Oecologia (Berl.) 17, 55—63 (1974)

Seed Production in a Prairie Legume (*Astragalus canadensis* L.)

Interactions between Pollination, Predispersal Seed Predation, and Plant Density

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Received July 8, 1974

Summary. The effects of pollination, predispersal seed predation, and plant density upon seed production of *Astragalus canadensis* L. in a tall-grass prairie were studied by experimental manipulation of plant density. Seed production was greater at high than low plant densities; this was inferred to result from differences in pollination success. Predispersal seed predation was lower at high than low plant densities. The relative seed production of different densities of *A. canadensis* was predicted based upon pollination success and the host detection ability of the predator. Increased seed production and modification of the environment by high densities of *A. canadensis* appears to maintain a clumped distribution of this species, while also producing new clumps at a low rate.

Introduction

The spatial distribution of plant species in complex communities may be influenced by a wide array of environmental variables. In tallgrass prairies many plant species exhibit a clumped distribution. Several individuals comprise a clump, the total size of which is increased by vegetative reproduction of the individuals present. Establishment of new clumps occurs by seed dispersal from parent clumps. Two factors that should be important in determining the number of seeds available for dispersal are seed production and the losses due to predation upon the seeds. If the individuals within the population exhibit a clumped distribution, this should influence both seed production and the loss to seed predation, and ultimately the distribution patterns of future generations of the population.

Astragalus canadensis L. (milk vetch), a legume with a wide distribution in North America (Barneby, 1964) and abundant on tallgrass prairies in Iowa, was used to test aspects of this hypothesis. On the Cayler Prairie Preserve in northwestern Iowa (*cf.* Aikman and Thorne, 1956), *A. canadensis* occurs as isolated plants and small clumps scattered between high density clumps composed of several cloning individuals.

The extent to which the density of *A. canadensis* influences seed production and predispersal seed predation by a Curculionid weevil were investigated by experimental manipulation of plant densities in clumps. Seed production and seed predation prior to dispersal were measured at the different experimental plant densities. Field observations were used to supplement data obtained with experimental techniques. From the data obtained, a qualitative model was developed to predict how interactions between the distribution of individuals within the population, seed production, and predispersal seed predation might maintain clumped distributions of *A. canadensis*.

Methods

Forty 10 × 10 m quadrat sites containing *A. canadensis* were established on Cayler Prairie in June, 1972. Thirty-two quadrats contained low plant densities, each having one plant trimmed to a single basal stem. When necessary, other *A. canadensis* plants were removed from low density quadrats. No more than 8 basal stems were removed from any low density quadrat. The 8 high density quadrats contained 100–250 basal stems of *A. canadensis* from several (10–20) individuals. A 5 m buffer zone around high density quadrats was obtained by removing *A. canadensis* plants in this area.

Mature seeds were harvested in the fall of 1972 by collecting stalks of plants after the first frost and before dehiscence occurred. Seed production was measured by counting the number of pods which matured on a randomly selected 5 cm length from each raceme on the stalk. This length was sufficient to detect differences in seed production. A distinct knob was present on the raceme if a seed pod was present, whereas no knob was present if the flower had aborted. Thus accidental loss of seed pods before or after collection did not affect measurements of seed production. This method of measurement was not sensitive to seed set within pods, and thus the fecundity of *A. canadensis*, but did indicate gross seed production. Within seed pods attacked by predators 98.1 ± 0.3 percent of the seeds were destroyed. Seed pods not containing larval exit holes when collected in the fall had not been attacked by the predator. Thus, seed predation by the Curculionid weevil was accurately estimated by measuring the percent of the pods per raceme containing exit holes of the larvae.

During the summers of 1972 and 1973 observations were made on pollinator and predator activity in the experimental quadrats. Exclosures of mosquito netting were placed over five clumps of *A. canadensis* to determine if insect vectors were necessary for pollination. In two high density and two low density clumps that were caged pollen was transferred from anthers to the stigma of the same flower and between flowers of different individuals within the exclosures. In July, 1973, sweep samples of *A. canadensis* in high ($n = 19$; 100–250 basal stems) and low ($n = 17$; 1–25 basal stems) density clumps were made to estimate relative densities of the Curculionid weevil.

