

A Remnant Greensword Population from Pu'u 'Alaea, Maui, with Characteristics of *Argyroxiphium virescens* (Asteraceae)¹

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ABSTRACT: Two unusual greenswords occurring on Pu'u 'Alaea in 1989 reportedly possessed vegetative features characteristic of the presumed extirpated species *Argyroxiphium virescens* Hillebr. One of these Pu'u 'Alaea plants flowered in August 1989, allowing detailed comparisons with preserved specimens of *A. virescens* as well as other species and hybrids of *Argyroxiphium* native to East Maui. These comparisons suggest that the unusual Pu'u 'Alaea greenswords represent remnants of hybridization between the now presumably extinct *A. virescens* and the more common Haleakalā silversword, *A. sandwicense* subsp. *macrocephalum* (A. Gray) Meyrat, that still occurs at and adjacent to this site. The estimated pollen fertility of 62% in the Pu'u 'Alaea plant is consistent with this interpretation. Recovery of a few embryos from fruits of the plant that flowered in 1989 and the possibility of tissue culture of the remaining living plant at Pu'u 'Alaea apparently represent the last opportunities to conserve any vestige of *A. virescens*.

THE HIGHER SLOPES and summit areas of Haleakalā, East Maui, compose the aboriginal home of three distinctive species of the genus *Argyroxiphium*. The most common and conspicuous of these is the well-known Haleakalā silversword, *A. sandwicense* subsp. *macrocephalum* (A. Gray) Meyrat. This striking plant is widespread around the summit area and is particularly abundant on the cinder cones within the crater. More restricted in distribution is the greensword *A. grayanum* (Hillebr.) Degener, which, nevertheless, is locally abundant, primarily in bogs and adjacent areas of the northeastern slopes of Haleakalā and in and around the summit bogs of West Maui. A second greensword, *A. virescens* Hillebr., was once found on the upper slopes of Haleakalā. This unique East Maui greensword has been seen by few living persons.

Originally described by Hillebrand (1888), *Argyroxiphium virescens* was collected about a dozen times between 1840 and 1945, from Ko'olau Gap and adjacent slopes, and from the eastern summit of Haleakalā. The most recent specimen known is that of *St. John & Mitchell 21153*, taken in 1945, from the pass north of Kuiki [2135 m elev.] (Carr 1985). Thirty years after its last documented observation in nature, *A. virescens* was considered possibly extinct (Fosberg and Herbst 1975). Fifteen years later, with no evidence to the contrary, the federal government listed the species as extinct in the wild (Anonymous 1990). Because there was no known cultivation or seed bank of this species, it seemed that *A. virescens* would never again be seen.

Knowing the plight of the ill-fated greensword, a few local botanists have been intrigued for several years by two unusual plants on Pu'u 'Alaea, Haleakalā, that seemed to bear a striking resemblance to *A. virescens*. In 1989, one of these plants flowered and material was collected for this study. In this paper we document the similarity of the Pu'u 'Alaea specimen to *A. virescens* and conclude that it likely represents a hybrid product be-

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tween previously existing *A. virescens* and the Haleakalā silversword, *A. sandwicense* subsp. *macrocephalum*, which is still found in the same vicinity. These plants may represent the only hope of saving some of the genes that were once embodied in the unique greensword *A. virescens*.

MATERIALS AND METHODS

The materials from the field that were used in this study were collected by A.C.M. from a single flowering plant at Pu'u 'Alaea, Haleakalā, East Maui, in August 1989. The material collected included 14 basal leaves, 8 cauline leaves, and 7 flowering heads with peduncles partially or wholly intact. These structures were photographed and then preserved as dried, pressed herbarium material. Later, a representative flowering head was rehydrated and dissected to determine numbers and sizes of component structures. The detailed description of the plant is based on these materials augmented by interpretations from photographs taken in the field. Herbarium specimens available at the B. P. Bishop Museum (BISH) and at the University of Hawai'i Herbarium (HAW) provided a means for comparing the Pu'u 'Alaea plant with other representatives of *Argyroxiphium*. Pollen from the heads of the Pu'u 'Alaea plant and a nearby individual of *A. sandwicense* subsp. *macrocephalum* collected on the same day was mounted on a microscope slide in cotton blue (Maneval 1936). The stain reaction of more than 500 grains was scored, and stainability was considered an estimate of pollen fertility in these plants. The herbarium material of the Pu'u 'Alaea plant will be deposited at BISH.

