# Fire and the life history of shooting star, *Dodecatheon meadia*, in Iowa tallgrass prairie

by

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# INTRODUCTION

Most often, tallgrass prairies have been examined on the community level by plant ecologists and range managers (e.g., Weaver 1954; Curtis 1959). This has been especially true with research on fire response and management; production and yield have been the foci of most prairie fire research.

By comparison, only a small amount of work has been done on the autecology of prairie plants. Most of this work has concentrated on the prairie grasses, the dominant species. Less research has been done on the autecology of prairie forbs and their response to fire. There has been an increase in interest in prairie preservation and restoration in the past 20 years. Thus, it is important to have life history and fire response data on all prairie species to ensure their proper management.

Shooting star, Dodecatheon meadia L., a perennial, spring-flowering forb, was chosen as a subject for this study. It is commonly found in tallgrass prairies, especially in the eastern two-thirds of the prairie peninsula. Relatively little is known about its life history; even less about its response to spring fire, a common prairie management technique. This is also true for many other prairie forbs, especially spring-flowering species. Consequently, shooting star may potentially serve as a model for spring-flowering prairie forbs.

This study was designed to answer the following questions:

1. What are the basic life history characteristics of shooting star?

2. How does fire affect the biomass, phenology, and sexual and asexual reproduction of shooting star?

# TAXONOMY, PHYTOGEOGRAPHY AND ECOLOGY

## Taxonomy of Dodecatheon

Shooting star was first collected about 1675 by an English botanist, Reverend John Bannister, who found it in the colony of Virginia and sent seeds to London (Meehan 1894, Wherry 1943). In 1743, Mark Catesby, another English botanist, named Bannister's plant. He called it *Meadia meadia*, in honor of his sponsor, Dr. Richard Mead, the physician to England's royal family and a patron of science (Meehan 1894, Thompson 1953). Linnaeus (1753) renamed the genus *Dodecatheon*, but retained the species name *meadia*. *Dodecatheon* (dodeca, twelve, and theos, god) was a name used by Pliny for a species of primrose. Linnaeus apparently changed the generic name because Dr. Mead was not a great botanist (Meehan 1894, Thompson 1953).

The American botanist, Asa Gray, described the genus *Dodecatheon* as a single species, *meadia*, with six varieties (Gray 1878). A more extensive collection and closer examination of *Dodecatheon* in the western United States made this classification obsolete. Gray (1886) developed a new classification, recognizing five species in the genus. The German botanists Pax and Knuth (1905) divided *Dodecatheon* into 30 species with 17 subspecies. Fassett (1944), working with the *Dodecatheon* found east of the Mississippi River, recognized two species, *D. meadia* and *D. amethystinum* (*D. radicatum*), and five varieties of *D. meadia*. Thompson (1953) conducted a comprehensive study of the genus *Dodecatheon*. He divided it into three sections and 14 species. Thompson placed *D. meadia* into the section *Dodecatheon* and recognized three subspecies -- *meadia*, *brachycarpum*, and *membranaceum*. Gleason and Cronquist (1963) reduced the subspecies to varieties and called *D. meadia* var. *membranceum* by an older name, *D. meadia* var. *frenchii*. Olah and DeFilipps (1968) determined that this variety was actually a distinct species, *D. frenchii*.

*D. meadia* and *D. amethystinum* are very similar morphologically. The most reliable way to distinguish them is by their mature capsules (Fassett 1944; Schwegman 1984). *D. meadia* has thick capsule walls (160-250 micrometers, mean 196), while *D. amethystinum* capsules have thin (90-120 micrometers, mean 100), flexible walls. *D. meadia* flowers are white, lavender, or pink, while *D. amethystinum* usually has purple, rarely white, flowers (Fassett 1944; Schwegman 1984). *D. amethystinum* starts blooming about two to three weeks before *D. meadia*, though there is some overlap in flowering time (Fassett 1944, Hartley 1966, Iltis and Shaughnessy 1960, Schwegman 1984). Macior (1968) reported that *D. amethystinum* in Dubuque, Iowa bloomed May 10-30, 1966 and May 1-25, 1967.

