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REGENERATION OF INTRODUCED SPECIES OF CISTUS (CISTACEAE) AFTER FIRE IN SOUTHERN CALIFORNIA

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Establishment of vegetative cover for erosion control on barren or disturbed wildland sites is an important aspect of watershed management in Southern California. Disturbances resulting from construction activities pose a particularly serious problem. Early attempts to extend the cover provided by native chaparral shrubs onto these sites by direct seeding and transplants were of only limited success (Juhren, 1956). A number of introduced shrubs from areas of similar Mediterranean climate were subsequently tested to find species that might perform more satisfactorily in low-maintenance plantings (Juhren, 1956; Hellmers and Ashby, 1958; Ching, 1959).

Among the most promising introductions were species of *Cistus* (rockrose) native to the Mediterranean Basin (Juhren, 1956). These deep-rooted, evergreen shrubs occur widely as components of the Mediterranean macchia (maquís) and garrigue plant associations (Knapp, 1962; Le Houerou, 1974), which are analogous to the California chaparral and coastal sage scrub (Naveh, 1967; Zinke, 1973). The results of several studies (Martin and Juhren, 1954; Laure et al., 1961; Ching and Stewart, 1962; Montgomery and Cheo, 1969) have indicated that individual plants and stands of *Cistus* may be less flammable than most dominant chaparral shrubs. Thus in addition to providing cover, wildland plantings were thought to have potential in reducing the incidence of brush fires along mountain roads, near homes, and around campgrounds (Martin and Juhren, 1954; Stewart, 1961).

Despite the interest in *Cistus* for erosion control and fire hazard reduction, little attention has been given to the ecology and ultimate fate of these plants in Southern California. Knowledge of their response to fire is of particular interest. Recurring fires are a natural and inevitable part of the chaparral environment (Cooper, 1922; Hanes, 1971). Given enough time, fire would eliminate plantings of *Cistus* or any other shrub unless the species possesses adaptations to enable it to survive and recover after burning. Stands of *Cistus* destroyed by fire in the Mediterranean Basin regenerate very rapidly, and the species are well adapted to frequent burning (Knapp, 1962). Naveh (1974) found that *C. villosus* and *C. salvifolius* in Israel are facultative resprouters; they regenerate after fire by new growth from dormant buds in the root crown of the burned plants as well as from seed. It has also been shown that *Cistus* seed germination increases after fire (Naveh and Dan, 1973). *Cistus* species are classified as active pyrophytes and are often encountered as pure stands in areas of the Mediterranean Basin where the frequency of fire is particularly high (Le Houerou, 1974).

The first observations of the response of *Cistus* to fire in Southern California were reported by Martin and Juhren (1954). Following burning tests of several species grown under garden conditions, large numbers of seedlings appeared around the base of burned plants. Relatively few seedlings were found beneath unburned controls. In addition, many of the burned shrubs resprouted from the root crown (Martin and Juhren, 1954). These observations substantiate the "fire-type" nature of *Cistus,* but they do not answer the question of whether wildland stands can become reestablished spontaneously after fire. Of critical importance in this regard is the ability of the plants (seedlings and/or resprouts) to compete successfully with native species during the early stages of postfire succession.

A major wildfire in 1968 partially destroyed one of the *Cistus* field plantings and provided an opportunity to investigate further the fire ecology of *Cistus* in Southern California. Presented in this paper are the results of analysis of the burned and adjacent unburned areas carried out four years after the fire.

Study Area

The *Cistus* field planting involved in fire is located at Dillon Divide on the coastal exposure of the San Gabriel Mountains approximately 10 km northwest of the city of Sunland, California, at 820 m (2700 ft) on a 30–35° north-facing slope. The general climate of the area is Mediterranean defined by a relatively short winter of cool temperatures and occasional heavy rain storms alternating with a long, hot dry season. Mean annual precipitation at the site extrapolated from isohyetal maps (Los Angeles County Flood Control District, 1975) is 50 to 60 cm. Soils were classified as Entic Haploxerolls (USDA Soil Conservation Service, 1973). They are granitic in origin (pH 6.0 to 6.5) with a dark grayish brown A-horizon of loamy-sand texture overlying a pale brown C-horizon of highly weathered parent rock. Depth varies from less than 50 cm near the top of the slope to 150 cm or more at the base of the slope.