RESULTS AND DISCUSSION

Argyroxiphium virescens

There is no convincing evidence that this greensword was ever very common or widely distributed. Its historical occurrence in only a few sites is documented by herbarium speci-

mens (Figure 1). Although Degener made extensive collections (*Degener 3528*, *Degener 7489*) from what may have been the last substantial stronghold of *A. virescens*, his discussion of the species (Degener 1930) and his failure to acknowledge the existence of *A. grayanum* on Haleakalā suggest that he confused the two greenswords occurring on East Maui at that time. The brevity of Hillebrand's original description of *A. virescens* and his restricted view of *A. grayanum*, which he described as a new species of *Wilkesia*, probably fostered similar confusion among other early collectors as well. However, the extremely narrow green leaves attributed to *A. virescens* by Hillebrand (1888) in his original description of this species are virtually diagnostic within the entire silversword alliance and leave little doubt regarding proper application of this name. Carr (1985) published an expanded description of *A. virescens* that provided a better means to identify this poorly understood species. At the same time he reported the occurrence of the putative hybrids *A. grayanum* × *A. virescens* and *A. sandwicense* subsp. *macrocephalum* × *A. virescens*.

Description of the Pu'u 'Alaea Greensword

At first glance the Pu'u 'Alaea greensword (Figure 2) appears similar to small individuals of *A. sandwicense* subsp. *macrocephalum*, but with reduced pubescence resulting in a distinctly greener (versus silver) overall appearance. However, inspection of the leaves (Figures 3–7), flowering heads (Figure 8), and florets (Figures 9–10) reveals a number of features by which the Pu'u 'Alaea greensword differs from any extant species. The very narrow leaves with hairy, but not silvery-floccose surfaces; the well-developed, nearly white rays; the nearly total absence of pappus; and other, less obvious attributes compose a unique combination of features not known in any other member of the genus *Argyroxiphium*. To facilitate detailed comparisons, a comprehensive characterization of the Pu'u 'Alaea greensword in the same format as existing species descriptions (Carr 1985) is presented below. See