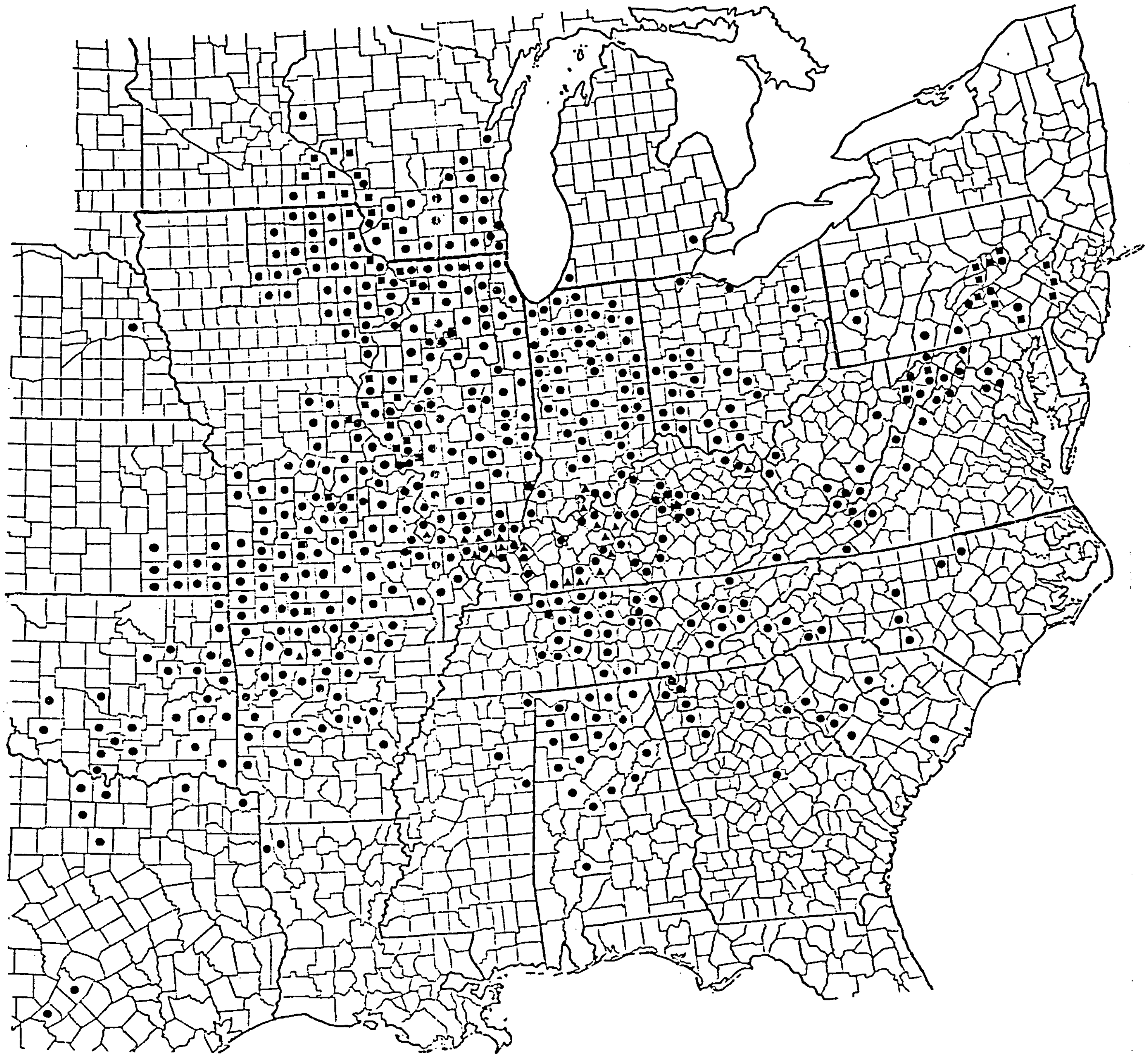
## Phytogeography of *Dodecatheon*

The majority of the species in the genus *Dodecatheon* are found in the western United States and Alaska; one species reaches northern Mexico (Munz 1974) and another is found in northeastern Soviet Asia (Shishkin and Bobrov 1952). Three species are found east of the Mississippi River. French's shooting star, *D. frenchii* (Vasey) Rydb. (=*D. meadia* L. var. *membranaceum* A. Gray) has a restricted distribution in the central United States and is one of the rarest of all shooting stars (see Fig. 1). Jeweled shooting star, *D. amethystinum* Fassett (=*D. radicatum* Greene), has been reported from counties near or bordering the upper Mississippi River valley, West Virginia, and Pennsylvania (see Fig. 1). The identification of West Virginia specimens as *D. amethystinum*, rather then *D. meadia*, has been questioned by some taxonomists (Strausbaugh and Core 1964).

*D. meadia* has one of the widest distributions of any shooting star, being found in the midwest, east, and south (see Fig. 1). It is considered endangered in Michigan (Kim Chapman, Michigan Natural Features Inventory, Lansing, personal communication 1983), Minnesota (Welby Smith, Minnesota Natural Heritage Program, St. Paul, personal communication 1984), and Mississippi (Ken Gordon, Mississippi Natural Heritage Program, Jackson, personal communication 1985), but it is locally abundant in the central United States.

Iowa has two species of shooting star. *D. amethystinum* is restricted to four counties in northeast Iowa (see Fig. 1), primarily from sites near the Mississippi River. *D. amethystinum* has been reported from moist sandstone or limestone cliffs and talus slopes in Iowa (Hartley 1966). Schwegman (1984) reported that in Illinois *D. amethystinum* is almost always associated with a bedrock outcrop. *D. meadia* is found primarily in the eastern half of Iowa (Fig. 1). It was reported from Kalsow Prairie State

Fig. 1. Distribution map for *Dodecatheon meadia* (●), *D. amethystinum* (■) and *D. frenchii* (▲).



Preserve (Moyer 1953). However, no herbarium record could be located from Kalsow Prairie and Brotherson (1969) did not report it from this site. In Iowa D. meadia is primarily found in tallgrass prairie communities or in open forest sites (Lammers 1983; this thesis). While the two species are very similar morphologically (see Taxonomy), their habitats are distinct, and they have never been reported growing together in Iowa.

## Habitat

D. meadia has been reported from a diversity of habitats: fens (Frederick 1974, Friesner and Potzger 1946, Osorio 1982, Swink and Wilhelm 1979); dry calcareous prairie (Dix 1959, Lovell et al. 1983, Mason and Iltis 1965); sandy prairie (Fay 1951, Fay and Thorne 1953); hill prairie (Evers 1955, Fell and Fell 1956, McFall 1984, Schwegman 1984); dry gravelly to low, alkaline prairie (Musselman et al. 1971); sand prairie (Curtis and Greene 1949); dry, dry-mesic, mesic, wet-mesic, and wet prairie (Curtis 1959, Michigan Natural Features Inventory 1982, Swink and Wilhelm, 1979); oak savannah (Bray 1960); oak woods (Musselman et al. 1971, Mohlenbrock and Voight 1965, Swink and Wilhelm 1979); white pine woods (herbarium specimen, ISC 331125); cedar glades (Aldrich and Bacone 1984, Baskin, Quarterman, and Caudle 1968, Curtis 1959, Nelson and Ladd 1983, Turner and Quarterman 1968); and wooded or open, moist to dry bluffs, sandstone or limestone ledges and cliffs (Ebinger 1982, Fassett 1944, Mohlenbrock and Voight 1959, Olah and DeFilipps 1968, Ozment 1967, Winterringer and Vestal 1956).

Although D. meadia may be found in dry prairie, most of the habitats are mesic to wet-mesic. Curtis (1959) noted that it is most common in mesic, wet-mesic, and wet prairie, reaching its greatest abundance on wet-mesic prairie. Partch (1962) compared the water holding capacity of soil to the frequency of shooting star at Faville Grove Prairie in Wisconsin; it was most common in mesic and wet-mesic prairie. Zimmerman (1972) noted that seedlings are very sensitive to drying out their first two years. Adequate moisture is obviously an important factor influencing the distribution of shooting star.

Some of the habitats listed, such as cedar glades and hill prairies, are generally dry or dry-mesic. In these cases, shooting star may grow in a microsite that is not representative of that habitat's general moisture regime. Turner and Quarterman (1968) found shooting star in a portion of a cedar glade where runoff and seepage kept conditions atypically moist. Fell and Fell (1956) found it on gravel hill prairies, dry or dry-mesic communities, but in some cases it grew in areas more moist than the surrounding prairie.

A habitat may not be dry or dry-mesic all year. Erickson et al. (1942) noted that in dolomitic glades of east-central Missouri, where *D. meadia* has been found (Nelson and Ladd 1983), continual seepage often occurs during late fall-spring.

