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Factors Affecting Seed Germination of the Mauna Kea Silversword in Hawai'i[1]

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ABSTRACT: The Mauna Kea silversword, *Argyroxiphium sandwicense* DC, is endemic to the slopes of Mauna Kea on the island of Hawai'i. Once abundant, it is now reduced to a total of less than 500 individuals. We examined germination of silversword seeds subjected to various experimental and field conditions. Under experimental conditions, germination was optimal in moist, shady environments. Removal of the pericarp greatly enhanced germination, but cold and heat pretreatments did not alter germination. Germination of field-collected seeds was highest for seeds <2 yr old and for seeds collected from flower stalks. The ability to germinate was much lower for seeds collected from on or under the soil surface. In mesic environments, grasses competed with silversword seedlings. We suggest that seed germination and early seedling establishment are major obstacles to reestablishment of the Mauna Kea silversword.

THE MAUNA KEA SILVERSWORD (MKSS; *Argyroxiphium sandwicense* DC) is a federally listed endangered plant and is endemic to the alpine slopes of Mauna Kea on the island of Hawai'i. The current population consists of about 40 naturally occurring individuals in one population and about 400 individuals that are the result of outplanting at three locations by the Hawai'i State Division of Forestry. The largest population of outplants is located on the eastern slope of Mauna Kea between 2800 and 2900 m elevation at Waipāhoehoe Gulch. Two smaller outplanted populations are located on the western slope of Mauna Kea at Pu'u Nānaha (2770 m) and along the Skyline jeep trail (2970 m). The MKSS is a giant rosette plant of the family Asteraceae, and individuals are either monocarpic or polycarpic (have one or several rosettes [Powell 1992]). Showy flower stalks are produced that reach 2–3 m in height. The MKSS is less well known than its relative, the Haleakalā silversword (*Argyroxiphium macrocephalum* A. Gray), a threatened species endemic to Haleakalā Crater on the island of Maui. The Haleakalā and Mauna Kea silverswords are variously considered subspecies (Carr 1985, Wagner et al. 1990) or separate species (Degener, pers. comm.; Powell 1992) based on morphological characteristics. Genetic analyses of variation between and within the Haleakalā and Mauna Kea populations are currently in progress (R. Robichaux, pers. comm.). This study considers the MKSS as a distinct species (Powell 1992).

Recovery of the MKSS to population levels that will allow it to be removed from the endangered species list is mandated by the Endangered Species Act (Rohlf 1991). Two approaches are being attempted to reestablish the MKSS. The Hawai'i State Division of Forestry has conducted an extensive program of outplanting shadehouse-grown seedlings on Mauna Kea (1974–present [Powell 1992; S. Bergfield, pers. comm.]). However, outplanting is costly and labor intensive and survival rates of outplants have been low (14–42% survival in 1987 [E.A.P., unpubl. data]). In addition, shadehouse- or greenhouse-grown plants may be selected for characteristics not common in the natural populations (Powell 1992). The second approach is to examine the feasibility of sowing seeds directly at potential regeneration sites

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to avoid the problems associated with outplanting. In both approaches, artificial cross-pollination of flowers in the field is necessary to obtain adequate numbers of filled seeds because the MKSS is self-incompatible and seed set is pollinator-limited (Powell 1992).

In this paper we report on experiments that examined the germination of MKSS seeds from achenes subjected to greenhouse and field conditions. Specifically, we looked at the effects of various shade and water regimes, pericarp removal, and cold and heat treatments on germination of MKSS seeds in the greenhouse. We also compared germination of seeds that remained on flower stalks, fell to the ground, or were buried in the soil. Finally, we examined the numbers of seedlings established from MKSS achenes sown in different microhabitats in the field. The results of these experiments will help determine if sowing MKSS achenes in the field is a viable alternative to outplanting and what the optimal conditions are for germination.

MATERIALS AND METHODS

Greenhouse Experiments

In July 1988 we conducted three experiments designed to determine factors affecting germination of MKSS seeds. The experiments were conducted at Hawai'i Volcanoes National Park (HAVO) on the island of Hawai'i (1200 m elevation). Achenes (fruits) were collected in September 1987 from 20 flowering silverswords from the Waipāhoehoe and Skyline populations on Mauna Kea and stored at 5°C. Contributions from individual plants varied between 0.5 and 10% of the total seed collection. Only achenes with filled seeds (containing intact embryos) were used for the three experiments.

