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Reproductive Biology of *Pulsatilla patens* (Ranunculaceae)

ABSTRACT: The pasque flower, *Pulsatilla patens* ssp. *multifida* (Ranunculaceae), is common over a range of elevations in the western two-thirds of Colorado. It blooms early in the spring. The flowers are cross-pollinated by early emerging bees and flies. They can effect self-pollination as well since unpollinated protogynous stigmas will remain receptive through much of anthesis. No evidence of self-incompatibility is present.

Pulsatilla patens (L.) Miller ssp. *multifida* (Pritzl) Zamel (Ranunculaceae), commonly called pasque flower, is found over much of western North America. It is common throughout the western two-thirds of Colorado from 1650-3800 m (Harrington, 1964; Weber, 1972). Our purpose was to investigate reproduction in the pasque flower. It is among the earliest of the spring wild flowers to bloom and set seed throughout its elevational range in Colorado. Reproduction occurs during a period of highly unstable climatic conditions (Marr, 1973), when frequent cold, snowy periods are interspersed with intervals of warm, sunny days.

METHODS AND RESULTS

Our work was carried out in the lower montane region of the Rocky Mountain Front Range (*sensu* Marr, 1961) between 2600 m and 2700 m in 1971, 1972 and 1973. At this elevation, pasque flower blossoms usually appear above the snow in late February or early March before the leaves emerge. After this first appearance, these blossoms, and subsequent ones through April, are repeatedly covered by snow and re-exposed after melt-off. Only two other species commonly flower as early, *Townsendia hookeri* Beaman (Compositae) and *Thlaspi alpestre* L. (Cruciferae).

We have observed honeybees (*Apis mellifera*), two species of andrenid bees (*Andrena* spp.), syrphid flies (*Syrphidae*) and bumblebees (*Bombus* spp.) on the pasque flowers. Insect activity was rare at ambient temperatures below 15.5 °C (60 F) or on windy or rainy days. Insect pollination is therefore sporadic during the period that pasque flowers are in bloom. Honeybees and andrenids were responsible for over 95% of the flower visitations (516 of 541 observed visits) and for all the observed pollinations (431 observations), so they were singled out for further study.

Behavior patterns during visitations were the same in both genera. When the flowers were open, the bees landed on the stigmas, rested for a second or 2,

then crawled in a circular pattern over the stamens. Each flower has numerous stigmas (and carpels) and stamens. The outer stamens are modified as nectaries. In approximately 20% of the timed visits (32 of 145), the insect returned to the stigma before leaving the flower. Exact observations on bee behavior on unopened flowers were difficult to make. The bees forced the sepals apart, crawled down into the flowers, moved about the stamens and departed. Individual bees exhibited fidelity for *Pulsatilla* and tended to go directly from one pasque flower to another even when other kinds of flowers (*Townsendia* and *Thlaspi*) were available in the same area ($n = 222$). This fidelity was reflected in the honeybee pollen loads, which consisted of 92% mature *Pulsatilla* pollen and 8% foreign pollen ($n =$ eight loads, 200 gr/load). Similarly, the andrenid loads were 94% *Pulsatilla* and 6% foreign pollen ($n =$ six loads, 200 gr/load). Honeybees visited an average of nine flowers before returning to the nest ($n = 34$ bees). The number of visits per andrenid trip is unknown.

Cross-pollination was encouraged in two ways: protogyny and insect behavior patterns. Ramaley and Gill (1911) stated that *Pulsatilla* is protogynous, *i.e.*, the female reproductive structures mature first. We also found this to be true. We made hand pollinations ($n = 18$), waited for 6-24 hr, fixed, stained, squashed and microscopically examined the carpels according to Buchholz's (1931) technique. Pollen tube growth occurred in those cases where the stigmatic surface appeared moist at the time of the crosses (11 of 18). Therefore, moistness of the stigmatic surface was used as an indicator of receptivity.