Nevertheless, it appears that shooting star does inhabit some truly dry or dry-mesic sites. Fassett (1944) found it on steep open hillsides with *Petalostemon* and *Bouteloua*, typical dry prairie genera. He also reported that *Anenome patens*, a dry prairie species, covered gravel hills in early spring that were overgrown with shooting star by the end of May. Curtis (1959) reported finding it on dry calcareous prairies. Evers (1955) and Schwegman (1984) found shooting star on hill prairie. Nelson and Ladd (1983) listed it as a characteristic species of dolomite cedar glades. Shooting star's habit of going dormant by mid-summer may allow it to survive in such dry habitats.

Bliss and Cox (1964) reported that *D. meadia* grew in a tallgrass prairie which had a pH of 5.0. Clark (1977) found shooting star in an Arkansas tallgrass prairie with a soil pH of 5.1. Birdseye and Birdseye (1951) noted that shooting star can grow in a garden setting at pH 4.5-6.0. However, relatively high soil pH appears to be common for most shooting star habitats. Turner and Quarterman (1968) reported a pH 7.6 for a *D. meadia* woodland site. Dix (1959) describes shooting star growing on dry calcareous prairie which had pH's in excess of 7.5. However, most reports fall in between these values, primarily in the 6s or low 7s (Curtis 1959, Freeman 1964, Frick 1939, Iltis and Shaughnessy 1960). Shooting star apparently favors a soil pH that is circumneutral, perhaps coupled with mesic or wetter conditions.

## Fire

The published literature on the response of *Dodecatheon* spp. to fire is very limited. Rock (1981) noted that D. meadia reacts negatively to spring fire. Pauly (1984) reported that D. meadia bloomed profusely on a calcareous prairie after fire, even after a late fire that burned the basal leaves. Shooting star did not bloom without a spring fire, which removed matted grasses and allowed light to reach the basal rosettes. Reichert and Reeder (1972) found that on a dry calcareous prairie D. meadia had a higher cover and relative frequency on a burned area then on an unburned area after an April fire. Antos et al. (1983) found that a late June fire in foothills grassland of Montana produced no change in the cover of D. conjugens, but their sample size was small. DeBenedetti and Parsons (1984) found that a summer fire in a California subalpine meadow severely inhibited a Dodecatheon species. It did not reappear until the third year after the fire, with cover increasing the fourth year.

## Life History

Shooting star seeds are generally spherical to oblong in shape, sometimes flattened on five or six sides. They are olive green to brown in color and 0.5 to 1.5 mm long.

The seeds require stratification for significant germination, although a few seeds may germinate without this treatment. Greene and Curtis (1950) obtained 35 to 44% germination after eight weeks of stratification at 4.5° C, depending on the year the seed was produced. Threlfall (1972) observed 70% germination after two weeks of stratification at 5-10° C, 85% after three weeks. She noted that one year old seeds germinated as successfully as seed of the year. Turner and Quarterman (1968) obtained 80% germination after 12 weeks of stratification at 1° C. In general, the longer the stratification period, the greater the germination percentage and rate of germination (Christiansen 1967, Threlfall 1972, Turner and Quarterman 1968). Increased stratification also decreased the light and temperature requirements for germination (Christiansen 1967). Woodland seed grown under a temperature regime of 10-27° C after stratification produced higher germination then at a regime of 5-30° C. Germination of glade seed was more influenced by the length of stratification than temperature after stratification (Turner and Quarterman 1968).

As the seed germinates, petiolate cotyledons and a taproot emerge. After the seedling taproot reaches a certain size, a fleshy lateral caudex develops and the taproot degenerates. At about the same time, a bud forms near the node of the cotyledon stalk and the caudex (Sorenson 1984). By early summer the cotyledons wither, the plant having produced no new leaves. Thompson (1953) reports that other species of Dodecatheon produce true leaves during their first growing season.

The plant spends the rest of the growing season just below the soil surface (Sorenson 1984) or on top of it (Zimmerman 1972). This leaves the plant vulnerable to drying out in late summer and susceptible to frost heaving during the first winter (Zimmerman 1972).

In the early spring of its second growing season, the juvenile bud produces 1-4 leaves, each 1-2 cm long (Sorenson 1984, Zimmerman 1972). It goes dormant again by early summer. This ephemeral habit is characteristic of shooting star throughout its life. Consequently, growth is slow and the plant takes several years to mature. The third and subsequent years bring about a further increase in the size of the leaves and caudex. Rock (1981) reports that shooting star can flower in its third year, but most estimates range from the four to nine years (Prairie Nursery 1984, Smith and Smith 1980, Zimmerman 1972).

A mature caudex in spring is composed of two parts, an upper and a lower part. The upper portion is formed during the previous growing season and bears leaves, and possibly an inflorescence. By the end of the present growing season, the upper caudex has enlarged, becoming the lower caudex, and will have roots in the following growing season. This lower caudex has a new upper caudex. Foerste (1884) states that the lower caudex provides food for the growing plant. In the following year, a constriction develops between the more recent lower and upper caudex and the old lower caudex, after which the latter dies. Consequently, the plant never has parts that are much over two years old. Barring predation or disease, the plant could potentially live for decades.

Flowering plants produce a scape topped by an umbel of 1-125 flowers (Thompson 1953); Iowa plants average about 12 flowers per scape (this study). Anthesis begins in March in the southern United States, April or

May further north. Flowers start out as erect buds. The pedicel gradually elongates and bends over. The petals curve back, revealing the stigma and tube of connate filaments with connivent anthers. Macior (1964, 1968) observed that shooting star is pollinated by bumblebees, Bombus sp., and by bees of the genera Augochloropsis and Lasioglossum. Insect pollination is required for seed production (Macior 1964, Turner and Quarterman, 1968), although this does not necessarily mean the species is self-incompatible.

After anthesis, the pedicel gradually elongates and becomes erect again. The green capsule matures and turns brown, opening at the tip by valves. The ovary has free central placentation, bearing about 200 anatropous ovules (Ingram 1963, Thompson 1953). In Tennessee, shooting star from a woods averaged 39 seeds/capsule and 394 seeds/plant, while those from a glade averaged 89 seeds/capsule and 1065 seeds/plant. Many seeds are aborted (Turner and Quarterman 1968).

Shooting star also reproduces vegetatively. Mature and juvenile plants produce small buds on the roots at the point where the root attaches to the caudex. This bud, if separated from the parent plant or if the parent plant dies, can give rise to a new shooting star (personal observation). At least two years must elapse before vegetative buds will produce flowers (Glover 1985, Sperka 1973). Vegetative buds are found underground and have no means for significant dispersal. Consequently, plants produced from vegetative buds are found near parent plants. Fassett (1944) reports that D. meadia forms clones.

