



Estimates of cross- and self-fertility of cicer milkvetch (*Astragalus cicer* L.)
by John George Scheetz

A thesis submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of
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Abstract:

The mode of pollination of cicer milkvetch was studied in 1969 and 1970. The floral structure was examined and the common pollinators were identified. Estimates of cross-fertility by open-pollination and self-fertility by artificial selfing by hand and by artificial selfing without hand manipulation were made for 20 cicer milkvetch plants in 1969. Estimates of cross-fertility by open-pollination and self-fertility by artificial selfing by hand were made on 30 plants in 1970. Estimates of cross-fertility by open-pollination and estimates of self-fertility by natural selfing in isolation by bees and artificial selfing by hand were made on four clones of cicer milkvetch in 1970. Seeds obtained from the four clones were seeded in flats in the greenhouse to study the effect of inbreeding on cicer seedlings.

The floral structure was found not to eliminate self-pollination. Three species of bumble bees were found to be the common pollinators of cicer milkvetch. Apparently, honey bees are not common pollinators of cicer. Cicer flowers were more fertile during the first few weeks of the flowering period both years. The average artificial self-fertility of all cicer milkvetch plants was 13.10%. The average natural self-fertility of four cicer milkvetch clones was 58.86%. The average cross-fertility of all cicer milkvetch plants was 62.65%. Selfing had an adverse effect on the growth of cicer seedlings. It was concluded that cicer milkvetch is naturally cross-pollinated with a relatively high degree of self-fertility.

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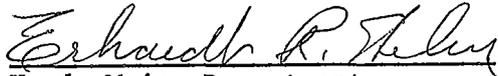
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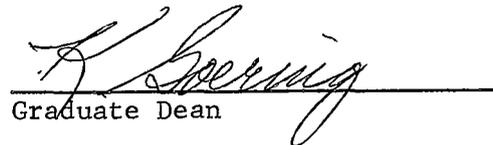
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ABSTRACT

The mode of pollination of cicer milkvetch was studied in 1969 and 1970. The floral structure was examined and the common pollinators were identified. Estimates of cross-fertility by open-pollination and self-fertility by artificial selfing by hand and by artificial selfing without hand manipulation were made for 20 cicer milkvetch plants in 1969. Estimates of cross-fertility by open-pollination and self-fertility by artificial selfing by hand were made on 30 plants in 1970. Estimates of cross-fertility by open-pollination and estimates of self-fertility by natural selfing in isolation by bees and artificial selfing by hand were made on four clones of cicer milkvetch in 1970. Seeds obtained from the four clones were seeded in flats in the greenhouse to study the effect of inbreeding on cicer seedlings.

The floral structure was found not to eliminate self-pollination. Three species of bumble bees were found to be the common pollinators of cicer milkvetch. Apparently, honey bees are not common pollinators of cicer. Cicer flowers were more fertile during the first few weeks of the flowering period both years. The average artificial self-fertility of all cicer milkvetch plants was 13.10%. The average natural self-fertility of four cicer milkvetch clones was 58.86%. The average cross-fertility of all cicer milkvetch plants was 62.65%. Selfing had an adverse effect on the growth of cicer seedlings. It was concluded that cicer milkvetch is naturally cross-pollinated with a relatively high degree of self-fertility.

INTRODUCTION

Cicer milkvetch has been shown to have a high potential as a forage legume. It has the potential of higher hay yields than alfalfa in areas having a short growing season. With no cases of float being reported, cicer milkvetch has a potential of being important as a pasture forage.

The mode of pollination of a species is very important in determining the type of breeding program that is used for improving existing varieties or developing new varieties of that species. There are a number of problems that can occur if a breeding program is developed without the knowledge of the mode of pollination. If the plant breeder believes the crop to be exclusively cross-pollinated and sets up a number of two clone crosses, a high degree of self-fertility can alter his whole study. This is especially true in a crop that has indeterminate flowering as cicer milkvetch does. One clone may have 70% of its flowers open while the other clone may have only 40% of its flowers open at one particular time during the season. If the crop is highly self-fertile, this could result in a high percentage of selfed seeds when the breeder actually believes these seeds to have been developed from cross-pollination. On the other hand, if the breeder knows the crop is predominantly self-pollinated, he does not have to worry about foreign pollen from the neighboring plant. Knowledge of the mode of reproduction of a crop also indicates whether or not pollinators are needed for seed

set.

