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SOME STUDIES ON INTRODUCING *CASTILLEJA COCCINEA*, INDIAN PAINTBRUSH, INTO PRAIRIE VEGETATION

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ABSTRACT

Indian paintbrush, absent from many prairie remnants in Arkansas, behaves as a biennial in certain central Arkansas prairies, growing as a small rosette one season and flowering the next. It is known to be an indiscriminate root parasite. Field sowings were made in October, March and June. Annual change in population size was monitored for one of these sowings. Laboratory studies of germination were conducted to investigate the effects of light, temperature, water potential, and host species. Haustorial connections to host roots were examined. Based on these studies, a strategy for establishing the species in prairie was developed.

INTRODUCTION

Castilleja coccinea, showy Indian paintbrush, is one of the most striking forbs of midwestern seral prairies (Steyermark, 1975). Near the southern and western limits of its range in Arkansas, this paintbrush occurs in widely scattered prairie patches, yet is totally absent from many prairies. In the Conway area there is one robust population on about 40 hectares of unplowed native hay land, but numerous similar sites have no paintbrush. As part of a prairie restoration project (Culwell and Wright, 1984), a study was designed to explore methods of introducing the paintbrush into prairie sites.

The Castillejas are among the many root parasites found in the Scrophulariaciae and Orobanchaceae. All Castillejas are designated as hemiparasites; that is, they are rooted photosynthetic plants which draw a portion of their water, minerals, and metabolites from autotrophic host plants through haustorial attachments between roots (Atsatt, 1972). *Castilleja chromosa* has been shown to maintain stable carbohydrate and water balances in comparison with its host, *Artemisia tridentata*, in the White Mountains of California (Hansen, 1979).

The hemiparasites are variously believed to have evolved as a compensating response to disease (Atsatt, 1976) or as an outcome of the tendency to form root grafts (Malcolm, 1966). Although hemiparasitic Scrophulariaceae are capable of living for some time without a host, anthesis and seed production generally depend on numerous haustorial connections (Kuijt, 1969; Atsatt and Hansen, 1978). *Castilleja coccinea* has been shown to remain in a stunted condition until haustorial connections are developed (Malcolm, 1966). As is typical for many of the herbaceous hemiparasites in the Scrophulariaceae (Werth and Riopel, 1979) *Castilleja coccinea* forms indiscriminate haustorial connections with a wide range of host species, including some that are not native (Malcolm, 1966; Heckard, 1962).

The showy Indian paintbrush generally behaves as a biennial, forming a rosette one season and flowering the following Spring. The tiny seeds, 18,000 per gram, are shed by early summer and are believed to germinate either then or the following spring. No vernalization is needed, but light is a requirement for germination (Malcolm, 1966).

MATERIALS AND METHODS

Phenological observations of the native Conway population located on the Henze prairie (Culwell, 1980) were made during the 1981 growing season. Phenology of sowings on the UCA prairie (Culwell and Wright, 1983) was observed from April, 1982 to April, 1984. These sowings consisted of broadcasting about 15 g of seed collected at the Henze prairie in a 7 x 20 m plot early in March 1981, and making duplicate sowings of 8 or 6 g of seed in 2 x 10 m plots on October 19, 1982, March 25, 1983, and June 1, 1983. Germination potential of the seed sown in 1982 and 83 was determined in November, 1982. Precipitation and temperature were monitored throughout the study.

Haustorial connections were examined in specimens from the field and from the greenhouse. Greenhouse trials were conducted to compare success of the *Castilleja* with different hosts and different densities of a given host.

Response of seed germination to temperature was determined in a lighted incubator under temperature regimes of 10 to 15 °C, 22 to 25 °C and 25 to 30 °C. Approximately 500 seeds were tested at each temperature. Seeds were maintained on filter paper saturated with distilled water in petri dishes for the duration of the test. Emergency of cotyledons was taken as evidence of germination.