Dix (1959) reported that shooting star is very susceptible to cattle grazing on Wisconsin's calcareous prairies. Drew (1947) reported that it was more common on grazed than ungrazed prairie in Missouri, but his sample size for shooting star was small. In addition, the grazed prairie he studied had also been mowed for hay, which likely confounded analysis of shooting star's response to grazing.

D. meadia serves as a host for Phyllosticta dodecathei Trel., a leaf spot fungus (United States Department of Agriculture 1960). No fungi are known to attack shooting star in Iowa (Dr. Lois Tiffany, Department of Botany, Iowa State University, personal communication 1983).

## STUDY AREAS

Three study sites were chosen, based on the criteria that the areas have burn management and/or large populations of D. meadia. These sites were Rochester Cemetery Prairie, Clay Prairie State Preserve and Hayden Prairie State Preserve.

### Rochester Prairie

Rochester Cemetery Prairie is located in south central Cedar County, T79N R3W Sec 12 SE 1/4. The cemetery is divided by a gravel road into an approximately 1.0 hectare eastern and a 4.0 hectare western section. Only the western portion was used in this study. The cemetery was established in the 1840s, at a time when the region had just been opened to European settlement. The site was grazed in the past (Dr. William Furnish, Atalissa, Iowa, personal communication, 1983). In each of the last 21 years, and possibly longer, the cemetery has been mown in early summer and early fall (Cedar County Historical Society 1974). The cemetery is owned by the township of Rochester.

The Rochester Cemetery flora is primarily composed of dry-mesic to mesic prairie vegetation. Some deciduous forest herbs, such as mayapple, Podophyllum peltatum, and wild geranium, Geranium maculatum, also occur here, especially in the shade of trees. The site is dominated by about 10 large white oaks, Quercus alba, and so might be called a sand savannah. The Cedar County Historical Society (1974) developed a plant species list for the cemetery. Macior (1968) included a picture that illustrates the density of shooting star that can be found here.

Rochester Cemetery prairie is part of the glacial Lake Calvin Basin. Prior (1976) describes this basin as an alluvial plain that developed during the Wisconsin glaciation. It is characterized by clearly defined valley walls, broad floodplains and terraces, and sand dunes. The cemetery is located just east of the Cedar River, whose floodplain was the source of the aeolian sands that comprise the soils of the cemetery. The topography of the cemetery is gently rolling, with an overall relief of about 10 m.

### Clay Prairie

Clay Prairie State Preserve is located in southeastern Butler County, T91N R16W Sec 18 NE 1/4. The prairie is slightly more than 1 ha in area and has about 3 m of topographic relief. It was originally a part of the cemetery for the now defunct town of Butler Center. Local residents say the prairie was mowed yearly in the fall for hay and burned in the spring, probably until the prairie was purchased as a preserve in 1967.

The vegetation is composed of mesic to wet-mesic prairie species, with some Eurasian weeds, especially in the disturbed southern end. Lantz (1969) provides a fairly complete species list for the prairie.

### Hayden Prairie

Hayden Prairie State Preserve and National Natural Landmark is located in northwestern Howard County, T100N R13W Sec 33. The prairie was cut for hay for 78 years and occasionally pastured prior to its purchase in 1945 as the Iowa's first prairie park (Roosa 1976). Hayden Prairie is about 94 ha in size, composed of a 78 ha and a 16 ha tract, separated by a gravel road. It is the largest tallgrass prairie preserve in the state.

Hayden Prairie has a gently rolling topography; maximum elevation differences are about 16 m. The site is rich in mesic to wet tallgrass prairie species, with sedges, _Carex_ spp., and cordgrass, _Spartina pectinata_, dominating in some drainageways and lowlands. Some of the upland areas have Cresco loam soils which have seasonally perched water tables (Buckner and Highland 1974). This produces an unusual situation where wet prairie species such as cordgrass and bluejoint, _Calamogrostis canadensis_, are found with mesic prairie species.

Hayden Prairie has a spectacular display of shooting star in the latter half of May, the single largest population in Iowa and probably one of the largest in the United States (see picture in Roosa 1976). Dr. Paul Christiansen (Biology Department, Cornell College, Mt. Vernon, Iowa) has developed an unpublished plant species list for the prairie.

Clay Prairie and Hayden Prairie are found on gently rolling drift plains of the Iowa Erosion Surface (Prior 1976). The erosion surface was formed during the Wisconsin glaciation and cut into Kansan or Nebraskan glacial till. It is covered by a layer of late Wisconsin loess or loam sediment deposited during late glacial or postglacial times. Consequently, the soils have two layers, the upper layer formed in loess or loam sediment, the lower layer formed in the underlying eroded till, with a stone line separating the two at a depth of 30 to 75 cm (Oschwald et al. 1965; Ruhe 1969).

# METHODS

The distribution of *Dodecatheon amethystinum*, *D. frenchii* and *D. meadia* in the United States was mapped by county. State and regional floras, as well as journal articles, were consulted. Label information or occurrence records were requested and received from 40 herbaria and Natural Heritage Inventory programs within the known range of these species. Specimens were examined at the Iowa State University herbarium and field work in Iowa produced one new county record. This information is displayed on the map, Fig. 1.

## Plots

Field work began in 1981 with the establishment of systematically placed permanent 0.25 $m^2$ (0.5 x 0.5 m) plots. Flowering adults were marked by placing two nails (nails were used because they would survive fire) next to them. Plants that had flowered in 1980, but not in 1981, were marked with three nails (1980 flowering plants were identified by an old scape near the base of the 1981 rosette). Plants that had flowered in both 1980 and 1981 were marked with four nails. Vegetative adults (plants with four or more leaves at least 8 cm long, but no scape) were marked with one nail and seedlings were marked with a slanted nail.

### Clay Prairie

Permanent plots (0.25 $m^2$) were set up at Clay Prairie in April and May 1981. Three transects were spaced six paces apart; plots within transects were five paces apart. A total of eleven plots were established on both north and south halves of the prairie, restricted to a single soil type. The south half was burned in 1981 and 1983; the north part was burned in 1982.

### Hayden Prairie

In May 1981, ten permanent plots (0.25 $m^2$) were set up on a north site and nine more plots on an adjacent south site, spanning several soil types. Three or four plots were placed on three areas within each site. Plots were spaced 5 paces apart. In 1981 and 1983, the north site was burned; in 1982 the south site was burned.