The site was cleared as part of the Kagel-Mendenhall Fuelbreak in the mid-1950's (unpublished maps and field reports, Angeles National Forest). Regrowth of native chaparral shrubs from crown sprouts and seedlings was controlled with herbicides. The site originally supported a dense stand of mixed chaparral dominated by *Adenostoma fasciculatum, Quercus dumosa,* and *Ceanothus crassifolius.*

The *Cistus* planting was established in June 1961 (unpublished field reports, LASCA). The Reese fire of the preceding year had burned off the plant cover leaving only charred stumps of the larger shrubs. A total of 1,000 nursery-grown seedlings of *C. villosus* and *C. ladaniferus* in tar paper tubes were set out over an area of 0.4 ha. The plants were irrigated at the time of planting. They received no supplemental water or care thereafter. Initial mortality was high, but by 1964 the population had stabilized at 150 plants (90 and 60 individuals of *C. villosus* and *C. ladaniferus,* respectively). Volunteer seedlings of *Cistus* were not observed in early inspections, although both species had flowered heavily and produced seed. Further observations in the mid-1960's revealed that *Bromus rubens* and several other naturalized annual weeds dominated large areas of the site and that the native shrub cover was becoming reestablished only to a limited degree (unpublished field reports, LASCA).

In September of 1968 the upper third of the *Cistus* stand burned in the large Limerock Canyon fire. The lower part of the planting and an adjacent strip of mature chaparral were left as an island of vegetation within the burned area. The fire appears to have died out as it moved downhill through the open shrub cover and herbaceous vegetation on the old fuelbreak. The leading edge of the fire produced a fairly distinct line extending across the face of the slope and down the western edge of the *Cistus* stand.

The present analysis of the site was undertaken in 1972. At that time the fire line was reconstructed as precisely as possible and marked with stakes. This line served to divide the site into burned and unburned (control) sub-plots.

METHODS

The study area was mapped using a method modified from Cain and Castro (1959). A Brunton compass was positioned along the western edge of the plot, and the area was partitioned into 10° "pie-slice" segments radiating outward for a distance of 30 to 60 m. Direct counts were made of all living *Cistus* plants beyond the cotyledon stage (i.e., larger than 5 cm high) that occurred within each segment. The position of these plants was then determined as the distance from the origin and from the two subtending radii. Care was taken to distinguish between volunteer seedlings and plants developing from root suckers, crown sprouts, or stem layers. Dead *Cistus* shrubs on the burn, where they could be identified, also were mapped. The height of each plant and area of the canopy (derived from paired measurements of width taken perpendicularly) were recorded. From these data estimates of volume were calculated, and the plants were grouped according to the following size classes: A, equal to or greater than 1.00 m^3; B, 0.10 to 0.99 m^3; C, 0.01 to 0.09 m^3; and D, less than 0.01 m^3.

Perennial vegetation on the site was sampled using line interception (Bauer, 1943; Hanes, 1971; Vogl and Schorr, 1972). Five parallel lines 100 m long were placed at 5 m intervals across the face of the slope in approximately a north-south direction from the bottom to the top of the slope. The point at which the intercepts crossed the fire line was recorded. Of the total length, 190.4 m (38.1%) was in the burned sub-plot and 309.6 m (61.9%) in the unburned sub-plot. Data for the large, woody shrubs were analyzed by species. Data for perennial herbs and small sub-shrubs were consolidated into a single group.

Annual grasses and forbs were sampled systematically in May 1973 by placing 1 m^2 quadrats at 10 m intervals along two of the intercept lines. In all, 22 quadrats were set out, nine located in the burned area and 13 in the unburned area. Within the quadrats, the number of individuals of each annual species was counted, and visual estimates of cover were made.

Voucher specimens of all species encountered in the line intercept and quadrat analyses are on file at LASCA. Nomenclature for native and naturalized species is according to Munz (1959); nomenclature for *Cistus* is after Dansereau (1939).