Results

Seed Production

Anthesis in *A. canadensis* occurred during the first week of July in 1972 and 1973, and flowering reached a peak within two weeks. The inflorescences of *A. canadensis* are emergent above the surrounding vegetation, and the flowers are large. Sporadic flowering occurred into late August, but these flowers usually aborted since bees rarely visited them. Only one flower out of more than 200 covered by the exclosures produced seeds. None of the self-pollinated flowers produced seeds. About 20 percent of the flowers which received pollen from a different individual set seed; no significant differences were obtained between seed pod production in low and high density clumps that had been hand pollinated. The number of racemes per basal stalk was not different at high and low densities, although the racemes occasionally were less conspicuous at low densities due to the presence of surrounding vegetation which partially concealed the lower racemes.

Although seed production was low at all experimental plant densities, the difference between seed production at high and low plant densities (Table 1) was significant ($P < 0.01$). Variation in seed production was larger for low than high plant densities since all flowers on some racemes aborted.

Table 1. The effects of the density of *A. canadensis* upon seed production and seed predation. Seed production is expressed as the mean number of pods per 5 cm of raceme ± standard error. Seed predation is expressed as the mean percent of seed pods attacked per raceme ± standard error. For high density $n = 1248$ racemes and for low density $n = 180$ racemes

	High density	Low density
Seed production	31.7 ± 0.2	25.2 ± 0.5
Seed predation	37.6 ± 0.6	61.0 ± 1.5

Table 2. Mean density ± standard errors of Curculionids collected from high and low density clumps of *Astragalus canadensis*

	High density	Low density
Weevils/plant stalk	1.65 ± 0.21	2.66 ± 0.36
Weevils/flowering raceme	0.77 ± 0.15	4.04 ± 1.14

Seed Predation

The larva of a snout weevil (Curculionidae: Tychiinae) feeds upon developing seeds of *A. canadensis* prior to seed dispersal in the fall. The life cycle of the seed predator is incompletely known, and the species involved has not yet been identified. Curculionid weevils were first observed on *A. canadensis* one to two weeks prior to anthesis. Weevils were observed in flight on numerous occasions. Adult weevils did not appear to exploit *A. canadensis* ovules extensively as a food source. Several females were observed with their proboscis penetrating the base of an ovary during copulation. Oviposition occurred in the hole produced and prior to the hardening of the seed coat. Usually one larva was present per seed pod. In late August the larvae bored out of the seed pods. Larvae kept in the laboratory pupated in the soil after boring out of seed pods. This species of Curculionid apparently is host specific to *A. canadensis*; it was not collected from other legumes blooming prior to or concurrently with *A. canadensis.*

More weevils were present per basal plant stalk and per flowering raceme at low than high densities ($P < 0.05$), as indicated in Table 2. The density of weevils was more variable on low than high density clumps. Differences in the relative density of weevils per flowering raceme were greater than those per basal stalk (Table 2). Decreases in the abundance of weevils paralleled decreases in the number of flowers over time. By August only a few Curculionids (0.1–0.2 weevils per stalk were collected in sweep samples.

Seed predation was significantly different ($P < 0.001$) at high and low plant densities; a much larger percentage of the seed pods contained larvae at low than high densities (Table 1). The losses to seed predation were more variable at low than high densities. These data are consistent with observations on the adult weevils, and indicate that seed predation by Curculionids is more intense on low than high density clumps.

Discussion

Plant communities in tall-grass prairies are complex. On Cayler Prairie most species are perennials. These species would be considered K-type species relative to r-type species found in less stable habitats in which density-independent mortality predominates (Gadgil and Solbrig, 1972; Abrahamson and Gadgil, 1973). Consequently, it is not surprising that the annual rates of seed production of prairie species are low compared to species in more disturbed habitats, and also that individuals reproduce vegetatively. Because establishment of new individuals within a clump and of new clumps is dependent upon the production of sufficient propagules to reach spaces available for colonization, seed production and predation can be important variables influencing the distribution of individuals in the population.