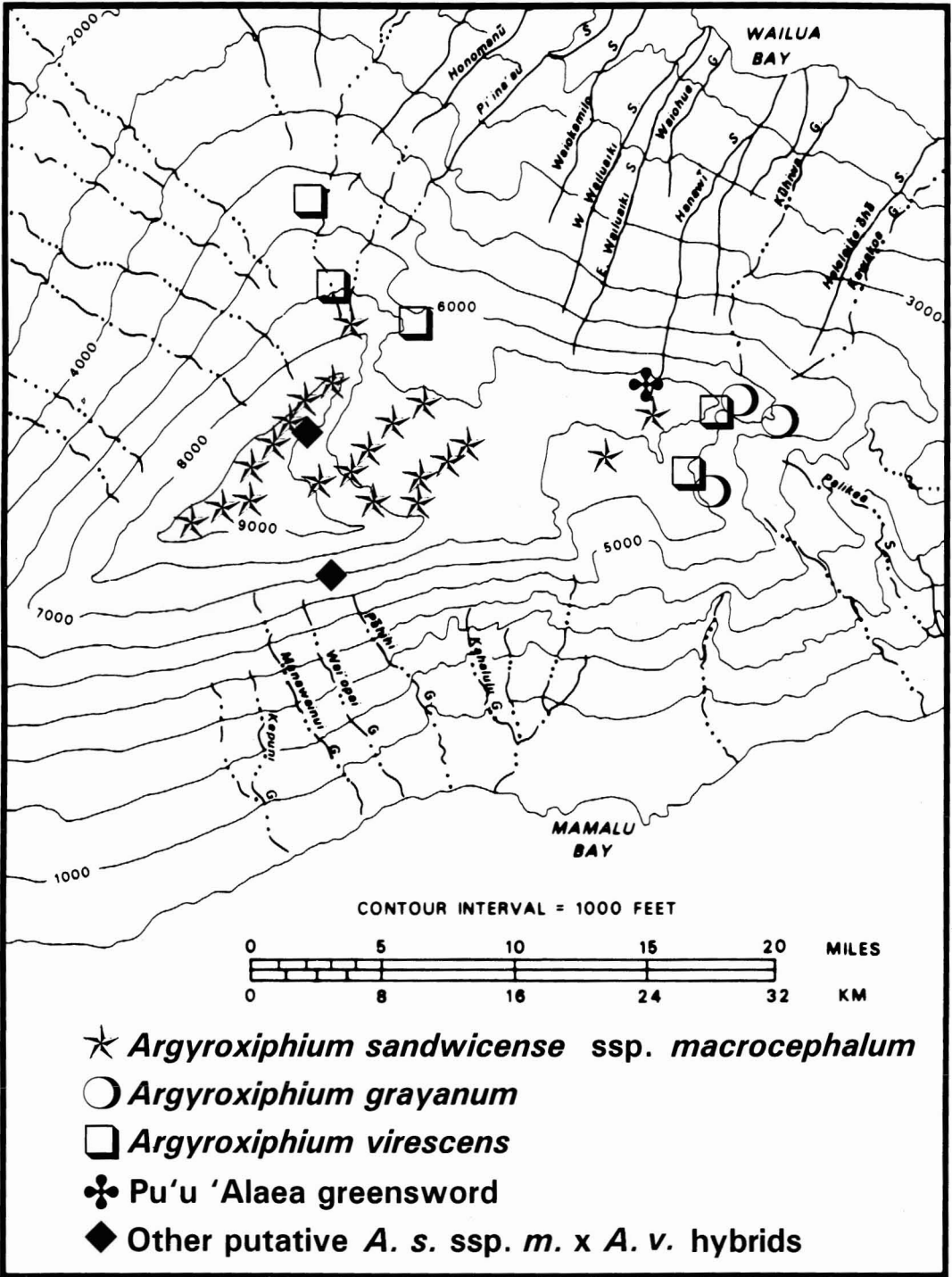


FIGURE 1. Locations of populations of *Argyroxiphium* on the summit of East Maui.

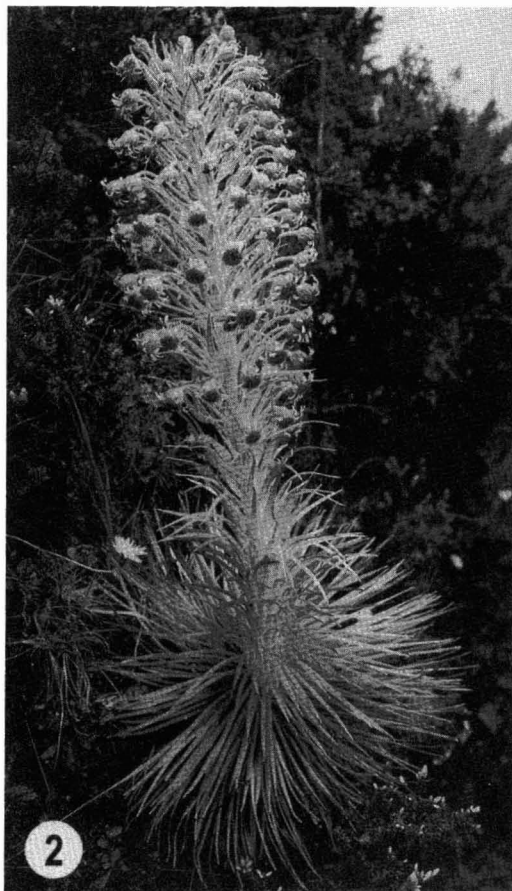
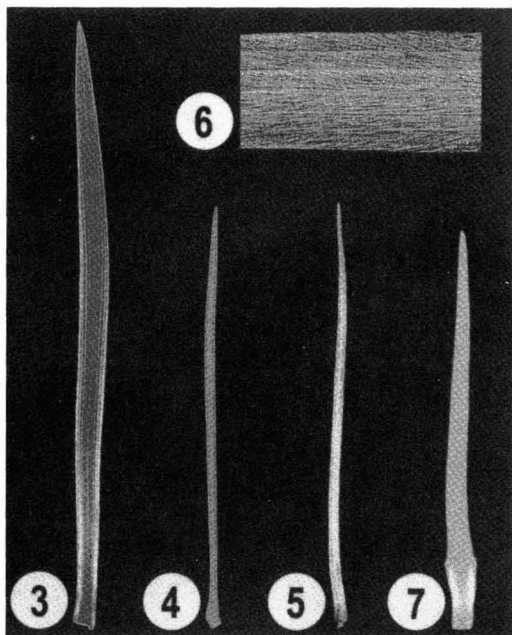


FIGURE 2. Pu'u 'Alaea greensword, in situ, August 1989.

Materials and Methods for clarification of the material sampled.