In August and September 1981, more permanent plots on the north and south sites were set up, restricted to Cresco loam soil. Transects were spaced six paces apart; plots within transects were four paces apart. The north site had 24 plots; the south site 12 plots. D. meadia had senesced by this time and many scapes had fallen over, making it difficult to distinguish vegetative adults from flowering adults. Consequently, only flowering adults with at least a portion of their scapes present were marked; no other plants were marked.

Transects

Rochester Prairie

In June 1982, transects were run on one soil type. Four transects were spaced four paces apart and plots within transects were placed two paces apart. Data were collected from a total of 50 plots. A 1 $m^2$ quadrat was used for recording the number of flowers and capsules per plant.

In June 1983, transects were run at Rochester in one soil type. Thirteen transects were spaced four paces apart. Plots within transects were also spaced four paces apart. Data were collected from a total of 128 plots. At each plot, a 0.25 $m^2$ quadrat was used for recording the number of flowers and capsules per flowering adult and the number of vegetative adults.

Hayden Prairie

In June 1982, transects were set up at Hayden on the north and south sites. Four transects were spaced six paces apart, as were plots within transects. At each of 32 plots, a 0.25 $m^2$ quadrat was used to record the number of flowering adults, vegetative adults, large juveniles (leaves at least 3 cm long) and small juveniles (leaves less than 3 cm long). A 0.5 $m^2$ quadrat (with the 0.25 $m^2$ quadrat nested within it) was used to record the number of flowers and capsules per D. meadia and the number of inflorescences destroyed by the larvae of the stalk borer, Papaipema nebris Guenee.

In July 1983, 20 transects were set up at the south Hayden site. Transects were three paces apart and plots within transects were four paces apart. Data were collected from a total of 260 plots. At each plot, two adjacent 0.25 $m^2$ quadrats were used to record flower and capsule number per plant; stalk borer damage and the number of vegetative adults were also noted.

Clay Prairie

In June 1982, five transects were set up on north and south halves of Clay Prairie. Transects were separated by 10 paces and plots within transects were separated by three paces. At every plot, a 0.25 $m^2$ quadrat was used to record flower and capsule number per *D. meadia* as well as to record the attacks of the stalk borer larvae. Data were collected from 130 of these plots on each half of the prairie. At every fourth plot, a 0.5 $m^2$ quadrat was used to record the number of flowering adults, vegetative adults, large and small juveniles. Data were collected from 31 south plots and 29 north plots.

In July 1983, nine transects were set up on both north and south halves of Clay Prairie. Transects were spaced eight paces apart and plots within transects were three paces apart. At each plot, two adjacent 0.25 $m^2$ quadrats were used to record flower and capsule number per *D. meadia* and to record the number of vegetative adults. Data were collected from 270 plots on the north site and 177 plots on the south site.

In July 1983, 10 additional transects were set up on both north and south halves of Clay Prairie. Plants were collected on 5 transects separated by 20 paces and collecting sites within the transects were separated by 8 paces. On Clay south, 35 flowering and 34 vegetative adults were collected; on Clay north, 35 flowering and 37 vegetative adults were collected. At each collecting site, the flowering and vegetative adults nearest to the right shoe of the investigator were cut off at ground level. Each plant was then placed in a plastic bag, labelled and sealed for transport to the laboratory.

A similar procedure was followed at Clay in June 1983, but collecting was restricted to the western half of that prairie. On Clay south, 40 each flowering and vegetative adults were collected; on Clay north, 40 flowering and 43 vegetative adults were collected.

In June 1982 and 1983, above ground biomass of flowering and vegetative adults was determined at the north and south sites of Hayden Prairie by the same procedure. On each site, collections were made from four transects separated by eight paces; six paces separated each collection site. On Hayden south, 40 flowering and vegetative adults were collected in 1982 and 1983. On Hayden north, 37 flowering and 36 vegetative adults were collected in 1982, and 40 of each in 1983.

For each plant harvested, the number of leaves per plant and the length of scape (if present) were recorded. The plants were then dried in paper bags at 70°C for two days. Total dry leaf weight, scape weight and total weight (leaf plus scape) were then measured on an electronic balance to the nearest 0.01 g.

Fire damage

In May 1983, transects were run at Clay to check on the damage to young inflorescences caused by fire. Transects and plots within transects were separated by four paces. Data were collected from 254 stations. At each station, a 0.1 $m^2$ quadrat was laid down, fire damage to *D. meadia* plants recorded, and the quadrat flipped ahead for a second recording. Inflorescences were recorded as healthy (no apparent damage), unusually small (no apparent damage but the inflorescence was small relative to the size of the healthy inflorescences), slightly damaged (burn damage evident, but flower buds appeared intact), moderately damaged (several flower buds destroyed) or destroyed.

Flower number

Flower numbers were obtained from permanent plots, transects, and plants collected for biomass studies.

Root bud number

Both above- and below-ground portions of adult plants were collected to determine the amount of vegetative reproduction. Three transects were spaced eight paces apart; collecting stations within transects were ten paces apart. Three or four plants were collected per transect. At each station, the vegetative and flowering adults nearest the right foot of the investigator were collected. Ten flowering adults and ten vegetative adults were collected from north both and south sites on Cresco loam at Hayden in July 1981 and July 1982. In 1983, only 12 flowering adults were collected. Plants, with their balls of soil, were stored in a cold room for one to two months, until they were processed. In some cases more than one adult plant was found in a ball of soil, increasing the number of plants used in the counts. For each caudex, counts were made of the number of roots that had a vegetative bud. Since this portion of the study was designed to determine how many roots produced buds, and because double buds were rare, roots with two buds were scored the same as those with only one.

Seed counts

Infructescences were collected for seed counts when the capsules were still green, starting to turn brown at the top. Previous experience had shown that infructescences picked earlier than this stage did not have fully developed viable seeds, which made it difficult to distinguish viable and aborted seeds.

In June 1982, 80 infructescences were collected at Rochester for seed counts. Five transects were spaced six paces apart; stations within transects were three paces apart. At each station, the nearest infructescence to the investigator's right foot was collected. A total of 80 infructescences was collected. These were randomized in the lab and 40 infructescences that had not been attacked by insects or fungi were chosen. Infructescensces were allowed to air dry in small beakers. Seeds were separated into viable and aborted seeds by capsule for all capsules in an infructescence. Aborted seeds were smaller and shrunken compared to viable seeds.