There were no studies on the mode of pollination of cicer milk-vetch (Astragalus cicer L.) reported in the literature. Thus, this study was set up to determine the mode of pollination of this species. The specific objectives were (1) examination of the flower structure, (2) to determine self-fertility by natural selfing in isolation and artificial selfing by hand, (3) to determine cross-fertility by open-pollination, and (4) to determine the effect of inbreeding on cicer seedlings.

LITERATURE REVIEW

Cicer milkvetch (Astragalus cicer L.) was introduced into the United States by the Plant Introduction Center from Sweden in 1926 (12). It has been evaluated primarily as a ground cover and secondarily as a forage legume at the western Soil Conservation Service Plant Materials Centers. However, recent studies at the Plant Materials Center, Bridger, Montana, have demonstrated the high potential of cicer milkvetch as a forage legume for the northern Rocky Mountain region and adjacent plains area (6, 10, 12, 26).

The flowers of cicer milkvetch are white to pale yellow in color and are borne in racemes (6, 28). Cicer has good palatability and livestock and big game animals consume it readily (23).

The acceptance of cicer has been limited because of poor stand establishment. A very high percentage of hard seed in cicer milkvetch results in poor germination and thus, poor stand establishment. Recent work at the Bridger Plant Materials Center and Montana State University showed that mechanical scarification increases the germination and field emergence (6). These workers have developed a commercial scarification procedure for cicer milkvetch.

Fertility and Inbreeding

The first step in determining whether a plant is self- or cross-pollinated is an examination of the floral structure. The next step is the isolation of single plants to observe whether or not seeds are

produced. The failure of a plant to set seed in isolation is an almost certain indication that the species is cross-pollinated. However, the reverse is not always true because the plant may be cross-pollinated but still be highly self-fruitful. If inbreeding can be carried out without adverse effects, the species is probably self-pollinated (1).

A typical legume flower consists of a standard petal, two wing petals, and two keel petals. The latter are usually partially united and enclose the stamens and stigma. Nine of the ten stamens have their filaments joined to form a ring around the style. The tenth stamen remains free from the others. The five petals are partially united to form a corolla tube (24).

Korean lespedeza, a self-pollinated legume, has two types of flowers on the same plant; chasmogamous and cleistogamous. In the cleistogamous flowers, the pollen germinated before dehiscence. The anthers are close to the stigma, and, therefore, some of the pollen tubes penetrate the anther wall and enter the stigma (24).

In sainfoin, the style protrudes past the anthers. It has been observed that appendages surround the stigma; more work is needed to determine the significance of these appendages. The above structures do not ensure cross-pollination because a bee tends to work all the open flowers on one plant before going to the next plant. This could result in a self-pollinated plant (11).

In red clover, the stigma protrudes slightly above the anthers at

the time of flowering. The keel petals form a receptacle, enclosing the staminal tube with a small opening at the tip. The weight of an insect presses the keel down exposing the anthers and stigma. Pollen is dusted onto the insect while foreign pollen carried by the insect is rubbed onto the stigma (24).

Pollen of birdsfoot trefoil is dispersed by a piston apparatus. The keel petals form a conical cavity above the anthers with a small hole at the apex of the cone. The weight of an insect depresses the keel forcing the stamens up into the cone. The pollen is forced out the opening in ribbons covering the underside of the insect with pollen. Further depression of the keel causes the stigma to protrude where it can be covered with foreign pollen carried by the insect (24).