Erect, unbranched monocarpic rosette shrub about 85 cm tall at flowering time. Leaves closely disposed in a helical fashion, 19–24 cm long, 4–5 mm wide at midpoint, linear-ligulate, straight or slightly arcuate-ascending, scarcely succulent, nearly flat, copiously sericeous on both surfaces but not totally obscuring the veins, pale greenish when fresh, drying silvery gray; margins entire, sericeous; apex acute, attenuate from above the midpoint; base linear from midpoint or above, abruptly dilated near point of insertion; venation of 5–7 parallel nerves, partially obscured by vesture. Heads about



FIGURES 3–7. Morphology of leaves of East Maui species of *Argyroxiphium*: (3) *A. grayanum*, narrowly elliptic-ligulate, broadest above the middle; (4) *A. virescens*, linear-ligulate, attenuate near the base; (5–6) Pu'u 'Alaea greensword: (5) whole leaf, linear-ligulate; (6) enlarged portion of leaf (note visibility of veins through the layer of hairs); (7) *A. sandwicense* subsp. *macrocephalum*, linear-lanceolate, dilated toward base.

90, disposed in a relatively lax racemiform capitulescence about 58 cm long and 24 cm wide, the peduncles ascending, about 8–12 cm long, distally recurved, glandular villous and also glandular puberulent to subfarinaceous; phyllaries (involucral bracts) mostly 9–12, about 14–17 mm long, linear-elliptic to linear-lanceolate, glandular hirsutulous with trichomes to 2 mm long, proximally adnate to the receptacular cup, the margins enfolding the ray achenes; ray florets mostly 9–12, the corolla narrowly tubular for 3–4.5 mm proximally, distally broadened into a limb 11.5–13 mm long and about 4 mm wide bearing 2–3 apical lobes 2–3 mm in length, the tubular portion sparsely puberulent and sometimes minutely glandular, pale greenish below and reddish above, the limb very pale greenish white, the pappus obsolete, the achenes (immature) 10–11 mm long, arcuate,



FIGURES 8–10. Floral features of the Pu'u 'Alaea greensword: (8) flowering heads (note pale ray flowers [mostly greenish white]); (9–10) florets (note virtual absence of pappus): (9) disk floret, pale (greenish) below and darker (reddish) above; (10) ray floret, note dark (reddish) stigmas against pale (greenish white) corolla.

slightly geniculate near apex, glabrous; receptacular bracts about 37, elliptic-oblongate, more or less uniseriate and coalescent into a cuplike structure enclosing the disk florets, 14–17 mm long, glandular hirsutulous; receptacle muriculate and minutely hispidulous; disk florets about 165, the corolla very pale greenish white proximally, reddish distally, 6.5–7.5 mm long, sparsely puberulent on narrowly tubular proximal portion, glabrous above, dilated gradually to about 1 mm wide in distal 1/3 to 1/2, the 5 triangular lobes glabrous, about 0.5 mm long, the pappus extremely reduced, represented by a minute rim, sometimes with a dorsal tooth up to 0.4 mm long, the achenes (immature) straight to slightly arcuate, 8.5–9.5 mm long, glabrous.

Identity of the Pu'u 'Alaea Greensword

Comparisons with Haleakalā species of *Argyroxiphium* indicate that the Pu'u 'Alaea plant resembles *A. virescens* in many ways. For example, leaf width in the Pu'u 'Alaea greensword falls within the range of leaf width seen in *A. virescens* (Table 1). This is especially important because the very narrow leaves of *A. virescens* are unique among the East Maui species of *Argyroxiphium*. The color of the ray and disk florets in the Pu'u

'Alaea plant also seem to match the sketchy information available for fresh florets of *A. virescens*. Many additional features of the Pu'u 'Alaea plant (Table 1) are similar to those of *A. virescens* but vary in the direction of *A. sandwicense* subsp. *macrocephalum*. These features include leaf shape, leaf vestiture, phyllary length, ray floret tube length, ray floret limb length and width, ray achene length, receptacular bract length, and disk floret corolla length. It is notable that the range of variation of these features in the Pu'u 'Alaea plant generally falls outside the range of the same features in *A. grayanum*.