Differences in the seed production of *A. canadensis* appeared to result from differences in pollination success. This species is obligately xenogamous. The most frequent visitors to flowers were bumblebees (*Bombus* sp.). Bumblebees tended to visit a number of flowers at one clump, then move to a different clump nearby. More bumblebees were observed on large than small clumps of *A. canadensis*. For example, in a two hour period on one day, ten bumblebees were observed on a large clump of *A. canadensis* and two were observed on a nearby small clump. The bumblebees spent between 5 and 10 min at the large clumps and moved between flowers of the same individual and between individuals. Upon leaving, they moved to other large clumps, often flying over small clumps between the large clumps. The bumblebees visiting the small clump were present about two minutes, then left and moved to the large clump nearby. These observations of the foraging behavior of bumblebees suggested that pollinators visited large clumps preferentially, and that this resulted in increased pollination success at high density. It is not possible to eliminate the alternate hypothesis that low density plants are under greater stress and thus fewer seeds are produced, although the similar seed sets of high and low density clumps that were hand pollinated suggest that this is not the case. Also the similar numbers of racemes/stalk and flowers per raceme present in high and low density clumps suggests that energy allocation for reproduction is similar in both high and low density clumps.

Two factors appear to be important in the pollination success of *A. canadensis*. Low pollination success at both high and low plant densities probably resulted from vegetative reproduction producing clones and thus considerable amounts of incompatible pollen were moved (Levin, 1969; Levin and Kerster, 1969; Levin and Anderson, 1970). This was indicated by the foraging behavior of bumblebees visiting *A. canadensis* clumps. A single bumblebee usually visited a minimum of 10–20 flowers on a individual before moving to the next individual. Second, low seed set may result from low numbers of visits by pollinators to flowers (Cruden, 1972). This was interpreted as the causal factor that resulted in differences in seed production at high and low plant densities.

The pollination success and observations on the foraging behavior of bumblebees indicate that a clumped distribution of *A. canadensis* (several cloning individuals forming a clump) should be selective as a result of the energetics of the pollinator (Heinrich and Raven, 1972). Levin and Kerster (1969) suggest that bee foraging areas are proportional to the distance between plants. The greatest energy return per unit expenditure would occur if pollinators foraged in regions of high plant density. Such preferential visits by pollinators to regions of high plant population density could result in clumped distributions due to intraspecific competition for pollinators (Levin and Anderson, 1970). The relationship between plant density and pollination success is unknown, but can be assumed to be sigmoid in nature and similar to that proposed by Levin and Kerster (1969).

Predispersal predation upon *A. canadensis* by Curculionids resulted in large losses of developing seeds similar to losses to predation noted by Breedlove and Ehrlich (1968, 1972) and Willson and Rathcke (1974). A much larger percentage loss to predispersal predation occurred at low plant densities; this apparently resulted from larger numbers of weevils present per raceme at low plant densities. Thus, the predispersal predation upon *A. canadensis* was different from postdispersal systems described by Janzen (1969, 1970, 1971), Smythe (1970), and Wilson and Janzen (1972). In postdispersal seed predation the distance of seeds from concentrations of seeds around the parent plant is positively correlated with the likelihood of escape from predation, and thus spacing of individuals in a population is enhanced by seed predation. In predispersal predation upon *A. canadensis*, a larger percentage of seeds escaped predation at high plant densities (and also at larger individual seed crops); therefore, clumping of individuals in a population could be enhanced by seed predation.

