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Reproductive Biology and Uniform Culture of *Portulaca* in Hawaii[1]

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ABSTRACT: Ten taxa of *Portulaca* that occur in Hawaii (*P. lutea*, *P. molokiniensis*, *P. oleracea*, *P. pilosa*, *P. sclerocarpa*, *P. villosa*, two imperfectly known species, and two cultivars) were included in a study of reproductive biology and uniform cultivation. The response of plants under uniform conditions upholds the merger of the reputed Hawaiian endemic *P. cyanosperma* with *P. pilosa*. All *Portulaca* taxa in Hawaii are autogamous, and in most instances large numbers of seeds are set even when the flowers are totally undisturbed. Some taxa are facultatively cleistogamous, but even in chasmogamous forms the flowers are open for only about 3–9 hr. The cultivars were the only taxa observed to attract pollinators, but *P. molokiniensis*, which was not studied in nature, appears to have adaptations for biotic pollination. Most of the portulacas studied have capsular fruit that require about 13–17 days to mature, but in *P. sclerocarpa* the fruits are thick-walled and indehiscent and require about 28 days for maturation. The life cycle ranges from about 8 weeks in most cases to several months in *P. molokiniensis*. However, individuals of most taxa typically flower and fruit many times during one growing season. Seeds were generally nondormant, but partial seed dormancy was encountered in *P. molokiniensis*.

THERE HAVE BEEN NO STUDIES focusing on reproductive aspects of *Portulaca* in Hawaii. The only available comparative information of this sort is found in the revision by Geesink (1969), which dealt with morphology, systematics, biosystematics, and typification of *Portulaca* from Indo-Australia and the Pacific. However, most of his work was based on herbarium studies. In his revision, Geesink (1969) recognized only three species of *Portulaca* in Hawaii. In contrast, the recent work of Wagner et al. (1990) recognized the occurrence of six named species and two unnamed taxa of *Portulaca* in the Hawaiian Islands. This disparity of treatments prompted a broad study of all taxa of *Portulaca* reported to be native or naturalized in the Hawaiian Islands (Yun 1989). The present paper provides information gained from a study of floral phenology, breeding systems, and uniform culture of 10 taxa of the genus *Portulaca* that occur in Hawaii.

MATERIALS AND METHODS

The taxa used in this study were *Portulaca lutea* Sol. ex G. Forster, *P. molokiniensis* Hobdy, *P. oleracea* L., *P. pilosa* L., *P. sclerocarpa* A. Gray, *P. villosa* Cham., two imperfectly known species designated *P.* "olowalu" and *P.* "ulupalakua," a cultivar of *P. grandiflora* Hook., and a second unidentified cultivar designated *P.* cv. 1. *Portulaca* "olowalu" is treated as a variant of *P. villosa* by Wagner et al. (1990). They suggest that it likely represents an undescribed endemic taxon. *Portulaca* "ulupalakua" corresponds to *P.* sp. A in the treatment by Wagner et al. (1990), who consider it to be a naturalized, as yet unidentified species. Plants were maintained and studied in the greenhouse for several months to 2 yr. Collection and accession data can be found in Yun (1989).

In the greenhouse study, randomly selected

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flowers (10–20) of each taxon were tagged at anthesis to determine the time required for seed maturation. The time of flower opening and closing and other aspects of floral biology were also noted and recorded. Fruits from these flowers and others sufficient to produce a minimum sample of 100 capsules for each taxon were harvested and the seeds were counted to assess seed productivity by unmanipulated flowers under greenhouse conditions. Fruits that did not have at least one apparently normal seed were excluded from the samples. To determine whether modes of reproduction such as autogamy or apomixis occurred in the group, flowers with normally developed anthers, flowers with aborted anthers, and emasculated flowers were bagged and checked daily for capsule development, seed production, or both. Several trips were made to the field to gather information on natural pollinating agents.

Because few seeds were set by unmanipulated flowers of *Portulaca molokiniensis* and one accession of *P. lutea* in the greenhouse, an experiment was conducted to determine the effect of artificial self-pollination of different flowers at approximately 2-hr intervals during the periods of 0830–0900, 1030–1100, 1230–1300, and 1430–1500 hours. A minimum of 15 tagged flowers was pollinated this way for each period. Daily observations were made until capsules were harvested at maturity. After the capsules were sorted according to the time of pollination, the number of seeds per capsule was determined and recorded. Fruits that did not have at least one apparently normal seed were excluded from the samples.