In July 1983, 60 infructescences were collected from both north and south sites of Clay. Ten transects were spaced five paces apart; stations within transects were four paces apart. At each station, the nearest infructescence to the investigator's right foot was collected. Sixty infructesences were collected from each site. These were randomized again in the laboratory and 30 from each site were used for seed counts. The two longest capsules (they were usually also the two largest) were used for seed counts. Correlations from the Rochester results showed that the averages for the two longest capsules on an infructescence can provide a good estimate of the average values per capsule for an entire infructescence. These correlations, for average number of viable seeds, average number of aborted seeds, and the average total number of seeds were r=.83, r=.94, and r=.96 respectively (n=40, all $p < 0.0001$).

## Statistics

At both Hayden and Clay prairies a single pair of burned and nonburned areas was used in the study. This design was necessary because of the predetermined fire management plan at both sites. Strictly speaking, this means that there is insufficient replication for standard statistical analyses. Individual plants can not be used as experimental units as acres of prairie, and not individual plants, were burned. Therefore, the results are interpreted in terms of mean trends, and so standard errors are presented to provide an idea of the amount of variation seen in a particular parameter. Nevertheless, the variation in plant response is interesting.

## Nomenclature

Species names used in this thesis conform to those of Gleason and Cronquist (1963), except for names of grasses (Pohl 1966) and *D. amethystinum* (Iltis and Shaughnessy 1960).

# RESULTS AND DISCUSSION

## Population Structure

The population categories of D. meadia in Table 1 are based on size, as precise aging of most species of herbaceous perennials is impossible without long term observation. Small juvenile represents plants in their second growing season and probably some plants in their third growing season. Large juvenile includes some plants in their third growing season, plus plants that have existed up to five growing seasons or more (see Life History). The vegetative and flowering adult categories encompass numerous age classes, with plants in both categories usually being at least five growing seasons old.

The numerical size of categories relative to each other varies from site to site and prairie to prairie (see Table 1). Small juvenile was the largest category at three out of four sites, while the second largest category included large juvenile, vegetative and flowering adult categories. This variation is probably primarily due to differences in soil moisture, length of a growing season and weather conditions during it, and seed production between years.

The most striking difference between Clay and Hayden prairies is in the number of small juveniles (Table 1). The higher numbers at Hayden may be due to the fact that Hayden's soils are more moist than those of Clay. Shooting star seedlings and small juveniles are very vulnerable to drying out (Zimmerman, 1972), because they have shallow root systems. The soil surface at Clay South may have been unusually dry in 1981 because of a fire; this may have contributed to a higher mortality. The low values for Clay South and also for the large juvenile category indicates that establishment was low for several years.

Hayden also had more flowering adults than Clay. This is, in part, due to the fact that Hayden has a higher percentage of flowering plants among its adults than Clay (Table 2). Hayden's greater soil moisture again may be responsible for this higher rate of flowering.

It is clear from field observations that Hayden had more seedlings

Table 1. Population structure of *D. meadia* at Clay and Hayden prairies in 1982. (B) indicates burned plots; values for *N* are plants/0.5m$^2$

| | Hayden North | | Hayden South(B) | | Clay North(B) | | Clay South | |
|---|---|---|---|---|---|---|---|---|
| | N | % | N | % | N | % | N | % |
| Number of quadrats | 32 | | 32 | | 29 | | 31 | |
| Flowering adults | 5.2 | 12.2 | 3.5 | 5.7 | 0.4 | 2.3 | 1.9 | 16.1 |
| Vegetative adults | 8.0 | 18.8 | 7.2 | 11.7 | 5.6 | 31.6 | 7.9 | 67.0 |
| Large juveniles | 5.2 | 12.2 | 4.9 | 8.0 | 5.7 | 32.2 | 1.5 | 12.7 |
| Small juveniles | 24.2 | 56.8 | 45.8 | 74.6 | 6.0 | 33.9 | 0.5 | 4.2 |

Table 2. Percentage of adult plants flowering

| | 1982 | | | | 1983 | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Clay | | Hayden | | Clay | | Hayden | | Rochester |
| | unburned | burned | unburned | burned | unburned | burned | unburned | burned | unburned |
| Number of adult plants flowering | 60 | 12 | 165 | 112 | 525 | 106 | 1096 | 1077 | 277 |
| Total number of adult plants | 304 | 173 | 420 | 342 | 2555 | 1305 | 1722 | 2353 | 877 |
| % of adult plants flowering | 19.7 | 6.9 | 39.3 | 32.7 | 20.6 | 8.1 | 63.7 | 45.8 | 31.6 |

per square meter than Clay. This is probably due in part to Hayden's greater density of flowering adult plants, and thus, greater potential for seed production.

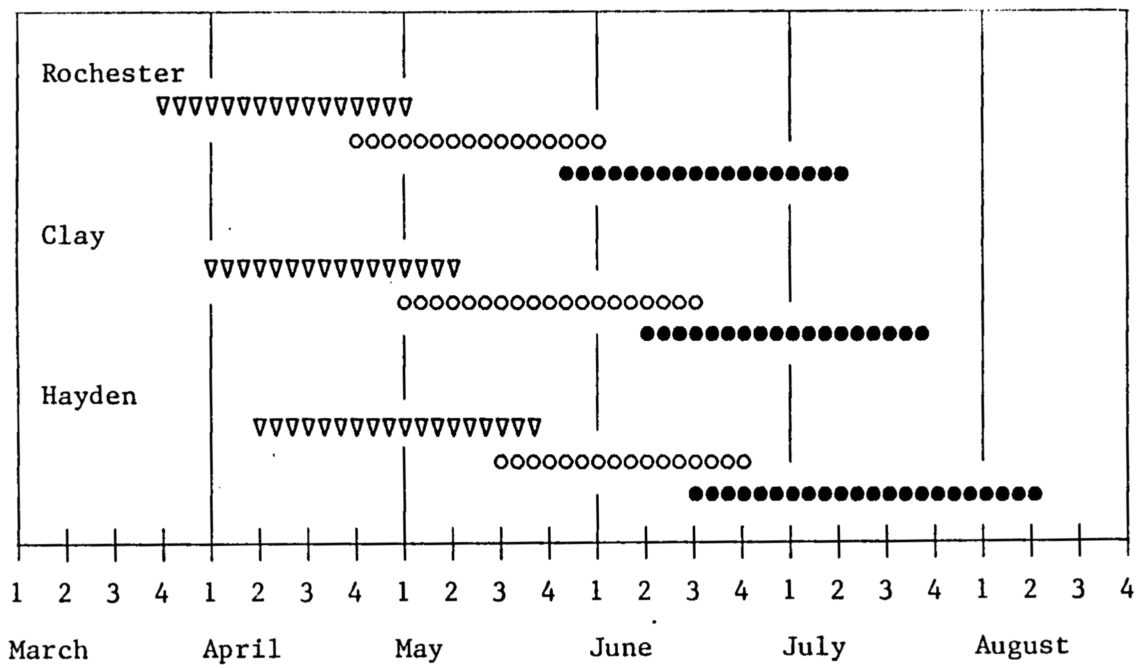
Of 57 seedlings marked at Hayden in 1981, 70.8% were found in the spring of 1982. This rate is rather high compared to other herbaceous species, where survival is often less than 20% (Harper, 1977). Such high survival may not be representative, as this is one year's data from one site. However, Auffenorde and Wistendahl (1983) reported that 98% of the seedlings of compass plant, Silphium laciniatum, survived into their second year at an Ohio prairie. This indicates that high survival rates may not be entirely abnormal for prairie species under some circumstances. It seems likely from these data that recruitment of prairie forbs may be markedly pulsed, rather than being a relatively low and more-or-less constant rate.