SHADE AND WATER EXPERIMENT. Forty-eight pots were placed in each of six shade treatments (0, 30, 55, 63, 80, and 96% reduction of ambient light by optically neutral shade cloth) on open-air benches at the greenhouse complex at HAVO. One achene (with filled seed) was sown in each pot on a surface of wet vermiculite (288 achenes total). Within each shade treatment, 24 pots were watered daily (unless it rained) and 24 were watered weekly. Seed germination (>1 mm elongation of the radicle) was monitored daily for 33 days (7 days after last germination occurred). The rate of germination was measured as the number of days to reach 50% of final germination (GT_{50}). Statistical differences among treatments were determined at the 0.05 level using chi-square analysis of contingency tables on the number of seeds that germinated.

PERICARP REMOVAL EXPERIMENT. Seventy-two achenes with filled seeds from the same September 1987 collection were removed from storage at 5°C and soaked in tap water for 3 hr before being subjected to one of three different treatments ($n = 24$ achenes per treatment): total, partial (one-fourth to one-fifth removed), or no removal of the pericarp (the hardened fruit wall). The achenes were placed on the surface of wet vermiculite in a greenhouse at HAVO and misted four times daily to maintain a moist surface. Seed germination was monitored for 33 days.

COLD AND HEAT EXPERIMENTS. Achenes with filled seeds from the same source as previously described were subjected to five different temperature regimes (room temperature [about +20], −15, +30, +55, and +75°C) for various lengths of time (30 min to 48 hr; total of 11–24 achenes per treatment, 16 treatments, 339 achenes total). After the heat treatments, achenes were soaked in tap water for 3 hr and the pericarp was partially removed. Achenes were then sown on a surface of wet vermiculite in pots at HAVO and misted four times daily. Seed germination was recorded daily for 33 days; treatment differences were evaluated with chi-square analysis.

Field Experiments

SEED GERMINATION: COLLECTIONS. Germination of seeds from stalks was determined from achenes collected from a total of 13 flower stalks in three populations (Waipāhoehoe, Pu'u Nānaha, and Skyline) in July

1988. The stalks were either 1 ($n = 6$ stalks), 2 ($n = 4$), or 3 ($n = 3$) yr old. In July 1989, achenes were collected from an additional six 1-yr-old flower stalks at Waipāhoehoe (total of 19 stalks). We did not collect from plants that flowered in multiple years or that were in close proximity to other flowering plants so age of achenes could be determined. When possible, five heads (capitula) with achenes attached were collected from each flower stalk, and all achenes were sorted to determine percentage of filled seeds. Germination of seeds was then tested. Achenes were first soaked in water for 3 hr, the pericarp was then partially removed, and the achenes were placed on moist vermiculite in greenhouse pots and misted daily. Germination was recorded for 33 days.

Germination of seeds and percentage of achenes with filled seeds from the ground surface were determined from achenes collected within a 1-m radius of (and in a northerly direction from) the same 19 flower stalks.

Germination of seeds found in the soil was also determined. Two bags of soil, each 5 by 10 by 1 cm deep, were collected around each of the same 19 flower stalks (13 in 1988, 6 in 1989) at each of three locations: directly under the old flower stalks, at 50 cm, and at 100 cm distance from the flower stalks in a southerly direction. These soil samples included any achenes that were on the soil surface as well as those achenes buried to 1 cm depth. The soil was sifted for achenes, and percentage achenes with filled seeds and percentage seed germination were determined. These data were also used to estimate density of achenes on and in the soil. The surface area of the two bags (100 cm^2) was used to extrapolate achene density in each of three concentric zones around each flower stalk. The sampled radius and area of each of the three zones was 0–25 cm (1963 cm^2), 25–75 cm (15,708 cm^2), and 75–125 cm (31,416 cm^2), respectively. Data from the 19 stalks were pooled by stalk age before germination was compared by stalk age and habitat (stalk or soil) with chi-square analysis; density of achenes was compared with a Kruskal-Wallis test.