Seeds were germinated on wet filter paper in Petri dishes or on the surface of a soil mixture containing vermiculite, sand, perlite, and potting soil. In the latter case, the soil mix was placed in 5 × 5 cm plastic pots on a greenhouse bench kept moist with an intermittent water mist. Apparent dormancy in *Portulaca molokiniensis* was effectively overcome by breakage of the seed testa with a razor blade or scarification of the seed with concentrated sulfuric acid for 90 sec.

Pollen viability was estimated for each taxon by observing the stain reaction of a minimum of 300 pollen grains in aniline (cotton) blue in lactophenol on a microscope slide. Fully stained pollen grains were considered viable, while partially or nonstained pollen grains were scored as nonviable. The percentage of stained pollen grains in a minimum of 20 samples for each of the 10 taxa was recorded.

RESULTS

In general, the results presented here and elsewhere (Yun 1989) are consistent with the recognition of two rather distinct groups of *Portulaca* in Hawaii. For convenience, these groups are identified as Group A (portulacas with broadly ovate leaves, cf. section *Portulaca* subsection *Portulaca*, Geesink 1969) and Group B (portulacas with oblong-oblanceolate to cylindrical leaves, cf. section *Portulaca* subsection *Stellulato-tuberculatae*, Geesink 1969) in the following text.

The cultivation of eight species representing many populations of *Portulaca* for observations of reproductive biology and other studies also afforded the opportunity to observe plants from a diversity of habitats under uniform conditions. Of particular interest in this regard are plants of *P. pilosa* from Barking Sands Beach, Kauai and Queensland, Australia. The Hawaiian plants had reddish branches in the wild, but their appearance changed considerably soon after being transferred to greenhouse conditions. The Hawaiian and Australian plants appeared almost identical after being grown in the same greenhouse environment for several months. This is of special significance because plants from the Barking Sands location were cited in the original publication of *P. cyanosperma* Egler (Egler 1937). Because of these results and data from observations of seed and pollen morphology (Yun 1989), *P. cyanosperma* is not recognized as distinct from *P. pilosa* in the present study.

The greenhouse study on reproductive biology indicates that flowers of portulacas in Hawaii are slightly protandrous. They are also autogamous, at least under experimental conditions, since numerous viable seeds are produced from bagged flowers that possess

TABLE 1

FLORAL PHENOLOGY AND SEED PRODUCTION OF *Portulaca* IN HAWAII

TAXON	TIME OF FLORAL RESPONSE		MEAN TIME TO SEED MATURITY (days)	MEAN NO. SEEDS PER CAPSULE
	OPEN	CLOSE		
P. cv. 1	0800–0830	1730–1800	N.A.	22.9
P. grandiflora cv.	0800–0830	1730–1800	N.A.	27.3
P. lutea	0845–0930*	1430–1500	13.2	30.9
P. molokiniensis	0630–0730	1430–1500	14.6	6.7
P. oleracea	0845–0930	1200–1230	12.7	40.7
P. "olowalu"	0800–0830	1500–1530	14.0	76.4
P. pilosa	0830–0900	1330–1415	13.9	60.7
P. sclerocarpa	0630–0730	1130–1230	28.6	232.3
P. villosa	0630–0730	1500–1530	14.9	66.8
P. "ulupalakua"	0815–0845	1030–1130	13.2	160.7

NOTE: Observations on floral phenology were made mostly under greenhouse conditions. Data on seed production were from unmanipulated flowers under greenhouse conditions and were based on a minimum of 100 samples except for the cultivar of *P. grandiflora*, for which only 4 samples were available. N.A. = data not available.

* Flowers of Necker Island plants opened at about 1100 hours, somewhat later than *P. lutea* from other locations.

normally developed anthers. No seeds are produced from flowers with aborted anthers or from emasculated flowers, indicating that these taxa are probably not apomictic, but pseudogamy has not been ruled out. Flowers of certain species are cleistogamous under conditions of reduced light and temperature. Such is the case in *Portulaca oleracea*, *P. pilosa*, and *P.* "ulupalakua," whose flowers are also fugacious. Flowers open fully only on bright sunny mornings, and self-pollination within closed buds without unfolding floral parts also frequently occurs. The diurnal phenology of flowering also varies among species. In some species flowers open early in the morning and last about 8–9 hr, while in others the flowers last only 3–4 hr and wilt rapidly (Table 1). Small-flowered species tend to have flowers that remain open for the shortest period. All flowers examined lasted only 1 day. No floral odor was detected except in *P. molokiniensis*, which has flowers that give off a faint fragrance. No apparent nectaries were found, and pollinators (honey bees) were encountered during flowering only in the cultivar of *P. grandiflora*. However, *P. molokiniensis* was not observed under field conditions. Occasionally, ants were observed at the base of the stamens in several species, but they are probably not effective as pollinators. Their activities were mostly limited to chewing at the filament bases and knocking the stamens off.