RESULTS

Direct counts of the *Cistus* plants at Dillon Divide grouped by size class are presented in Table 1. The location of each plant is illustrated in Figure 1 with size of the circles being proportional to the size classes. These size classes, when interpreted as age (Daubenmire, 1968), provide a general picture of the structure of the *Cistus* population in the

Table 1. Direct Counts of Cistus Plants at the Dillon Divide Study Site according to Age-size Class. Class A consists largely of old bushes from the original planting. Classes B through D include volunteer plants of decreasing age.

Sub-plot	Number of plants (% of total population)			
	class A ($1.00m^3+$)	class B ($0.10–0.99m^3$)	class C ($0.01–0.09m^3$)	class D ($<0.01m^3$)
Burned				
C. ladaniferus	0	0	39 (31.7)	84 (68.3)
C. villosus	0	14 (11.0)	40 (31.5)	73 (57.5)
Unburned				
C. ladaniferus	49 (77.8)	4 (6.3)	9 (14.3)	1 (1.6)
C. villosus	50 (61.0)	25 (30.5)	2 (2.4)	5 (6.1)

burned and unburned areas. Class A included the remaining original plants set out in 1961 and possibly a few volunteers 8 to 10 years old from seed. Class B included volunteer plants of intermediate age (mostly 4 to 8 years old). Class C was made up of young plants ranging in age from 2 to 4 years. Class D included seedlings 2 years old or less.

A total of 250 volunteer plants of *C. ladaniferus* and *C. villosus* from 1 to 4 years of age were recorded in the burned area (Table 1). The plants showed a distinct clumping pattern around charred stumps of parent shrubs (fig. 1). None of the burned *Cistus* bushes had resprouted from the root crown. In the unburned area, few *Cistus* plants less than 4 years old were found and, where they did occur, they tended to be restricted to openings in the shrub canopy.

Total perennial cover (Table 2) was much lower in the burned area (38.6%) than in the unburned area (72.1%). The burned area was dominated by *Eriogonum fasciculatum* and short-lived perennial herbs and sub-shrubs including *Eriophyllum confertiflorum, Dicentra chrysantha, Antirrhinum nuttallianum* (a biennial), *Lotus scoparius, Haplopappus squarrosus,* and *Helianthemum scoparium* var. *vulgare*. Several of these species are characteristic of the early stages of chaparral succession after fire (Hanes, 1971). Large, woody chaparral shrubs were poorly represented in the post-fire vegetation. Very few seedlings of these species were found. Scattered individuals of *Adenostoma fasciculatum* and *Quercus dumosa* had resprouted from the basal lignotuber (burl); *Eriodictyon crassifolium* was resprouting from rhizomes.

Perennial vegetation in the unburned area was predominately a mixture of *Cistus* and native chaparral shrubs (Table 2). The two species of *Cistus* accounted for over 30 percent of the relative cover. *Eriogonum fasciculatum* was quite abundant, but in many places it was becoming overtopped by *Ceanothus crassifolius. Rhus diversiloba* and *Eriodictyon crassifolium* accounted for most of the remaining cover. Perennial herbs and sub-shrubs were less abundant than in the burned area, but *Eriophyllum confertiflorum* and *Lotus scoparius* occurred extensively in openings between the dominant shrubs.