SEED GERMINATION: EXPERIMENT. To determine the effect of burial on seed germination, 10 achenes with filled seeds from the same September 1987 collection were placed in nylon mesh bags (10 by 7 cm; mesh size of 20 threads per centimeter). The bags were closed with wire ties and in July 1988 placed either on the surface of the soil at 1.5, 2.5, or 3.5 m or under 1 cm of soil at 1.0, 2.0, or 3.0 m from 12 of the 13 1988 flower stalks described above (total of 72 bags and 720 seeds). Bags at ≥ 2 m distance from the plant were retrieved after 1 yr; bags < 2 m from the plant were collected after 2 yr. Achenes were pooled by treatment (surface or buried) and date of collection for chi-square analysis, and seed germination was determined as previously described.

FIELD SOWING EXPERIMENT. This experiment was designed to determine the effect of organic soil versus cinder and the presence or absence of shade and grasses on MKSS seedling establishment. Two thousand achenes with filled seeds were obtained from the September 1987 collection on Mauna Kea (1000 from plant no. 23 at Skyline; 1000 from mixed sources). On 21 July 1988, 50 achenes with filled seeds were sown on the surface of the soil in 10 by 10 cm plots located in 10 areas (blocks) with four treatments per block (a total of 40 plots and 2000 seeds). The treatments were under māmane (*Sophora chrysophila* St. John) trees with 100% grass cover; under māmane with removal of all grass from a 25 by 25 cm area, leaving exposed organic soil; in adjacent open habitat on cinder without grass; and on adjacent open cinder habitat with 25–75% grass cover. The blocks were located at least 30 m apart in a 500 by 100 m area within the Waipāhoehoe Gulch silversword exclosure on Mauna Kea. Each treatment within a block was located randomly within the appropriate habitat along a 10- to 15-m transect and radiating out in a northeasterly direction from large māmane trees.

Achenes with filled seeds from the same sources and year were also sown on wet vermiculite in a greenhouse in Volcano, Hawai'i (1200 m elevation), and misted daily for

33 days to test viability of the field-sown achenes. Seedling establishment in the field was recorded in July 1989 (1 yr) and September 1990 (2 yr) as a percentage of achenes with filled seeds sown and compared with chi square analysis.

RESULTS

Greenhouse Experiments

SHADE AND WATER. Germination of seeds watered weekly differed significantly (chi square = 16.9; $P = 0.002$) among shade treatments and was highest at intermediate and high shade levels (Table 1). Germination of seeds watered daily was not significantly different (chi square = 4.7; $P = 0.40$) among shade treatments. Watering regime made less difference at higher shade levels, presumably because shade reduced water loss. Germination rates (GT_{50}) were fastest at higher levels of shade (Table 1).

PERICARP REMOVAL. Removal of the total pericarp resulted in the highest (87%) and fastest ($GT_{50} = 7$ days) germination, followed by partial (71%, 8 days), and no removal (42%, 18 days). The pericarp clearly inhibited germination of the MKSS seeds.

TABLE 1

GERMINATION OF SILVERSWORD SEEDS UNDER SIX SHADE AND TWO WATERING TREATMENTS

% SHADE	GERMINATION % DAILY[a]	% WEEKLY	RATE (GT_{50})[b] DAILY	RATE (GT_{50})[b] WEEKLY
0	46	12	21	21
30	62	46	19	19
55	58	nd	16	nd
63	75	58	13	14
80	62	67	17	14
96	54	54	14	13

NOTE: Twenty-four achenes with filled seeds were sown per treatment combination. nd, no data available.

[a] Watering regime.

[b] Time in days to reach 50% of final germination.

TABLE 2

GERMINATION OF SILVERSWORD SEEDS UNDER VARIOUS TEMPERATURE REGIMES

TREATMENT NO.	TREATMENT DESCRIPTION (temperature [°C], time[a])	n[b]	GERMINATION %	GERMINATION RATE (GT_{50})
1.	ambient, 0 hr	23	87	5
2.	−15°, 24 hr	24	92	3
3.	−15°, 48 hr	24	92	4
4.	+30°, 30 min	24	92	5
5.	+30°, 60 min	24	92	5
6.	+30°, 6 hr	22	77	5
7.	+30°, 24 hr	24	92	7
8.	+30°, 48 hr	24	92	6
9.	+55°, 30 min	23	96	5
10.	+55°, 60 min	23	78	4
11.	+55°, 6 hr	21	95	4
12.	+55°, 24 hr	24	87	4
13.	+55°, 48 hr	24	96	5
14.	+75°, 30 min	12	92	5
15.	+75°, 6 hr	12	92	5
16.	+75°, 48 hr	11	91	5

[a] Time in treatment after removal from 5°C and before sowing.