About 80–120 mature pollen grains were produced per anther. Pollen stainability tests suggest relatively high pollen viability (85–99%) in all species, excluding cultivars (Figure 1). Cultivars demonstrated low stainability by comparison, suggesting the possibility of a hybrid origin. Only 33% of the pollen grains of the cultivar of *Portulaca grandiflora* were stained, and the aborted grains were usually very reduced in size and shrunken in appearance.

Flowers of *Portulaca* exhibit sequential maturation throughout the growing season. Development of mature capsules from flowering usually required 13–14 days in most species (Table 1). In *P. sclerocarpa*, the maturation of the capsule required about 4 weeks. In cleistogamous flowers of *P. oleracea*, *P. pilosa*, and *P.* "ulupalakua," this process took only 7–10 days. The number of seeds in a capsule exhibited great variability by species (Table 1). It ranged from as low as a mean of 6.7 seeds per capsule in *P. molokiniensis* (Group A) to as high as 232.3 seeds per capsule in *P. sclerocarpa* (Group B). The two other species of Group A, *P. lutea* and *P. oleracea*, also had fewer seeds per capsule than

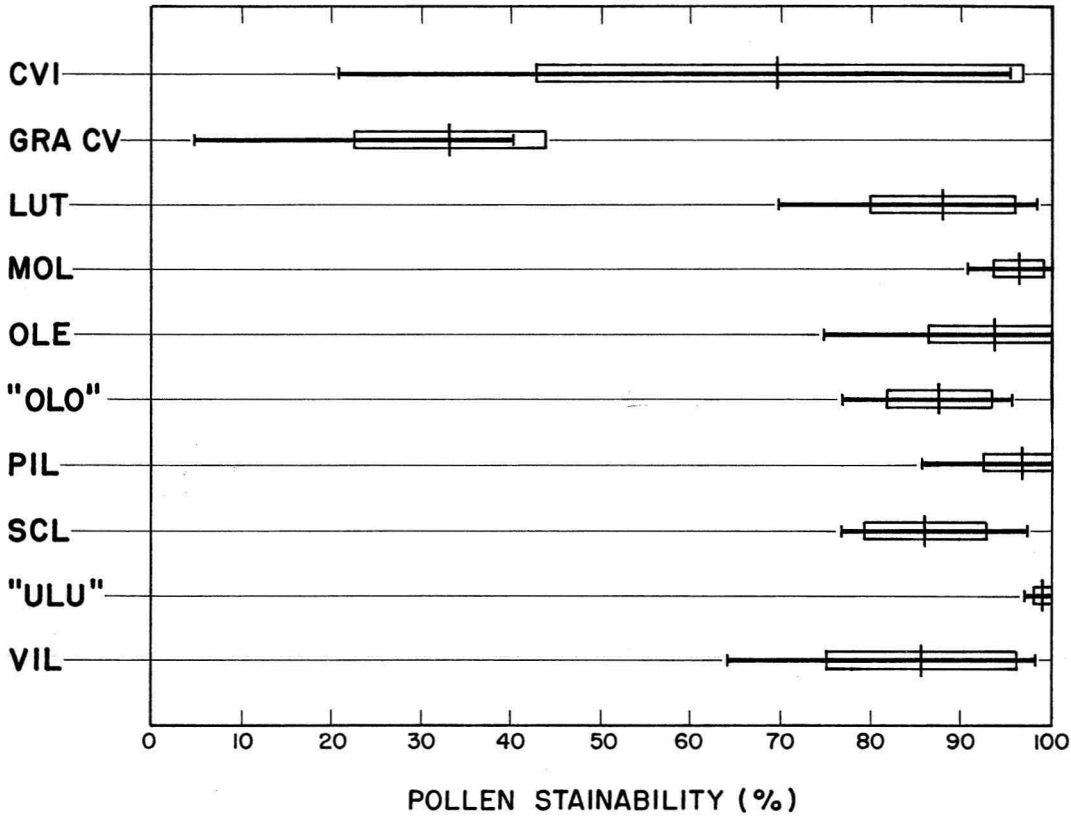

FIGURE 1. Pollen stainability of *Portulaca* in Hawaii. For each species the range is indicated by the horizontal line, the mean by the vertical line, and the standard deviation by the box. CV1 = cv. 1, GRA CV = *P. grandiflora* cv., LUT = *P. lutea*, MOL = *P. molokiniensis*, OLE = *P. oleracea*, "OLO" = *P.* "olowalu," PIL = *P. pilosa*, SCL = *P. sclerocarpa*, "ULU" = *P.* "ulupalakua," and VIL = *P. villosa*.

species of Group B. However, infraspecific variation in seed productivity was also noted when population samples were compared.