The pollen of alfalfa is dispersed by an explosive action known as tripping. When an insect lands on the keel, his body weight presses the keel down causing the anthers and stigma to snap upward and free of the keel. The staminal column strikes the insect covering his underside with pollen. At the same time, foreign pollen carried by the insect is rubbed on the stigma (24).

In the only reference found on cicer milkvetch fertility, Townsend (32) observed many open-pollinated heads contained 200-300 seeds each. When the isolated flowers were rolled between the thumb and fingers, most plants set some selfed seed, although the amount was generally low. Several plants were fairly self-compatible because 50-62

selfed seeds per head were obtained.

Pharis (21) found that in alfalfa an average of 31.6% of selfed flowers formed pods whereas 74.8% of the flowers that were crossed formed pods. The pods obtained from selfing contained 1.7 seeds per pod and the pods from crossing contained 3 seeds per pod.

In one study, the range of self-fertility in alfalfa was 0.24-4.84 seeds per flower tripped with a mean of 1.72 (17). In another, the mean range in self-fertility extended from 0.12-1.84 with a mean of 0.75 seeds per flower tripped (35). It was noted by Tysdal (34) that self-fertilization results in much less seed production per flower than cross-fertilization. Piper and co-workers (22) found that when alfalfa flowers were tripped they set selfed pods freely, although cross-fertilization resulted in more pods. They also found that cross-fertilization resulted in more seeds per pod than did self-fertilization. An unanticipated high degree of selfing in several two-clone crosses of alfalfa was reported by Hanson and co-workers (14). Additional research must be conducted to determine the extent of natural crossing in alfalfa. In general, alfalfa flowers must be tripped to produce seed, and that ordinarily there is not sufficient automatic tripping to produce satisfactory seed crops (33). Other researchers (2, 7, 15, 20) have shown that untripped alfalfa flowers will form some pods, but the number of pods formed in this way is quite low in comparison to the number of pods formed when the flowers have been tripped. Armstrong and White (2)

showed that pollen germination occurred in 84% of the tripped alfalfa flowers and in less than 1% of the untripped flowers. In 1936, Brink and Cooper (5) found that the environment had a great influence on whether or not alfalfa flowers have to be tripped to form pods. In the greenhouse, the flowers must be tripped; whereas, if the environment is right, the flowers set pods freely without tripping.

Temperature and other environmental factors have been shown to greatly influence the magnitude of self-fertility in alfalfa (27, 35). Self-sterility in alfalfa was approximately twice as high in the greenhouse as in the field (35). Self-fertility indices in alfalfa are highest during the first weeks of flowering. In latter weeks, there is considerable variation among plants (19). Kehr and LaBerge (16) reported that the degree of self- and cross-pollination in alfalfa may differ, depending upon materials, planting method, and environment.

In alsike clover, self-compatibility in the greenhouse was significantly correlated with self-compatibility in the field (30). Self-seed set in tetraploid alsike clover is reported not to be limited by the metabolites needed for seed production, but seed set is primarily dependent on the genetic mechanisms controlling self-compatibility (31).

Hanna (13) reported that in sainfoin open-pollinated seed set ranged from 3.7-78.3% with a mean of 35.6%. Self-fertilization ranged from 0-21.4% with a mean of 4.8%. He also stated that this measurement of self-fertility by tripping did not agree with what he observed on

plants in isolation. Haaland (11) reported 48% seed set with open-pollination in sainfoin on S_0 plants. When the same plants were crossed by honey bees in two clone combinations, 25% seed set was obtained. When these isolated S_0 clones were selfed with honey bees, 29% seed set was obtained. However, when sainfoin was selfed by hand tripping, only 6% seed set was obtained on the same S_0 plants. He concluded that self- and cross-fertility, as estimated by percent seed set, where flowers were selfed and crossed by honey bees were not significantly different. He also concluded that selfing by bees is more effective than selfing by hand tripping.

In birdsfoot trefoil, artificial pollination data cannot be interpreted in terms of the natural pollination behavior of the plant. A significant difference between self and cross seed set with artificial pollination would suggest that under natural conditions an advantage exists in favor of cross-pollination (4).