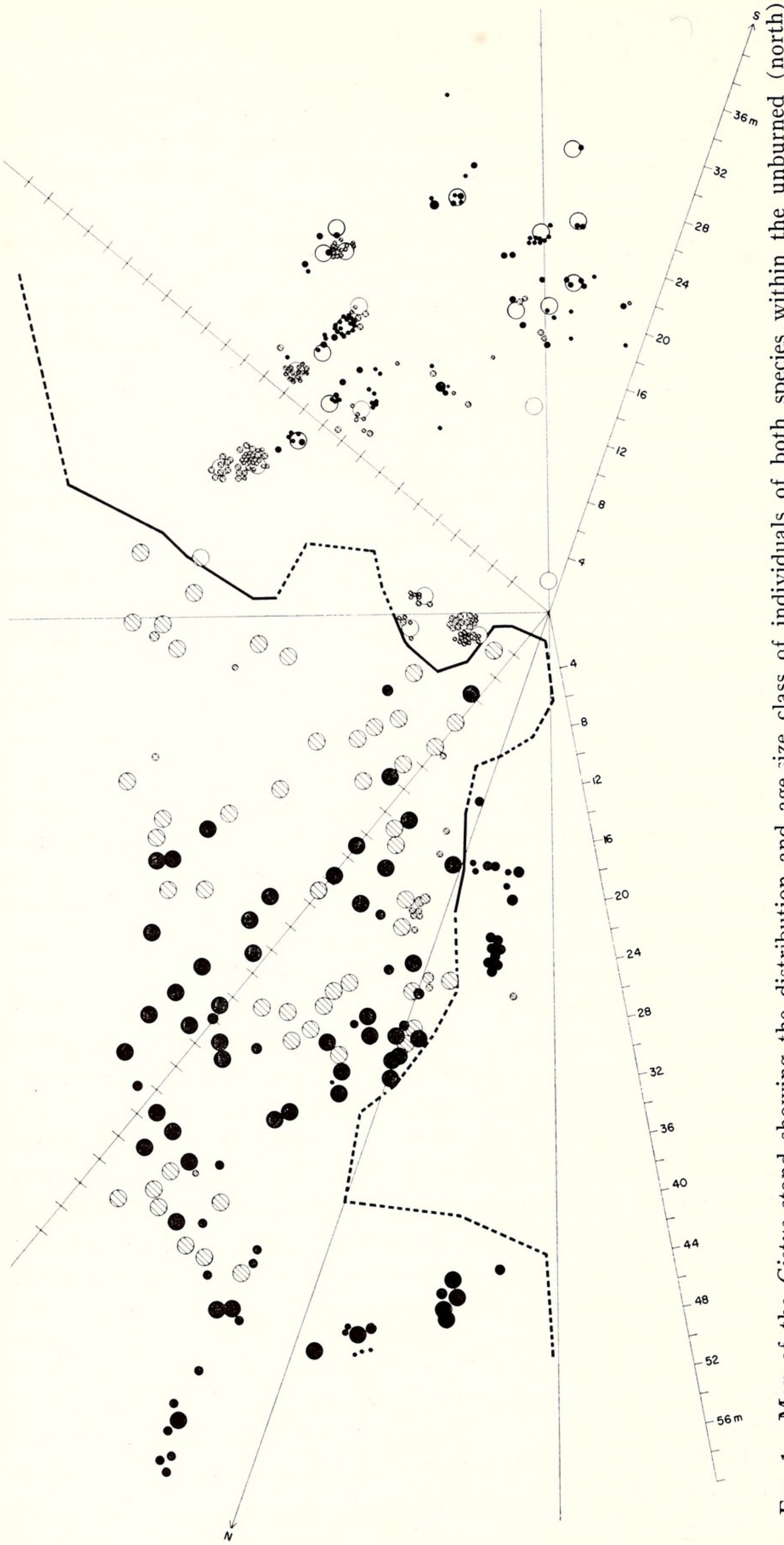

FIG. 1. Map of the *Cistus* stand showing the distribution and age-size class of individuals of both species within the unburned (north) and burned (south) portions of the planting. Size of the circles is proportional to the age-size classes. The fire line is represented by a heavy, solid line where it could be precisely reconstructed and by a heavy, broken line where it was less distinct. The solid black circles indicate *C. villosus*, and circles marked with diagonal lines indicate *C. ladaniferus*. Open circles in the burned area represent the stumps of dead *Cistus* bushes.

TABLE 2. CANOPY COVERAGE AND IMPORTANCE VALUES FOR PERENNIAL PLANTS AT THE DILLON DIVIDE SITE BASED ON LINE INTERSECT ANALYSIS. Total cover is the sum of data for the individual species and species group. Importance values were obtained by adding relative cover, relative density, and relative frequency. The sum of importance values for all species in each sub-plot equals 300 (differences between the data presented and 300 are accounted for by including perennial herbs and sub-shrubs).

