoides monilifera* into coastal dune communities, and found that it was dis-

TABLE 3. LINEAR REGRESSION COEFFICIENTS (r^2) FOR SEPARATE ANALYSES PERFORMED ON AVERAGE COVER m^{-1} TRANSECT (20 m LENGTH) OF FENNEL AND OTHER GROWTH FORM CATEGORIES (DEPENDENT VARIABLES) VERSUS AVERAGE DISTURBANCE INDEX (DI = INDEPENDENT VARIABLE) IN THE EIGHT SITES. Averages for each meter segment along the transect are from the six replicate transects per site. For each site and each analysis, $n = 20$, $df = 18$. Significance is indicated by $*P < 0.05$, $**P < 0.01$, and $***P < 0.005$. Trends are indicated as positive (+) or negative (–) even when relationships are not statistically significant.

Dependent variable	Regression coefficients			
	Upper, S	Upper, N	Lower, S	Lower, N
Chaparral sites				
Fennel cover	0.16+	**0.64+	0.03+	0.23–
Shrub + tree cover	0.14+	***0.83–	0.00	0.02+
Grass/herb cover	0.14–	0.07+	0.03–	0.21–
Coastal sage sites				
Fennel cover	0.22–	0.23–	0.03–	0.04+
Shrub cover	**0.68+	*0.54–	0.06+	0.00
Grass/herb cover	***0.82–	*0.51–	0.32–	0.02–