In general, there is a lower number of ovules in alfalfa entered by a pollen tube after selfing than after crossing. Cooper and Brink (8) reported that after self-pollination under greenhouse conditions, only 14.6% of the ovules of alfalfa became fertilized; this is in comparison to 66.2% after crossing. Individual plants vary significantly in the proportion of ovules that become fertilized after selfing, and most of these ovules are in the apical half of the ovary. They reported that pollen tube growth was more rapid after crossing than after selfing.

Sayers and Murphy (25) found that pollen tube growth after self-pollination closely paralleled pollen tube growth after cross-pollination. These groups of researchers (8, 25) have also shown that a larger percentage of the fertile ovules either abort or collapse after self-pollination than after cross-pollination.

In alfalfa, percent pods set was significantly correlated with both number of seeds per pod ($r = +0.88$) and number of seeds set per 100 flowers selfed ($r = +0.96$) (9). The same type of association was found in Montana (18). Pods per floret tripped was significantly correlated to seeds per floret tripped ($r = +0.88$) and to seeds per pod ($r = +0.67$). It was concluded that this indicates that all of these estimates of determining self-fertility were equally effective.

In alfalfa, selfing greatly reduces self-fertility and vegetative vigor. Wilsie (36) reported that after one generation of selfing, self-fertility was reduced 80-90% and vegetative vigor was reduced 20-30%. Melton and co-workers (18) concluded that inbreeding does not affect all genotypes of forage crops in the same way or to the same degree.

MATERIALS AND METHODS

Flower Morphology and Pollinators

Mature flowers were collected from cicer milkvetch plants under evaluation at the Montana State University field research center. The flowers were then taken into the lab, dissected, and photographed.

Flowers were collected from a 'Lutana' cicer milkvetch foundation seed field at the Bridger Plant Materials Center. About 50 flowers were taken into the lab, dissected, and all the floral parts measured. An average measurement was then calculated for each floral part.

Pollinating bees were collected from the foundation field of cicer. These bees were identified to species to determine the common pollinators of cicer milkvetch.

Self- and Cross-Fertility of Four Clones

This study was initiated in April 1969. Cuttings were made of four clones of cicer milkvetch that were currently under evaluation at Bozeman. These clones had been designated as 4-14-1-A, 4-14-1-B, 4-14-1-C, and 4-14-6-C and will remain so for this study.

In June of 1969, these clones were taken to the Bridger Plant Materials Center. One plant of each clone was transplanted along Bridger Creek with approximately one mile between plants to insure spacial isolation. Another plant of each clone was transplanted into the 'Lutana' cicer milkvetch breeders block at the Plant Materials

Center. Plants became established during the summer.

Three treatments (1) cross-fertility by open-pollination, (2) artificial selfing by hand, and (3) natural selfing in isolation by bees, were carried out on all clones in the summer of 1970. Estimates of cross-fertility were obtained from open-pollinated plants. Two different estimates of self-fertility were made. One was obtained from artificially tripped flowers and another from the spacially isolated plants. Fertility estimates were made during three periods of the summer. Treatment periods were started on June 29, July 13, and July 20.

The plants in the 'Lutana' breeders block were used to estimate cross-fertility and artificial self-fertility. Both of these treatments were carried out on a single plant of each clone. The decumbent growth habit of cicer milkvetch allowed half of the plant to be covered by a cage with the remaining half to be uncovered. Five racemes, with flowers unopened, were chosen at random, tagged, and left for cross-pollination by native bees on the uncaged half of each plant. Five racemes, with flowers unopened, were chosen at random, tagged, and artificially selfed by hand on the caged half of each plant. Artificial selfing by hand was accomplished by rubbing a toothpick over the anthers and stigma as each flower opened.

The plants along Bridger Creek were used for the natural selfing by bees treatment. Five racemes, with flowers unopened, were chosen at random, tagged, and left for selfing by bees on each clone.