A number of environmental factors could result in low relative densities of weevils at higher plant densities. The adult weevils do not necessarily oviposit on the plant beneath which they pupated; both sexes may fly for considerable distances before landing on a host. This implies that flowering hosts may be detected during flight, probably with chemical cues. If such cues are important, then the ability of the weevil to detect the presence of a suitable host will influence the distribution of weevils relative to plant density. Thus the distance at which a weevil can detect a host probably is important. Fig. 1A–C represents hypothetical cases of progressive increases in the range of detection of host plants by predators. Circles 1 and 2 represent low density clumps and circle 3 a high density clump of *A. canadensis*. The 3 lines represent randomly chosen flight vectors of weevils. When the host is detected by predator (asterisk), the weevil leaves the flight vector to alight on the plant. Once the predator detects a host, the chances of it encountering a second host are assumed to be zero. The arrows radiating from hosts represent the range over which hosts are detected by the predator. As graphically depicted in Fig. 2, increased ability to detect hosts results in increased predator densities at low plant densities and decreased predator densities at high plant densities. As the detection distance increases (from A to C in Fig. 2), the relative predator density, and thus the relative rate of predation, decreases as plant density increases. Basically, this relationship is a modification of type II predator response, in which the percent predation declines as prey densities increase (Holling, 1965, 1966). The numerical response becomes skewed towards saturation at lower plant densities as the range of detection increases. Thus a larger percentage of the developing seeds are destroyed at low than high plant densities. A relationship similar to that described in the present study has

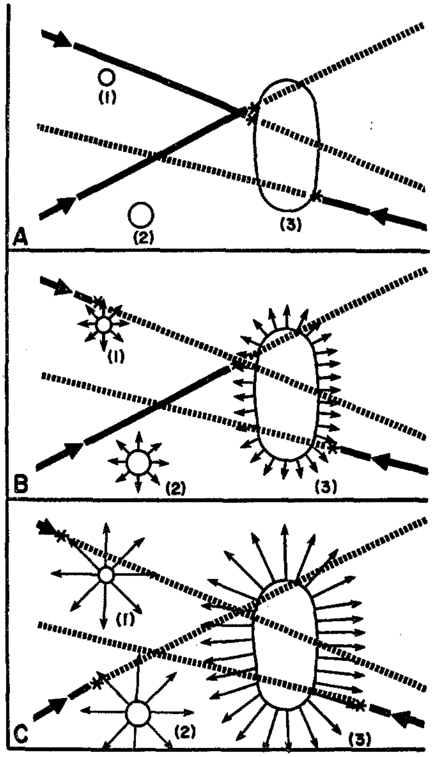

Fig. 1

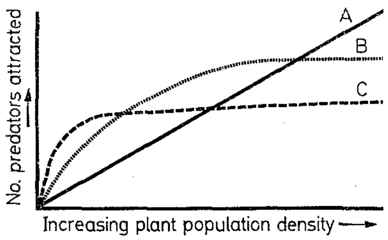

Fig. 2

Fig. 1 A—C. Hypothetical situations of progressive increases in the range of detection of the host plants by a predispersal predator. Circles *1* and *2* are low density, and *3* high density clumps of *A. canadensis*. The three lines are flight vectors of predators. When *A. canadensis* is detected by a predator (asterisk) it leaves the flight vector and alights on the host. The radiating arrows represent different ranges of detection of the predator. (A) represents low host detection capabilities. (B) represents intermediate host detection capabilities. (C) represents high host detection capabilities

Fig. 2. The hypothesized density of predispersal predators on hosts at different densities of *A. canadensis*. Curves *A*, *B*, and *C* correspond to the respective diagrams of host detection in Fig. 1. Curve *A* results from low host detection ability. Curve *B* results from intermediate host detection ability, and Curve *C* results from high host detection ability. The total number of weevils is assumed to be similar in all 3 curves

been described for predispersal squirrel predation upon seeds on ponderosa pines (Larson and Schubert, 1970).

Differences in the rates of predation as functions of host detection ability of the predator can be combined with seed production (pollination success) at different plant densities to predict the numbers of propagules available for dispersal at different plant densities. An interaction between pollination success and low host detection ability of the predator (type A) should result in small and equivalent rates of escape from predation at all plant densities. Low densities of plants might escape if the detection ability of the predator were low, and thus predation might be more intense at high than low plant densities. This type of predation may be typical of postdispersal predation. Predators locating seeds around a parent plant may be able to detect large numbers of seeds near the base of the plant, but those seeds located some distance away from the plant may not be detected. For Curculionid predation upon seeds of *A. canadensis* prior to dispersal, the hypothesized increased host detection ability would result in type B or C predation. A larger percentage of the seeds would escape destruction at high densities, and the more low density plants that are present in a community the greater would be the escape from seed predation at high plant densities. The extent of escape from seed predation at high plant densities would be enhanced by increased seed production due to increased pollination success.