[b] n = 11–24 achenes with filled seeds.

COLD AND HEAT. Germination percentages did not differ from the control at ambient temperature (chi square = 10.7; $P = 0.70$) following a wide range of temperature pretreatments (Table 2), suggesting that MKSS seeds are tolerant of freezing or heating for short periods of time.

Field Experiments

SEED GERMINATION: COLLECTIONS. The percentage of achenes with filled seeds (Table 3) declined with stalk (and therefore achene) age (chi square = 97.1; $P < 0.0001$) and was largest for achenes collected directly from stalks and smallest for achenes collected from in the soil (all three distances from stalk combined; chi square = 89.0; $P < 0.0001$). Percentage germination of seeds that remained on the stalks was >70% after 1 or 2 yr. Only one filled seed was found on the 3-yr-old stalks that were sampled, and that seed did not germinate. Seed survival is therefore pos-

TABLE 3

GERMINATION OF SILVERSWORD SEEDS COLLECTED FROM STALKS, FROM THE GROUND SURFACE, OR FROM THE TOP 1 CM OF SOIL

STALK AGE (yr)[a]	NO. STALKS	% FILLED SEEDS			% GERMINATION OF FILLED SEEDS		
		ON STALKS	ON SOIL SURFACE	IN SOIL	ON STALKS	ON SOIL SURFACE	IN SOIL
1	12	2.9 (2,667)	2.5 (798)	1.9 (465)	70.5	60.0	22.2
2	4	1.5 (533)	0.8 (247)	0.0 (101)	75.0	100.0	NA
3	3	0.4 (238)	0.0 (85)	0.0 (71)	0.0	NA	NA

NOTE: Seed age equals stalk age. Numbers of seeds collected are in parentheses. NA, not applicable.
[a]From July 1988 collection (stalk ages 2 and 3 yr) and both July 1988 and July 1989 collections (stalk age 1 yr).

sible on the stalks or soil surface for 2 yr but probably not for 3 yr. Burial reduced seed survival to a maximum of 1 yr.

Density of achenes with or without filled seeds on or in the soil declined rapidly with distance from flower stalks (Kruskal-Wallis $H = 24$; $P < 0.0001$), but did not decline consistently with stalk age (Kruskal-Wallis $H = 0.8$; $P = 0.68$ [Table 4]). However, achenes that had been in the soil for 3 yr were probably not viable (Table 3).

SEED GERMINATION: EXPERIMENT. After 1 yr, the percentage of achenes that still contained filled seeds was greater (chi square = 19.7; $P = 0.04$) for achenes buried in the field in mesh bags (38%) than for achenes placed in mesh bags on the soil surface (28%). Retrieval of filled seeds after 2 yr was minimal for achenes that were buried (two seeds [1.7%]) and for achenes on the soil surface (three seeds [2.5%]). Germination of surviving seeds was not significantly higher (chi square = 17.6; $P = 0.09$) for buried achenes in year 1 (buried: 83%; surface: 65%). In year 2, one of the filled seeds germinated from the buried achenes and two from the surface achenes. All but 5% of the achenes were recovered, but most had been damaged by fungi, broken, dried out, or contained seeds that germinated and then died.

TABLE 4

DENSITY OF SILVERSWORD ACHENES AT THREE DISTANCES FROM FLOWER STALKS

STALK AGE (yr)[b]	NO. STALKS	ACHENE DENSITY (no./cm^2)		
		0–25 cm[a]	25–75 cm	75–125 cm
1	12	0.35 ± 0.15	0.04 ± 0.01	0.03 ± 0.01
2	4	0.13 ± 0.01	0.04 ± 0.01	0.08 ± 0.07
3	3	0.18 ± 0.07	0.03 ± 0.01	0.03 ± 0.01

NOTE: Densities were calculated using number of achenes with or without filled seeds from the soil surface and top 1 cm of soil divided by the area of each of three concentric bands around the stalks.
[a]Range of radial distances from flower stalk.
[b]From July 1988 collection (stalk ages 2 and 3 yr) and both July 1988 and July 1989 collections (stalk age 1 yr).