## Phenology

The time of appearance, flowering, fruiting, and senescence of shooting star varied from prairie to prairie (Figure 2). In any one year, Rochester was approximately one week ahead of Clay in phenological development and Clay was about one week ahead of Hayden. These differences probably are due to the length and beginning of the growing seasons. Rochester, the southernmost of the three sites, has the longest growing season, 160-170 days, Clay has a growing season of 150-160 days, and Hayden, the furthest north, has a growing season of only 140-150 days (United States Department of Agriculture, 1941).

Variation of shooting star phenology also occurred from year to year within a prairie. Flowering began in late April 1981 at Rochester, while in 1982 it began in early May. On May 10, 1981, shooting star had already been flowering for several days at Clay Prarie. However, on May 15, 1983, only a few plants had begun to flower there. These differences probably are due to year-to-year variation in the beginning of the growing season and by the average daily temperature during bolting and flowering.

The timing of fire (Table 3) greatly influenced the phenology of shooting star. In 1981, burning at Hayden occurred at a time when plants




∇ = shoot appearance and leaf/scape expansion
o = flowering
● = fruit formation and senescence

Fig. 2. Phenology of shooting star at Clay, Hayden, and Rochester Prairies

Table 3. Burn dates for Clay and Hayden Prairies. "Timing" is timing of burn relative to D. meadia phenology

| Year | Clay | Hayden | Timing | Condition of D. meadia |
|---|---|---|---|---|
| 1981 | April 10 | March 20 | very early | still underground or just coming up. |
| 1982 | April 26 | April 28[a] | early | leaves nearly fully expanded; most scapes still protected by leaves. |
| 1983 | May 2 | April 27 | late | scapes taller than leaves. |

[a]In 1982 development of D. meadia at Hayden was approximately a week behind the stages seen in 1981 and 1983.

were below ground. At Clay, the 1981 burn occurred when shoots were beginning to appear above ground, but the leaves were still furled. At each of the prairies, flowering began approximately a week earlier on the burned areas than on the unburned areas. The removal of litter and resulting higher soil temperatures earlier in the growing season are the most likely reasons for the advanced phenology. Ehrenreich's (1957) study at Hayden found that soil temperatures 12.5 cm below the surface were as much as 2.8° C higher in April on burned sites compared to unburned sites. This difference increased to as much as 5.6° C in May. Air temperatures 2.5 cm above the ground were as much as 5.6° C higher on burned areas compared to unburned areas. The relationship between litter removal and earlier plant growth in prairie has been well-documented experimentally by Hulbert (1969), Old (1969) and Peet et al. (1975).

Late fires at Hayden and Clay in 1983 delayed flowering on burned areas by approximately a week compared to unburned areas. This is the opposite of the result of an early burn. The important difference lies in the stage of phenological development of the plants. The 1983 fires occurred at a time when the leaves were unfurled and expanded, and the inflorescence was taller than the leaves so that more of it was exposed to the flames than in the very early fires of 1981. The heat apparently "shocks" the scape, delaying development. Since flowering was delayed, fruiting and senescence were also delayed.

## Herbivory

At Clay and Hayden prairies, the larvae of the stalk borer moth, *Papaipema nebris*, family Tortricidae, attacked shooting star scapes. Larvae were not observed at Rochester, but evidence of their presence was found. This is the first report of stalk borer feeding on shooting star. They attack many medium-sized species of herbaceous plants in spring, but move on to larger plants like corn (*Zea mays*) and giant ragweed (*Artemisia trifida*) in the summer when the larvae are larger.

The larva chewed its way into the base of the scape. It ate its way up the scape until it reached the vicinity of the umbel and then ate its way out. As the larva worked its way up the scape, the inflorescence began to wilt and fell over at or near the base of the umbel. The inflorescence eventually dried and fell off, frequently taking a portion of the scape with it. As low as 1.2% and as much as 21.0% of the scapes were attacked (Table 4).

Fire dramatically reduced the incidence of stalk borer attacks. Overwintering eggs on dead plant matter or newly hatched larvae were destroyed when the prairie was burned. Larvae only move a short distance when looking for new hosts (Decker 1931, Bailey 1985), and so burned sites generally had much lower attack rates.

Rochester's low incidence of attack probably indicates that the stalk borer was not common there. This may have been due to the fact that few suitable plant hosts were present nearby for the later stages of the larva's life history.

Larvae in the moth family Tortricidae were found attacking green Dodecatheon capsules at Clay in July 1982. They had used their silk to join the inner portions of several capsules and had eaten their way into one or more of them, destroying some ovules.

Larvae in the moth family Geometridae were also discovered attacking D. meadia at Clay in 1982 and 1983. They ate their way into the bottom of the capsule and destroyed some ovules. Of 58 capsules from Clay North 1983 (unburned) that were used for seed counts, 13.8% had been attacked by the geometrid larva. Clay South 1983 had been burned, and none of 60 capsules had been attacked by the geometrid larva. Although a small sample, this indicates that fire reduces geometrid attacks, again probably by destroying overwintering pupae, eggs or young larvae.

Of 323 capsules from Rochester 1982, 3.1% had been attacked by unknown insect larvae. Three of these had holes at the base of the capsule, indicating that the same geometrid larva that attacked capsules at Clay may also have been present at Rochester.