Species	Burned area		Unburned area	
	Percent cover	Importance value	Percent cover	Importance value
Eriogonum fasciculatum	13.71	89.70	13.82	53.62
Adenostoma fasciculatum	4.04	18.26	1.07	3.51
Eriodictyon crassifolium	2.63	22.25	13.70	60.28
Cistus villosus	2.26	17.27	6.94	25.35
Cistus ladaniferus	0.53	8.77	13.57	39.72
Salvia mellifera	0.32	3.62	0.00	0.00
Quercus dumosa	0.26	5.27	3.00	14.93
Ceanothus crassifolius	0.05	1.52	3.97	12.80
Rhus diversiloba	0.00	0.00	7.20	30.06
Ceanothus leucodermis	0.00	0.00	0.58	1.67
Others (perennial herbs and sub-shrubs)	14.81	—	8.24	—
Total	38.61		72.09	

Importance values (Curtis and McIntosh, 1951) for each shrub species were calculated from the line intercept data as the sum of relative cover, relative frequency, and relative density (Table 2). By far the most important shrub on the burn was *Eriogonum fasciculatum*. Several plants in the unburned area, including both species of *Cistus*, were of about equal importance.

Annual plant cover consisted largely of naturalized Mediterranean grasses. The dominant species was *Bromus rubens* with average covers of 18.1 and 4.3 percent in the burned and unburned areas, respectively. This species accounted for 83.0 percent of the total annual vegetation in the burned area and 63.2 percent in the unburned area. *Avena fatua* also was abundant in the burned area (2.7% cover). Several other naturalized annuals were encountered in the quadrat analysis but did not contribute to the cover. The native, *Plagiobothrys californicus* var. *fulvescens*, was found in moderate abundance (0.3% cover in the burned area and 0.9% in the unburned area).

DISCUSSION

The present study indicates that it is possible for wildland stands of *Cistus*—at least under certain conditions—to become reestablished and naturalize after fire in Southern California. Regeneration of *C. landaniferus* and *C. villosus* at the Dillon Divide site has been entirely by means of seedlings. Neither species demonstrated the ability to resprout from the root crown. This observation appears to be inconsistent with reports that *Cistus* species are adapted as resprouters (Martin and Juhren, 1954; Knapp, 1962; Naveh, 1974). However, Naveh emphasized that root crown regeneration in facultative resprouters such as *Cistus* varies greatly from fire to fire according to the age, vitality, and successional status of the plants.

At the time of our analysis, the post-fire *Cistus* stand was composed of volunteer plants ranging in age from 1 to 4 years. Most of the plants appearing in the first and second years after fire must have come from seed produced by the *Cistus* bushes present in the pre-fire stand. Since *Cistus* begins to flower and set seed in two years, these initial seedlings would have provided a seed source to account for more recent germinations. The *Cistus* population is distinctly segregated by species into clumps of plants that are located around the base of the burned parent shrubs. There has been very little spread of the stand into areas not previously occupied by *Cistus*. These observations suggest to us that neither species is aggressive enough to naturalize after fire at the expense of native plants or to become a dominant component in the post-fire succession of chaparral. Mortality within the clumps will probably be high in the next few years, the result being to thin the population to a relatively small number of individuals.

There are certain similarities between our observations and the typical pattern of *Cistus* seed reproduction after fire in the Mediterranean Basin. Naveh (1974) reported that *Cistus* species in the maquís and garrigue vegetation of Israel exhibit a post-fire population explosion that is followed by a drastic reduction in seedling densities probably due to moisture stress and competition. Although germination is quite variable, populations of volunteer seedlings numbering 100 or more plants/m^2 are often found around the base of burned parent shrubs. The greatest increase in germination occurs in the first winter after fire, but seedlings may continue to appear in the second year in microhabitats not occupied by other perennials or by annual invaders (Naveh, 1974).

Two effects of fire are implicated in the regeneration of *Cistus* at Dillon Divide. First, the fire may have directly improved seed germinability. Le Houerou (1974) pointed out that seed germination in *Cistus* is stimulated by fire but added that the effect of burning on the physiology of the seed is not well understood. Unpublished experiments carried out by the first author show that germination in *C. villosus* and, to a lesser extent, *C. ladaniferus* increases substantially following scarification by heating. The second effect involves changes in the site produced by fire, which may have created a more favorable habitat for *Cistus* germination and seedling establishment. Disturbance by fire removed the vegetative cover, thereby increasing the amount of light reaching the ground and reducing competition with shrubs and herbs for soil moisture. Other changes such as the removal of litter, increase in soil fertility, and destruction of phytotoxins as discussed by Hanes

(1971) and by Christensen and Muller (1975) could also have been involved.