Water relations of germinating seeds were investigated using a graded series of non-nutritive polyethylene glycol solutions. Carbowax 2000 (Union Carbide Corp.) was dissolved in distilled water to create solutions with water potentials ranging from −0.5 bar to −4.0 bar in increment of −0.5 bar. Five ml of solution was introduced into standard petri dishes; approximately 100 seeds of *Castilleja coccinea* were added to each dish, and the dishes sealed with tape. Plates were incubated in a lighted growth chamber at 22 °C for eight days. Emergence of cotyledons was taken as evidence of germination.

RESULTS

Phenology of the Local Native Population.

Widely scattered *Castilleja coccinea* plants in early anthesis were found March 31, 1981 on the Henze prairie. A systemtic search revealed 10 plants in ½ hectare. By April 23, the normal peak of flowering, some hundreds of *Castilleja* were visible over a 20 hectare area, still widely scattered. (By contrast, the previous season there had been many tens of thousands.) The nearest neighboring plants were from 1 cm to 15 cm distance, and included species of *Andropogon, Asclepias, Carex, Senecio, Smilax, Solanum,* and several unidentified grasses and composites. On May 28 the *Castilleja* ranged from late anthesis to mature seed, and some were growing away from any other perennial forbs or grasses. A search was made on September 23, but failed to reveal plants of *Castilleja coccinea* in any stage. (Nevertheless in Spring 1982 the density of flowering plants was much higher than in 1981.) Nineteen-eighty was a year of severe drought, with under 2 cm of precipitation recorded at the University of Central Arkansas in Conway for the July-August

period. In 1981 a total of 15.8 cm was recorded for the same period. In 1982, 9.9 cm of precipitation occurred in July and August; in 1983 the total was 11.3. June had 10 cm or more for each of the years 1980-1983.

Phenology of Sowings Made at UCA Nature Reserve.

In early March 1981, approximately 15 g of seed of *Castilleja coccinea*, collected on 1980 on the Henze prairie, was broadcast on a 7 x 20 m plot of undisturbed prairie at the UA Nature Reserve (later named the Jewel E. Moore Nature Reserve). On April 1, 1982, six paintbrush plants were observed in early anthesis. On May 18, 1982, 17 flowering individuals were counted. The most abundant plant in the plot was *Panicum linearifolium*, a small annual grass, although numerous other prairie species were represented. On May 1, 1983, 97 individuals of paintbrush were counted in the plot. On May 1, 1984, 158 paintbrush plants were located in the plot.

The three sets of duplicate field sowings made in 1982 and 1983 were from seed collected in 1982 and stored dry at 5°. Germination potential of this seed at 24° on moist filter paper in petri dishes in a lighted growth chamber was determined to be 60%. Numbers of *Castilleja coccinea* plants visible on May 1, 1984 were as follows:

October 19, 1982 sowing
plot A, 8 g seed, 5 individuals
plot B, 8 g seed, 31 individuals
March 25, 1983 sowing
plot A, 8 g seed, 4 individuals
plot B, 8 g seed, 14 individuals
June 1, 1983 sowing
plot A, 6 g seed, 0 individuals
plot B, 6 g seed, 0 individuals

The entire prairie was burned in February of 1982, 1983, and 1984. Combustion typically stopped 2 to 3 cm above the soil.

Mean temperatures at UCA for the possible germination periods were as follows: March 1981, 11.8°; April 1981, 18.5°; March 1983, 11.0°; April 1983, 13.1°; May 1983, 22.1°; June 1983, 24.8°.

On April 16, 1985, a qualitative survey indicated increased numbers in all plots, including the June 1983 sowing.

Host Dependence.

The haustorial association proved difficult to work with. Although pot trials clearly demonstrated the dramatic difference in growth between *Castilleja* plants that had and had not made haustorial connections to host broccoli plants, the hemiparasite did not respond when grown in pots of different native host *(Pentstemon alluviorim, Rudbeckia hirta, Helianthus angustifolia, Echinacea purpurea, Gnaphalium obtusifolium),* or different densities of *Rudbeckia hirta.* One certain haustorial connection to the annual *Oenothera linifolia* was found on a field specimen of a current-year seedling on May 28, 1981.