The host detection ability of the weevil results in decreased seed predation at high plant densities only if life history characteristics of the weevil do not result in total destruction of seed crops. If the fecundity of the predator were high the range of detection would not be important, since a few females could oviposit on a large number of seed pods. Also, if seeds were susceptible to predation for an extended period of time predator densities might increase to a point that most of the seed crop would be destroyed (Janzen, 1972). However, the reproductive rates of the Curculionid in the present study were not sufficient to enable a few females to oviposit on all developing seed pods in a clump, and the seasonality of the environment prevents multiple generations in a single year. Other factors, such as mortality rates in larval and pupal stages of life, may be important in lowering the density of emergent adults and preventing destruction of seed crops by high densities of adults. The data indicate, however, that escape mechanisms of the plant population (Beattie *et al.*, 1973; Willson, 1973) other than satiation of the predator are not necessary. The use of host detection ability to generate observed predator distributions at different densities *A. canadensis* is a hypothetical explanation, but is consonant with known life history data of the predator and characteristics of the plant population.

While the pollination success and seed predation both result in greater seed production at high plant densities, this alone is insufficient to explain the clumped distribution of *A. canadensis* populations. Dispersal of seeds and establishment of seedlings also must be considered. *Astragalus canadensis* has no mechanism for long-distance seed dispersal. The seeds are small and have no pappus. They are released from the pods in the late fall and winter after the pod cracks open and when the wind whips the exposed seed stalks back and forth. The distribution of dispersed seeds should be such that most seeds are located relatively close to parent plants.

Establishment of seedlings is often considered the most critical period in the life history of a plant (Harper and White, 1970; Willson, 1972). The effects of large clumps of *A. canadensis* upon vegetation beneath and at the edge of the clump may enhance recruitment to the population. Fewer species of plants occur beneath clumps or at the edges than in areas not containing *A. canadensis* (Platt, unpublished data). Over 90 percent of all *A. canadensis* seedlings are located near or at the edge of established clumps. Increased seed production at high plant densities may be advantageous since few openings for colonization are available elsewhere, except possible after fire. Competitive interactions between species and the presence of considerable litter (Koelling and Kucera, 1965; Kucera *et al.*, 1967) would reduce the chances of seedling establishment and survival in areas away from parent clumps. Reduced competitive interactions and litter that is not as densely packed (the woody stalks of previous years growth of *A. canadensis* form a loose matrix of litter through which seedlings could grow) would enhance establishment of seedlings at the edge of parent clumps. The likelihood of seeds being dispersed only short distances, and appropriate environmental conditions for seedling establishment near parent clumps should result in most young plants being located near large adult clumps. This is consistent with field observations, and is probably enhanced by increased seed production at high plant densities, although similar results could be obtained if the seed crops of high density clumps were preyed upon more heavily then the seed crops of low density clumps. In this latter case the presence of a suitable site for colonization might override the predation factor and clumps would increase in size until losses to predation were so high that not enough seeds survived to produce any more adults. In this case high density clumps also would not be likely to produce new clumps located some distance from the parent clump. However, when losses to predation are low at high densities, then large clumps should produce new clumps (at a very low rate) as well as increasing the size of the parent clump. This pattern fits that observed in the field, and is enhanced by increased seed production (due to increased pollination success) and reduced seed predation at high plant densities.

Acknowledgements. We wish to thank Robert Cruden, Richard Bovbjerg, Michael Weis, and Margaret Platt for advice and suggestions on the study and manuscript. The Iowa State Preserves Board and Iowa Conservation Commission cooperated with this study on the Cayler Prairie Preserve.

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