Some of these features, for example leaf width and flower color, seem to indicate that the Pu'u 'Alaea plant is indeed *A. virescens*. However, the virtual absence of pappus in disk florets of the Pu'u 'Alaea plant strongly contrasts with the pronounced development of pappus in disk florets of all nonhybrid specimens of *A. virescens* recognized by Carr (1985). Likewise, the similarity of several features of the Pu'u 'Alaea plant with *A. sandwicense* subsp. *macrocephalum* would not be expected in nonhybrid individuals of *A. virescens*. Carr (1985) noted preserved specimens with characteristics similar to those of the Pu'u 'Alaea plant among mixed collections from areas of sympatry between *A.*

TABLE 1

COMPARISON OF THE PU'U 'ALAEA GREENSWORD WITH *Argyroxiphium grayanum*, *A. virescens*,
AND *A. sandwicense* SUBSP. *macrocephalum*

CHARACTER	<i>A. grayanum</i>	<i>A. virescens</i>	PU'U 'ALAEA GREENSWORD	<i>A. sandwicense</i> SUBSP. <i>macrocephalum</i>
Leaf				
Width	4–23 mm	3.5–6.5 mm	4–5 mm	8–23 mm
Shape	Narrowly elliptic-ligulate	Linear-ligulate	Linear-ligulate	Linear-lanceolate to linear-ligulate
Vesture	Glabrous to slightly canescent	Glabrous to moderately sericeous	Copiously sericeous, but not totally occluding the veins	Strongly silvery floccose-sericeous, totally occluding the veins
Apex	Gradually attenuate from near midpoint	Attenuate from well above midpoint	Attenuate from above midpoint	Gradually attenuate from midpoint or below
Base	Gradually attenuate from near midpoint	Linear from midpoint or slightly attenuate just above extreme base	Linear from midpoint or above	Gradually dilated from near midpoint or above
Capitulescence				
Length	1–10 dm	2–9 dm	ca. 5.8 dm	7–15 dm
Width	6–40 cm	10–25 cm	ca. 24 cm	23–78 cm
Peduncle vesture	Glandular pilosulous	Glandular villous and glandular puberulent to subfarinaceous	Glandular villous and glandular puberulent to subfarinaceous	Glandular pilose
Phyllary				
Length	7–13 mm	11–15 mm	14–17 mm	10–24 mm
Vesture	Glandular hirsutulous	Glandular hirsutulous and sometimes subfarinaceous	Glandular hirsutulous with trichomes to 2 mm long	Glandular puberulent to glandular pilosulous or glandular hispidulous
Ray floret				
Number	0–10	5–25	9–13	11–42
Corolla color	Pale yellow, sometimes reddish tinged	Greenish white to purplish	Tube pale greenish below, reddish above; limb very pale greenish white	Pink to wine-red
Tube length	1 mm	2–3 mm	3–4.5 mm	3–8 mm
Tube vesture	Glabrous	Puberulent	Sparsely puberulent and minutely glandular	Commonly pilosulous and minutely glandular
Limb length	1.5–3.5 mm	5–7 mm	11.5–13 mm	6–20 mm
Limb width	ca. 2 mm	2–3 mm	ca. 4 mm	2–6 mm
Pappus	Minute rim	Minute rim usually with 1–3 teeth 0.5–1.5 mm long	Obsolete or minute rim	Minute rim
Achene length	6–8 mm	8.5–10 mm	10–11 mm (immature)	7–14 mm

TABLE 1 (continued)

COMPARISON OF THE PU'U 'ALAEA GREENSWORD WITH *Argyroxiphium grayanum*, *A. virescens*, AND *A. sandwicense* SUBSP. *macrocephalum*

CHARACTER	<i>A. grayanum</i>	<i>A. virescens</i>	PU'U 'ALAEA GREENSWORD	<i>A. sandwicense</i> SUBSP. <i>macrocephalum</i>
Receptacular bract				
Number	20–45	14–50	ca. 37	32–115
Length	8–13 mm	12–16 mm	14–17 mm	10–24 mm
Disk floret				
Number	100–300	(40–)80–375	ca. 165	120–600
Corolla color	Pale yellow	Apparently purplish (probably only distally)	Very pale greenish white proximally, reddish distally	Yellowish proximally, pink to wine-red distally
Corolla length	3–4.5(–5) mm	4.5–6 mm	6.5–7.5 mm	5–8 mm
Pappus	2–9 unequal, oblong to oblanceolate scales 1–2(–3) mm long	5–9 unequal, linear to oblong-lanceolate scales, 0.5–4.5 mm long	Extremely reduced, a minute rim sometimes with a tooth up to 0.4 mm long	Rim with minute teeth or with 3–10 linear-lanceolate to oblong-truncate scales up to 5 mm long
Achene length	6–9 mm	8–11 mm	8.5–9.5 mm (immature)	7–15 mm

virescens and *A. sandwicense* subsp. *macrocephalum* and treated them as hybrids between these species [e.g., *Rock 8608*, p. p. (BISH); *Rock 8575* p. p. (BISH); *Rock 16036* (BISH)]. Unlike the Pu'u 'Alaea plant, these putative hybrids had well-developed pappus. However, many individuals of Haleakalā silversword also lack any substantial development of pappus in the disk florets. It may be that this feature was also variable in *A. virescens* or that hybridization involving an epappose individual of *A. sandwicense* subsp. *macrocephalum* accounts for the lack of pappus seen in the Pu'u 'Alaea plant.