Estimates of fertility were calculated as the number of pods formed per number of available flowers, number of seeds per pods formed, and number of seeds per available flower. All flowers were tripped in the artificial determination of self-fertility. It was assumed that under natural pollination, all treatment flowers of the plants in the breeders block and of the plants spacially isolated were, in fact, tripped.

The data were analyzed using a split plot design. Clones were used as replications, dates as main plots, and modes of pollination as subplots. Duncan's New Multiple Range Test was used for the mean separations between dates and between mode of pollination. Simple correlations between the three different methods of estimating self- and cross-fertility were estimated.

Self- and Cross-Fertility of a Larger Random Sample of Plants

The study was initiated in the summer of 1969. Five plants per date were chosen at random on June 19, July 8, July 21, and July 30 from the 300 plants in the 'Lutana' cicer milkvetch breeders block at the Bridger Plant Materials Center.

Three fertility estimates were made on these 20 plants. These estimates were (1) cross-fertility by open pollination, (2) self-fertility by artificial selfing by hand, and (3) self-fertility by isolation without hand manipulation of the flowers. The estimate of self-fertility by isolation without hand manipulation evaluated the

requirement of tripping.

Three racemes, with flowers unopened, were chosen at random and tagged on each of the plants. The number of flowers on each raceme was reduced to 20. One raceme was left for open-pollination by the native bees. The other two racemes were covered with glycine bags. The flowers on one of the racemes, covered with the bag, were artificially selfed by hand. The flowers on the other raceme, covered with a bag, were not tripped. The artificial selfing by hand was accomplished by rubbing a toothpick over the anthers and stigma of each flower. Bags were left on until all flowers had dried up.

A similar study was carried out during the summer of 1970. Ten plants were chosen at random on each of the dates of June 29, July 13, and July 20 from the 300 plants in the 'Lutana' breeders block.

Two estimates of fertility were made on these 30 randomly chosen plants. These estimates were (1) cross-fertility by open-pollination, and (2) self-fertility by artificial selfing by hand.

Ten racemes, with flowers unopened, were chosen at random and tagged on each of the plants being evaluated. Five of these racemes were left for open-pollination by the native bees. The other five racemes were covered with a cage and artificially selfed by hand. Artificial selfing was accomplished in the same manner as in the previous study.

On July 13, 1970, five additional racemes, with flowers unopened,

were chosen at random, tagged, and caged on five of the ten plants chosen for that date. This was also done on the four clones described in the previous section. These flowers were left for selfing without hand manipulation.

Estimates of fertility for 1970 were calculated as the number of pods formed per number of available flowers, number of seeds per number of pods formed, and number of seeds per number of available flowers. Estimates of fertility for 1969 and for the additional study on July 13, 1970 were calculated as the number of pods formed per number of available flowers. All flowers were tripped in the artificial determination of self-fertility. It was assumed that in the cross-fertility determination that all flowers were, in fact, tripped. Any flowers that formed pods in the selfing without hand manipulation treatment were assumed to be self-tripped.

The 1969 data were analyzed as a completely randomized design. The 1970 data were analyzed in the same manner with the exception that a sampling error could be estimated since five racemes were used for each treatment on each plant. When fertility was estimated by seeds per pod, one plant for each date was eliminated because no pods were formed for these plants in the artificial selfing by hand method of pollination. Simple correlations between the two different methods of estimating self- and cross-fertility in 1970 were estimated.

Effect of Inbreeding of Seedlings

The seed obtained from the natural selfing in isolation and from open-pollination in the study of four clones was used for this inbreeding study.

The seed from the three dates was combined, keeping each method of pollination for each clone separate. The seed was then hand scarified to increase the germination.