Protogyny encourages outbreeding because the pollen source cannot be supplied by the same flower when only the female system is in reproductive condition. But protogyny does not prevent geitonogamy (pollen from a different flower on the same plant) or, in this case, eventual self-pollination (*see below*). The anthers dehisced (Percival, 1965) for as long as 26 days with an average of 22 ($SD = 3.6$). They continued to shed pollen when the stigmas were no longer receptive. This does not directly encourage cross-pollination in the manner of protogyny, but it does provide pollen for cross-pollination. Cross-pollination also is encouraged by the behavioral patterns of the insect visitors. As mentioned above, the bees landed on the stigmas, crawled around on the stamens and moved on to another flower's stigma in most cases.

Self-pollination also was important. Even though the flowers were protogynous, the stigmas remained receptive for a considerable period (up to 17 days, $\bar{x} = 13$ days, $SD = 4.0$, $n = 43$), which overlapped anthesis (pollen-shedding) in that same flower. If cross-pollination had not occurred before anthesis, self-pollination could occur. The stigmas exceeded the stamens in height when they first became receptive, but as anthesis approached, the filaments of the stamens elongated. Simultaneously, the stigmas spread. Jostling by common spring winds would be sufficient to bring about self-pollination. Certain insect behavior patterns caused self-pollination. If a bee climbed back onto the stigma after crawling over the anthers on a flower, it could effect self-pollination, provided the stigmatic surfaces were receptive. In 346 observations, the insects were observed to return to the stigma after visiting anthers in 107 cases, and moved directly from the anthers onto a new flower in 159 cases. In the other cases (90) the bees either returned to their nests or were lost from sight for some other reason.

No self-incompatibility system was present. Twenty flowers were bagged before gynoecial maturity. At anthesis, 16 flowers were self-pollinated and the bags replaced. The other four flowers were not artificially pollinated. All 20 plants set normal numbers of seeds (*see below*). Emasculated flowers grown in the greenhouse did not set seed, so apogamy was not likely to occur here.

Once pollination had occurred, the stigmas that had spread apart moved back together and in almost all cases turned from white to pink or pinkish-brown in color. The number of ovules per capsule averaged 231 ($n = 46$, $SD = 51$). Seed set had a seasonal average of 166.6 seeds per flower and a range of 130-262 seeds ($n = 84$). Seed germinability in the Colorado pasque flower was 73.5% germination ($n = 600$ for 60 flowers, $SD = 8$). Of the sixty flowers, 20 were self-pollinated and 18 were cross-pollinated. The other pollinations were unknown. There was no significant difference in percent germination between self- and cross-pollinated flowers. Germination was defined as the emergence of the radicle to a length of 2 mm. The only requirements for germination were appropriate moisture and temperatures after a considerable (6 months in our case) after-ripening period (Sayers and Ward, 1966).

This species has reproductively adapted to the Colorado early spring with that area's unpredictable environmental conditions.

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Noncompetitive Effects of Common Milkweed, *Asclepias syriaca* L., on Germination and Growth of Grain Sorghum

ABSTRACT: Common milkweed, *Asclepias syriaca* L., is a wide-ranging perennial plant native to North America which is a major weed problem of N-central and northeastern United States and Canada. Previous studies in Nebraska have shown a significant reduction in grain sorghum yield and the number of sorghum plants per hectare caused by milkweed infestations (Evetts, 1971; Evetts and Burnside, 1973). Since these reductions were attributed to competitive mechanisms, we were interested in learning if the yield losses could be, at least in part, due to phytotoxins produced by *A. syriaca*. Aqueous extracts from fresh field-collected milkweed leaves inhibited growth of grain sorghum seedlings. Duplicate experiments with three dilutions of milkweed extract showed the reduction in sorghum dry weight to be proportional to the concentration of milkweed extract. Paper chromatograms prepared with aqueous leaf extracts of milkweed and developed in appropriate solvents showed several compounds which were characterized as phenolics. To determine