Floral features not observed in other portulacas in Hawaii were noted in *Portulaca molokiniensis* and in the plants of *P. lutea* from Lualualei, Oahu. Flowers of *P. molokiniensis* and the atypical plants of *P. lutea* (Lualualei) share a number of similarities, including long-exserted stigmas that receive little or no self-pollination. Consequently, very few seeds were produced when these plants were left undisturbed in the greenhouse, but when flowers were artificially self-pollinated at ca. 2-hr intervals, seed production increased substantially (Table 2). In *P. molokiniensis*, the highest production was obtained from artificial self-pollination at 1030–1100 hours, yielding a mean of 92.2 seeds per capsule compared to a mean of 6.7 seeds per capsule from unmanipulated flowers under greenhouse conditions. A similar pattern was detected in *P. lutea* (Lualualei), although the amount of seed produced was relatively small, with a peak production mean of 35.7 seeds per capsule resulting from the 1430–1500 hours pollination, compared to a mean of 10.5 seeds per capsule from unmanipulated flowers.

Portulaca seeds used in this study were largely nondormant, although seeds of *P. molokiniensis* demonstrated partial dormancy that was overcome by breaking the testa or by scarification in sulfuric acid. In general, a high percentage of germination was achieved in 1 to 2 weeks, and the response was best in the

TABLE 2

SEED PRODUCTIVITY IN *Portulaca molokiniensis* AND *P. lutea* AFTER ARTIFICIAL SELF-POLLINATION AT 2-HR INTERVALS

TAXON	TIME OF POLLINATION	NO. FLOWERS	NO. SEEDS PER CAPSULE	
			MEAN	RANGE
P. molokiniensis	0830–0900	15	62.8	7–110
	1030–1100	15	92.2	44–126
	1230–1300	15	76.7	46–116
	1430–1500	15	51.9	5–98
	Control	376	6.7	1–106
P. lutea (Lualualei)	1030–1100	15	26.7	7–41
	1230–1300	15	28.9	13–50
	1430–1500	15	35.7	12–88
	Control	15	10.5	1–33

NOTE: Control = seed production by unmanipulated flowers under greenhouse conditions.

treatment utilizing a potted soil mixture on greenhouse benches subjected to misting.

With one exception, the species of *Portulaca* in this study reached maturity (seed germination to flowering) in a relatively short period. Most species flowered 6–8 weeks after seed germination, and the seeds ripened soon after flowering. Species such as *P. oleracea*, *P. pilosa*, and *P.* "ulupalakua," which have weedy characteristics and frequently exhibit cleistogamy, tend to reach maturity earlier than others. Data regarding *P. molokiniensis* are incomplete, but three seedlings about 8 months old were still in a primary growth stage. This species is an endemic Hawaiian perennial *Portulaca* (Hobdy 1987, Wagner et al. 1990) that has a stout, thick stem with a corky layer of secondary growth. Plants established from cuttings generally commenced flowering within a few weeks of being transferred from the field.

DISCUSSION

The observations on floral phenology recorded in the present study are in close agreement with those made in *Portulaca* by other workers (Hobdy 1987, Khoshoo and Singh 1966, Miyanishi and Cavers 1980, Sharma and Bhattacharyya 1956, Vengris et al. 1972, Wagner et al. 1990, Zimmerman 1977). Zimmerman's (1976) report of self-compatibility and the absence of apomixis in *P. oleracea* is consistent with results from the present study, not only for the Hawaiian populations of *P. oleracea*, but also for seven other species of *Portulaca* found in Hawaii. Self-pollination within floral buds occurs in cleistogamous species under unfavorable environmental conditions, as reported previously (Vengris et al. 1972). The relatively low number of pollen grains (80–120) found in anthers of Hawaiian *Portulaca* has also been reported previously in other autogamous taxa (e.g., autogamous species of *Linum* in which Faegri and Iversen [1950] estimated ca. 100 pollen grains per anther). The relatively homogeneous populations frequently observed during greenhouse and field study, as mentioned by many earlier workers, are consistent with the notion that all known members of Portulacaceae are self-pollinating (cf. Geesink 1969).