The history of disturbance at Dillon Divide may have been a particularly important factor in the regeneration of *Cistus* after fire. The effects of clearing and herbicide use in the 1950's were still evident in 1972. Large, strongly woody chaparral shrubs were not well represented. They had been replaced, in part, by species adapted as invaders on disturbed sites including *Eriogonum fasciculatum, Eriodictyon crassifolium,* and *Bromus rubens.* Because of the "impoverished" condition of the native shrub cover, succession after fire has been quite different than described elsewhere for chaparral (Hanes and Jones, 1967; Hanes, 1971; Vogl and Schorr, 1972). Seedlings and/or resprouting individuals of large chaparral species were notably absent on the burn. The cover was dominated by *Eriogonum fasciculatum, Bromus rubens,* and a number of fire-succession perennial herbs and small sub shrubs. The absence of regenerating chaparral shrubs and the rather low, open, predominately herbaceous cover appear to be of great benefit to *Cistus.* Even after four years, the vegetative canopy had not become sufficiently dense to limit *Cistus* germination and seedling growth. In a more typical post-fire chaparral succession, it is unlikely that new germinations would have been found beyond the first or second rainy season.

This study is limited to observations of *Cistus* on a single site after one fire. Additional data are needed to define fully the fire ecology of these Mediterranean shrubs in Southern California and to determine cause-effect relationships. Studies are currently underway to obtain such information. Based on the Dillon Divide analysis, however, we suspect that other wildland stands of *Cistus* located on sites with a similar history of mechanical disturbance would have a high potential for recovering after fire and for persisting as part of the vegetative cover. Stands located on relatively undisturbed sites, on the other hand, might be eliminated in the early stages of post-fire succession because of more intense competition with regenerating chaparral shrubs.

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MORPHOLOGICAL EVIDENCE OF HYBRIDIZATION BETWEEN ARCTOSTAPHYLOS GLAUCA AND A. PUNGENS (ERICACEAE)

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Arctostaphylos is a large genus of evergreen shrubs common in western North America. Although species in the group occupy various habitats throughout this region, their greatest diversity is found in the chaparral covered coastal ranges of California. The diversified topography of this area, with its exceedingly complex mosaic of habitats, has doubtlessly contributed to the diversity of the group. Jepson (1939) suggested that much of the variation in this genus was associated with minor climatic differences and was related to the geological history of the region. Similar factors have been proposed by Gankin and Major (1964) to account for the origin of *A. myrtifolia* Parry, and Vasek and Clovis (1976) have also suggested that recent climatic selection has resulted in a complex pattern of variation in *A. glauca* Lindl.

Hybridization has been implicated in explanations of variation in at least 30 species, subspecies, or varieties (Baker, 1932; Eastwood, 1934, 1937; McMinn, 1939; Jepson, 1939; Adams, 1940; Howell, 1955; Munz, 1959; Roof, 1962; Hoover, 1964; Gankin and Hildreth, 1964; Gankin, 1966; Wells, 1965, 1968, 1972). Despite the frequency of reports of suspected hybridization in *Arctostaphylos,* relatively little biosystematic evidence for it has been published. Epling (1947) made the first attempts by quantifying leaf proportions along a transect from a stand of "pure" *A. mariposa* Dudl. in Eastw. to a stand of "pure" *A. patula* Greene. He, and later Dobzhansky (1953), concluded that although hybrids between these two species were abundant and vigorous, both species remained quite distinct along the zone of contact. More recent and complete studies have clearly indicated hybridization between *A. nissenana* Merriam and *A. viscida* Parry (Schmid et al., 1968) and between *A. viscida* and *A. canescens* Eastw. (Gottlieb, 1968). The results of the latter study led Gottlieb to conclude that several species maintained in standard floras are hybrids.