FIELD SOWING. One year after sowing, seedling establishment of silverswords was highest (chi square = 27.0; $P = 0.003$) under māmane with grass removal (4.2 ± 1.7% [mean ± SEM] of the viable seeds sown; 12 seedlings total in five plots) followed by open cinder with grass (3.6 ± 2.5%; 10 seedlings in two plots). Only one seedling was found under māmane with grass, and no silverswords established in the open habitat without grass. No seedlings survived for 2 yr.

DISCUSSION

Germination may be a major factor limiting reestablishment of the Mauna Kea sil-

versword. Under experimental conditions, germination was optimal in moist, shady environments. However, establishment of MKSS seedlings under the shade of large trees was apparently prevented by dense cover of grasses. Competition between grasses and seedlings of long-lived alpine rosette plants has been found in other studies (Smith 1984, Augspurger 1985).

The pericarp (fruit wall) of the MKSS clearly inhibits germination, probably due to chemical inhibitors that Siegel et al. (1970) detected in extracts from both achenes and inflorescences of the related Haleakalā silversword. Germination was highest in our study when the entire pericarp was removed. Partial removal of the pericarp resulted in intermediate germination. When the pericarp was only punctured (Siegel et al. 1970), germination was not enhanced. Germination of the MKSS probably occurs following natural weathering of the inhibitory pericarp. This weathering may occur most rapidly in mesic environments.

Dry MKSS achenes tolerated extreme temperatures for short durations in our study. Wide ranges in soil surface temperatures are typical of Hawaiian alpine areas, with freezing temperatures common at night and daytime maxima exceeding 40°C (Kobayashi 1973). Yet Siegel et al. (1970) found that germination of the Haleakalā silversword was heat sensitive, with best germination (of imbibed seeds) at alternating temperatures of 8 and 15°C, and no germination in any regime (continued for 3 weeks) involving 8 hr or more at temperatures of −15 or +35°C. Our study did not have a comparable 3-week temperature regime, and we only used temperature as a pretreatment, subsequently placing seeds in a moist environment at ambient temperature to germinate. However, Siegel et al. (1970) found that germination was reduced after a pretreatment for dry achenes of just 15 min at 60°C. Our results showed no effect on germination even after a pretreatment of 48 hr at 60°C. Removal of the pericarp after the heat treatments may have enhanced germination of heat-treated seeds.

Seed viability declined more rapidly when the seeds were in the soil than when they remained on the flower stalks. Wetting of achenes in the soil may make the seeds more susceptible to extreme temperatures, desiccation, or attack by fungi. Primary causes of seed mortality on flower stalks appeared to be seed herbivores (notably tephritic fly larvae that parasitized the developing embryos [Powell 1992]).

Dispersal of the MKSS achenes appeared to be primarily limited to 1–2 m from the parent plant. Long-distance dispersal by water or wind is possible but has not been documented (beyond one example of apparent water dispersal downslope a distance of 8 m [L.R.W., pers. obs.]). We found no evidence of animal dispersal. In the absence of active dispersal mechanisms, germination of the few filled seeds (0.5–5% of the total [Powell 1992]) may be inhibited by leachates from the pericarps of thousands of achenes with unfilled seeds that also fall near the parent plant (see Fenner 1985).

Sowing MKSS achenes in optimal microsites away from the potentially inhibitory effect of parent plants and other achenes may improve germination in the field and prove to be a less costly and more logistically feasible option than outplanting. Because the seeds have no dormancy requirement (typical of monocarpic plants [Young and Augspurger 1991]), achenes may be sown immediately after collection. Seed viability declined rapidly in the soil, so collections should be made directly from the stalks. Further experiments are under way to evaluate the effects of elevation and other microsites on germination. Elevation, for example, can affect microclimate and the morphology, physiology, and reproduction of alpine plants (Baruch 1979, Smith 1980). Powell (1992) noted higher production of achenes with filled seeds but lower seedling establishment for plants at the Skyline exclosure than for plants at the lower-elevation Waipāhoehoe Gulch.

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