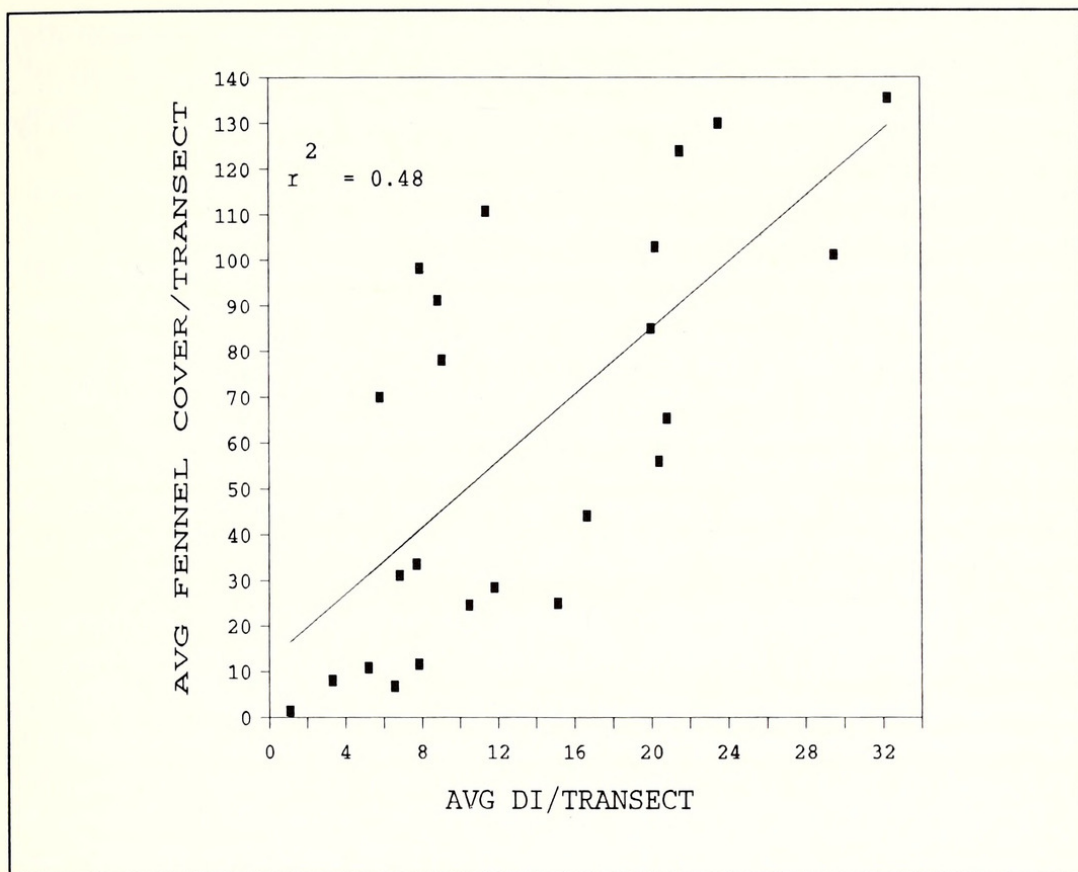


FIG. 5. Linear regression for average fennel cover against average disturbance index (DI), in grassland halves of the chaparral transects (4 sites, 6 replicate transects/site = 24 observations; $df = 22$). Averages are of values in the first 10 meter segments on each transect. The r^2 value is 0.48, with $P < 0.05$.

placing a structurally similar dominant native species *Acacia longifolia* Willd.. Fennel is not similar in structure (deep rooted herbaceous perennial), phenology (summer growth and flowering), or climatic origin to native species on Santa Cruz Island. It does not appear to be a true ruderal species, since it is abundant in areas with and without surface disturbance. The success of fennel in island communities may relate to its ability to exploit resources during the summer when most species are not active (see also Howard and Minnich 1989) in combination with both dispersal and maintenance by grazers. In a related study Beatty (1991) found species richness in fennel-infested grasslands to be lower, with mostly naturalized European annual grasses persisting in the densest fennel populations. Although there is no evidence that the presence of fennel has displaced native species to the point of local extinction, the potential for this will increase if fennel continues to expand in grassland and coastal sage communities.

Generally fennel is not successful in invading chaparral, but extends at least 10 m into coastal sage. Light limitations may be im-

portant in restricting fennel establishment. Lower chaparral boundaries had a higher proportion of trees and a lower proportion of shrubs than in the upper margins, resulting in a much more open understory. This may have contributed to the greater invasion of fennel into shrub canopies of lower topographic boundaries than upper boundaries, contrary to what we expected. A good predictor of fennel establishment under shrub canopies was the cover of fennel in the adjacent grassland communities (Fig. 3), although this relationship existed only for chaparral sites. In both chaparral and coastal sage sites fennel cover was often negatively correlated with shrub cover, but less notably for coastal sage which lacked tree (> 5 m tall) growth forms. The south-facing coastal sage sites showed the greatest decline of fennel in the canopy (Fig. 4), and had significantly taller shrubs than north-facing coastal sage sites (0.84 m vs. 0.51 m; t-test, $df = 22$, $P < 0.001$).

There is no evidence that disturbance is associated with fennel invasion into shrub communities, but it may play a role in fennel occurrence in grassland. Although fennel was positively correlated with disturbance across the entire transect in one site (Table 3), the confounding effect of a negative correlation of shrub cover with disturbance and with fennel in that site (Table 1) appears to preclude the prospect that disturbance is associated with fennel establishment in the shrub community. Indeed, the coastal sage site with a significant increase in disturbance (upper, south-facing site) had a significant decrease in fennel cover under shrubs. Thus greater disturbance under shrubs did not correspond to greater fennel colonization there. Only in grassland portions of chaparral sites was fennel cover significantly related to disturbance (Fig. 5). Further work will be necessary before causal mechanisms can be firmly established.

Vegetation on Santa Cruz Island has been affected by the introduction of a variety of grazers, particularly seen in the reduction of the distribution of coastal sage (Brumbaugh 1980). Grazing by cattle has probably kept fennel populations at moderate levels in frequently grazed pasture, but grassland areas adjacent to such pastures show the greatest infestation by fennel (Beatty 1991). The removal of all grazers will encourage recovery in the natural vegetation (Hobbs 1983). Prior to this study sheep were removed from the island (1985), and we avoided areas of active cattle grazing in our sampling so that grazing was not a direct factor affecting establishment of fennel. Currently all grazers including cattle (1989) have been removed from the island, but feral pig populations are still present (although recently in decline). The future vegetation dynamics will not be shaped by grazing pressures or by as varied a soil disturbance regime as in the past (which included compaction and denudation). Since fennel successfully colonizes grassland and coastal sage communities but not chaparral, the future expansion of fennel may be affected by the

distribution and degree of chaparral recovery. Conversely, the natural recovery of coastal sage and grassland communities may be adversely affected by continued occupation of these sites by fennel.

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