Temperature Response of Germination.

Germination at 10° to 15°C began on day 22. By 24 days it had reached 24%. No further germination had occurred by 27 days when the trial was terminated.

Germination at 22° to 25°C began on day 6. By day 11 it had reached 61%. No further germination occurred by day 14 when the trial was terminated.

Germination at 25° to 30°C began on day 7 and was complete by day 10. Total germination was 5%.

Water Relations of Germinating Seeds.

Control seeds placed on distilled water germinated at 90%. Seeds on Carbowax solutions of −0.5 bar and −1.0 bar water potential showed 50% germination. No germination occurred at −1.5 bars or lower water potential.

DISCUSSION

Since the goal of the study was to learn about introducing *Castilleja coccinea* into native prairie, results will be discussed in reference to cultural practices.

It is clear that establishment must be by field sowing, and that the numbers of seeds will be high. Natural sowing occurs in May and June from mature capsules that dehisce on the plant, allowing the very lightweight seeds to be blown or splashed out. May or June germination is possible, since the seed requires no after-ripening (Malcolm, 1966) and temperatures are favorable. Mean May and June temperatures of 19.7° to 26.8° are close to the 22° to 25° range of the highest laboratory germination. However, May-June germination is closely followed by a summer that is not only too warm for good germination but subject to periods of drought which would prevent it, as indicated by sensitivity of germination to water potential. It also seems likely that summer drought would take a heavy toll of seedlings that had not yet established haustorial connections, a process which may take some weeks (Malcolm, 1966).

Seeds that can survive until fall may germinate then or early the following Spring. Since stored seed has survived 3½ to 4½ years (Heckard, 1962) seed longevity would appear not to be a problem, but extreme sensitivity to drought as shown in the germination tests with polyethylene glycol may limit Fall germination. Thus this study appears to bear out the contention by Malcolm (1966) that early Spring is the time of field germination. The rosette discovered on May 28, 1981 was thus likely a current-season seedling, having made haustorial attachments to hosts in the previous several weeks. Early spring sowing is therefore recommended.

Field sown seed must of course reach soil and not be covered, owing to its small size and requirements of light during germination. It will parasitize plants its own age, such as the annual *Oenothera linifolia,* so presumbably could go onto lightly disturbed prairie, although the experimental sowings relied only on bare ground exposed by haying or burning. In nature as in the experimental sowings, a great many seeds are released. In the Henze and UCA prairies this study did not indicate requisite or preferred host species, but did show that establishment varies over several orders of magnitude from season to season, apparently correlated with drought during the first season of growth. It is easy to see how, without a carryover of ungerminated seed, a population could be eliminated by severe drought, and this may indeed account for the spotty distribution *Castilleja coccinea* in Central Arkansas.

It may require several seasons plus a good bit of luck for viable populations of *Castilleja coccinea* to become established. Increase of the 1981 sowing at the Jewel E. Moore Nature Reserve was several-fold from the 1982 to the 1983 season, and may have come from delayed germination of the original sowing as much as release of seed from the 1982 plants. Since from 150,000 to 300,000 seeds were sown in each plot, establishment was evidently very low. By May 1 of 1984, although sowings of the previous year had produced only a few visible seedlings, the 3-year-old plot continued to show increase in density.

Although the literature suggests that this species of hemiparasite establishes haustorial connections promiscuously, the current study does not bear this out. No connections were conclusively demonstrated in pot trials, and the low survival of field-sown seed may be partly attributable to failure to parasitize. Future field work should concentrate on a search for key host species that may correlate with field distribution in Arkansas.

In summary, introduction of *Castilleja coccinea* in central Arkansas prairie appears to be a chancy proposition. Given enough seed and time, along with good weather and the proper hosts, introduction may succeed, but it is far from certain to produce an established population.

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