However, self-compatibility is known to allow some outcrossing and variability in populations (Vengris et al. 1972), and evidence of outcrossing has been reported, even in the small-flowered species, *Portulaca oleracea* (Miyanishi and Cavers 1980). Cross-pollination, when it occurs in *Portulaca*, is believed to be accomplished primarily by wind (Mulligan 1972, Zimmerman 1976). Biotic pollination in *Portulaca* seems to be largely limited to cultivars, in which there have been frequent observations of honey bees foraging for pollen (Mogford 1980).

Among the Hawaiian taxa, *Portulaca*

molokiniensis appears to exhibit features that would promote outcrossing or at least imply its existence as a reproductive mode. These features include large, showy flowers, floral fragrance, a low incidence of seed production in undisturbed flowers, and increased seed production by flowers whose stigmas artificially receive pollen augmentation. This syndrome suggests that biotic agents may be involved in the pollination of *P. molokiniensis*, and fieldwork needs to be done to further evaluate this possibility.

The relatively high mean pollen stainabilities obtained in the portulacas from Hawaii are comparable to some of the previously reported estimates that were based on non-Hawaiian materials. For example, about 99% pollen stainability was recorded in *Portulaca oleracea* from India by Bir and Sidhu (1980), whereas Khoshoo and Singh (1966) reported 80%, 90%, and 100% stainabilities, respectively, for three distinct Indian forms of the same species. These are all within the range of pollen stainability obtained for the Hawaiian populations of *P. oleracea* (75–100%) in the present study. A. K. Singh (1979) reported a pollen stainability of 68–95% in the cultivar of *P. grandiflora*, but Hawaiian plants of this cultivar exhibited a range in pollen stainability of 4.6–40.1% and a mean of 33%. The low pollen stainability observed in the Hawaiian plants is very likely related to the unequal distributions of chromosomes seen at meiotic anaphase I in this cultivar by Kim and Carr (1990).

Little information is available on seed prodution among the many species in the genus *Portulaca* except in *P. oleracea*, where frequent estimates have ranged from 32 to 80 seeds per capsule (Dunn 1970, Egley 1974, Khoshoo and Singh 1966, Miyanishi and Cavers 1980, Vengris et al. 1972). Hawaiian populations of *P. oleracea* in this study produced an average of 40.7 seeds per capsule, with the range (13–86) included mostly within the range of estimates obtained by other workers. The number of seeds per capsule reported for *P. quadrifida* was 8–16 (Khoshoo and Singh 1966). Degener's (1932) estimate of 60 seeds per capsule for *P. lutea* is somewhat higher than the mean of 30.9 seeds per capsule reported here, but Degener probably worked from a much smaller sample. Among the Hawaiian taxa, seed size was inversely correlated with the number of seeds per capsule.

Completion of the life cycle in 6 weeks to 4 months has been recorded in *Portulaca* (Miyanishi and Cavers 1980, K. P. Singh 1973). In the present study, seedlings produced mature seeds within 8 weeks of emergence except in *P. molokiniensis*. Seedlings of this species 8 months old still appeared to be very immature. Another interesting variation in life cycle is found in *P. sclerocarpa*, in which the thick-walled indehiscent fruits required about four weeks for maturation. It might be worthwhile to investigate the possible relationship between this modification and the unusual volcanic fumarole habitat that seems to be favored by this species.

Seeds of *Portulaca* were classified into three groups, namely completely dormant, partially dormant, and nondormant, by Adachi et al. (1979) on the basis of germination responses in seven taxa. Two of them, *P. pilosa* and the cultivar of *P. grandiflora*, were also used in this study and showed the same results, nondormancy. Adachi et al. (1979) found the most rapid germination response in *P. pilosa*, with more than 50% germination in 3 days and almost 100% in 10 days. Similar results with fresh seeds were experienced in the present study, not only in *P. pilosa* but also in *P. oleracea*, *P. lutea*, and *P.* "ulupalakua." Other species tested in this study also had nondormant seeds, except for *P. molokiniensis*, which exhibited partial seed dormancy that was overcome by scarification.

Although the results from uniform culture indicate that *Portulaca cyanosperma* should be merged with *P. pilosa*, the taxa recognized herein appear to maintain differences sufficient to warrant their treatment as distinct species. These differences include, but are not restricted to, the reproductive aspects covered in the present paper (cf. Kim and Carr 1990, Yun 1989). Particularly noteworthy variations of the reproductive features of Hawaiian taxa include thick-walled indehiscent fruits in *P. sclerocarpa* and floral modifications in *P. molokiniensis* that appear to be related to bi-

otic pollination, a syndrome that has not been previously reported for portulacas other than cultivars.

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