Pollen of the Pu'u 'Alaea plant was 62% stainable compared with 99.7% pollen stainability in a sample of *A. sandwicense* subsp. *macrocephalum* that was collected nearby on the same day. The apparent fertility in the Pu'u 'Alaea plant is comparable with that of an artificial hybrid between *A. grayanum* and *A. sandwicense* subsp. *sandwicense* (64%, cf. Carr and Kyhos [1981], reported as *A. sandwicense* × *A. virescens*) and is consistent with the interpretation of the Pu'u 'Alaea plant as

an unstabilized hybrid involving two species of *Argyroxiphium*. Though the details are likely to remain obscure, we believe that the Pu'u 'Alaea plant represents a hybrid product between *A. virescens* that formerly occupied this area and *A. sandwicense* subsp. *macrocephalum* that is still found in the same vicinity.

When the Pu'u 'Alaea plant flowered in 1989, nearby individuals of *A. sandwicense* subsp. *macrocephalum* and *Dubautia menziesii* (A. Gray) D. Keck were also flowering. An abundance of potential insect pollinators (native bees, flies, and moths) visiting the capitulescences provided ample opportunity for hybridization between the Pu'u 'Alaea plant and at least two other members of the silversword alliance. Moreover, despite the widespread occurrence of self-incompatibility in the silversword alliance (Carr et al. 1986), some individuals have been known to produce substantial numbers of selfed progeny. Thus, the male parentage of any progeny of the Pu'u 'Alaea plant is necessarily uncertain. Nevertheless, 21 of several hundred fruits

collected from the Pu'u 'Alaea plant contained embryos, six of which germinated and are currently undergoing further evaluation (Bruce Baldwin, University of California, Berkeley, pers. comm.).

In the past, other plants similar to the Pu'u 'Alaea individuals have been observed on cliffs south of Hōlua Cabin within Haleakalā Crater (A.C.M., pers. obs.) as well as on the upper, outer rim of the crater southeast of the mountain summit (J. Tavares, pers. comm.) (Figure 1). Though unsubstantiated, these distinctly greenish silverswords may also represent hybrid products between *A. sandwicense* subsp. *macrocephalum* and *A. virescens*.

The vegetative putative hybrid plant at Pu'u 'Alaea is the only one known to be living at this time. Tissue culture was attempted at Mills College, Oakland, California, and at Lyon Arboretum, Honolulu, Hawai'i (Bruce Pavlik, Greg Koob, pers. comm.) but the cultures eventually died without regenerating whole plants. Similar efforts and the possibility of obtaining viable progeny from this plant or from fruits collected from the individual that flowered and died in 1989 represent the only apparent avenues to conserve the otherwise extinct Maui island endemic *Argyroxiphium virescens*.

LITERATURE CITED

- ANONYMOUS. 1990. Fed. Register 55(35), 21 Feb.
- CARR, G. D. 1985. Monograph of the Hawaiian Madiinae (Asteraceae): *Argyroxiphium*, *Dubautia*, and *Wilkesia*. Allertonia 4:1-123.
- CARR, G. D., and D. W. KYHOS. 1981. Adaptive radiation in the Hawaiian silversword alliance (Compositae-Madiinae). I. Cytogenetics of spontaneous hybrids. Evolution 35:543-556.
- CARR, G. D., E. A. POWELL, and D. W. KYHOS. 1986. Self-incompatibility in the Hawaiian Madiinae (Compositae): An exception to Baker's Rule. Evolution 40:430-434.
- DEGENER, O. 1930. Illustrated guide to the more common or noteworthy ferns and flowering plants of Hawaii National Park. Published privately, Honolulu.
- FOSBERG, F. R., and D. R. HERBST. 1975. Rare and endangered species of Hawaiian vascular plants. Allertonia 1:1-72.
- HILLEBRAND, W. 1888. Flora of the Hawaiian Islands. Williams & Norgate, London.
- MANEVAL, W. E. 1936. Lacto-phenol preparations. Stain Technol. 11:9-11.