Seed was planted in 14" x 20" flats in the greenhouse on September 21, 1970. A split plot design with four replications was used with the four clones as main plots and the type of progeny as subplots. A single flat was used as a main plot. Eighty seeds were seeded in two rows for the subplot in each flat. The plants were watered with nutrient solution each day. On October 9, 1970, the OP and S_1 seedlings were thinned. An attempt was made to reduce each row to a constant number for both the S_1 and OP in each replication. The seedlings were harvested on November 9, 1970 by cutting them off just above the bottom true leaves. At this time, the number of seedlings for each subplot was recorded. The harvesting was done in this manner so that the plants would not be killed and, therefore, be used for further evaluation. Dry weight in milligrams per seedling was used as the measurement criterion. A split plot analysis of variance was used to analyze the data (Appendix Table 21). Duncan's New Multiple Range Test was used for mean separations.

RESULTS

Self- and Cross-Fertility of Four Clones

The inflorescence of cicer milkvetch is an indeterminate raceme (Plate 1). Individual flower number for a raceme ranged from 13 to 62.

The flower of cicer milkvetch is a typical legume flower (Plate 2). The calyx consists of five sepals united near the top where they separate into sharp teeth 3 mm long. The entire calyx is 8 mm long (Plate 3). The corolla consists of 5 petals: one standard or banner petal 25 mm long and 8 mm wide, the apex emarginate (Plate 4); two wing petals 17 mm long and 3 mm wide, each consisting of a claw and blade (Plate 5); two keel petals which are united and enclose the reproductive parts. When united, the keel petals are 20 mm long and 7 mm wide (Plate 6). The stamens are diadelphous (Plates 9 and 1) and there is one pistil (Plates 7 and 8). The stamens and pistil are equal in length and about $\frac{2}{3}$ the length of the standard petal, or 16 mm long (Plate 9). This type of floral structure does not eliminate automatic self-pollination.

Observations on pollinator visitation were made at the Bridger Plant Materials Center. When a bee lands on a flower, the keel petals trip down much in the same manner as alfalfa. When the flower is tripped, there is a snapping noise. After the bee leaves, the keel petals move back up around the stamens and pistils again. The flower will not snap again even though a bee may land on it. It was noted that the bees worked several flowers on one raceme before moving to another

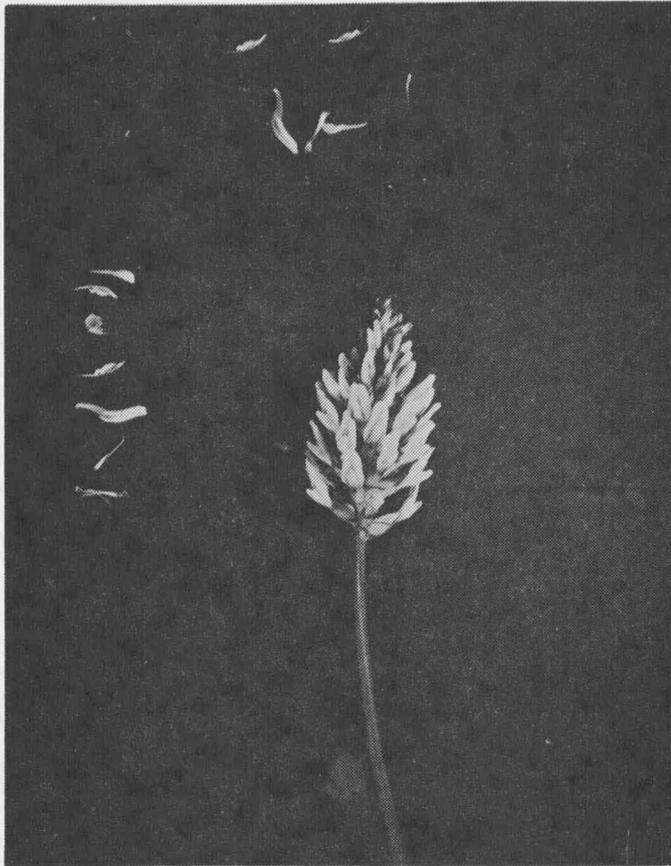


PLATE 1.--The inflorescence of cicer milkvetch