A combination of tortricid and geometrid larval herbivory can result in a significant reduction in D. meadia seed production. However, this level of insect herbivory is moderate compared to that found for the genus

Table 4. Stalk borer attack rates on *Dodecatheon meadia* at three different Iowa locations

| Site and Year | Number of Scapes | % Attacked |
|---|---|---|
| Clay South 1982 | 455 | 17.4 |
| Clay North 1982 (burned) | 137 | 2.9 |
| Hayden North 1982 | 331 | 18.7 |
| Hayden South 1982 (burned) | 236 | 1.7 |
| Clay North 1983 | 525 | 21.0 |
| Clay South 1983 (burned) | 106 | 0.9 |
| Hayden South 1983 | 657 | 11.9 |
| Hayden North 1983 (burned) | 555 | 8.7 |
| Rochester 1983 | 227 | 1.2 |

Baptisia on Missouri tallgrass prairie (Haddock and Chaplin, 1982). They report that seed predation by coleopteran and lepidopteran larvae over a two year period produced losses of 96% and 92% in Baptisia leucantha, while Baptisia leucophaea had losses of 89% and 65%. Hermann-Parker (1978) reports that a curculionid weevil larva reduced seed production in Psoralea esculenta by 10% and 55% at two Iowa tallgrass prairies.

## Plant Size

The response of average above ground dry weight of adult flowering plants to fire (Fig. 3) varied with the timing of the fire.

Average weight increased with an early burn (1982), but a late burn (1983) resulted in a lower average weight compared to unburned sites. The leaves were more expanded at the time of the late fire and so more damage resulted, damage apparently not compensated for by enhanced environmental conditions for photosynthesis.

The yield response of spring prairie forbs to an early fire is variable. Richards and Landers (1973) found that following a mid-April fire in north central Iowa, Fragaria virginiana and Viola petadifida had no change in yield, while Phlox pilosa and Zizia aurea had an increase in yield.

Average scape weight (Fig. 4), average weight per leaf (Fig. 5), and average total leaf weight (Fig. 6) for flowering adult plants followed the same pattern as average total aboveground plant weight, increasing after an early burn (1982), but decreasing following a late burn (1983), compared with unburned sites.

The average number of leaves per flowering adult plant decreased with burning (Fig. 7), although the difference, especially at Hayden in 1982, was very small. Burning at any time after the shoots are up seems likely to result in the loss of some leaves.

The response to fire of other spring prairie forbs with respect to leaf number is mixed. Lovell et al. (1983) conducted early (late March or early April) and late (mid May) burns on Wisconsin prairie. They reported that Zizia aptera and Viola pedatifida had an increase in leaf number

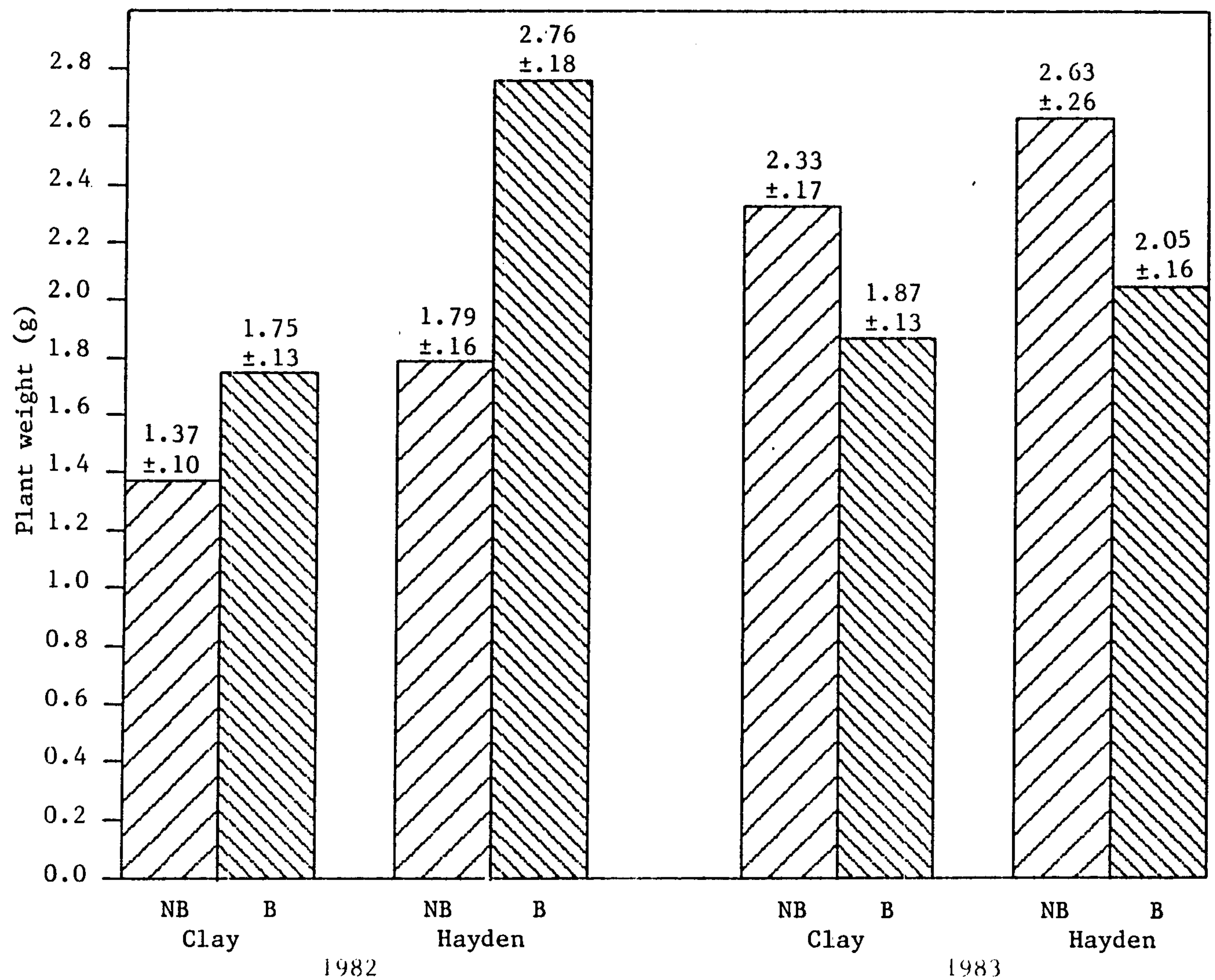



Fig. 3. Mean weight of flowering adult plants

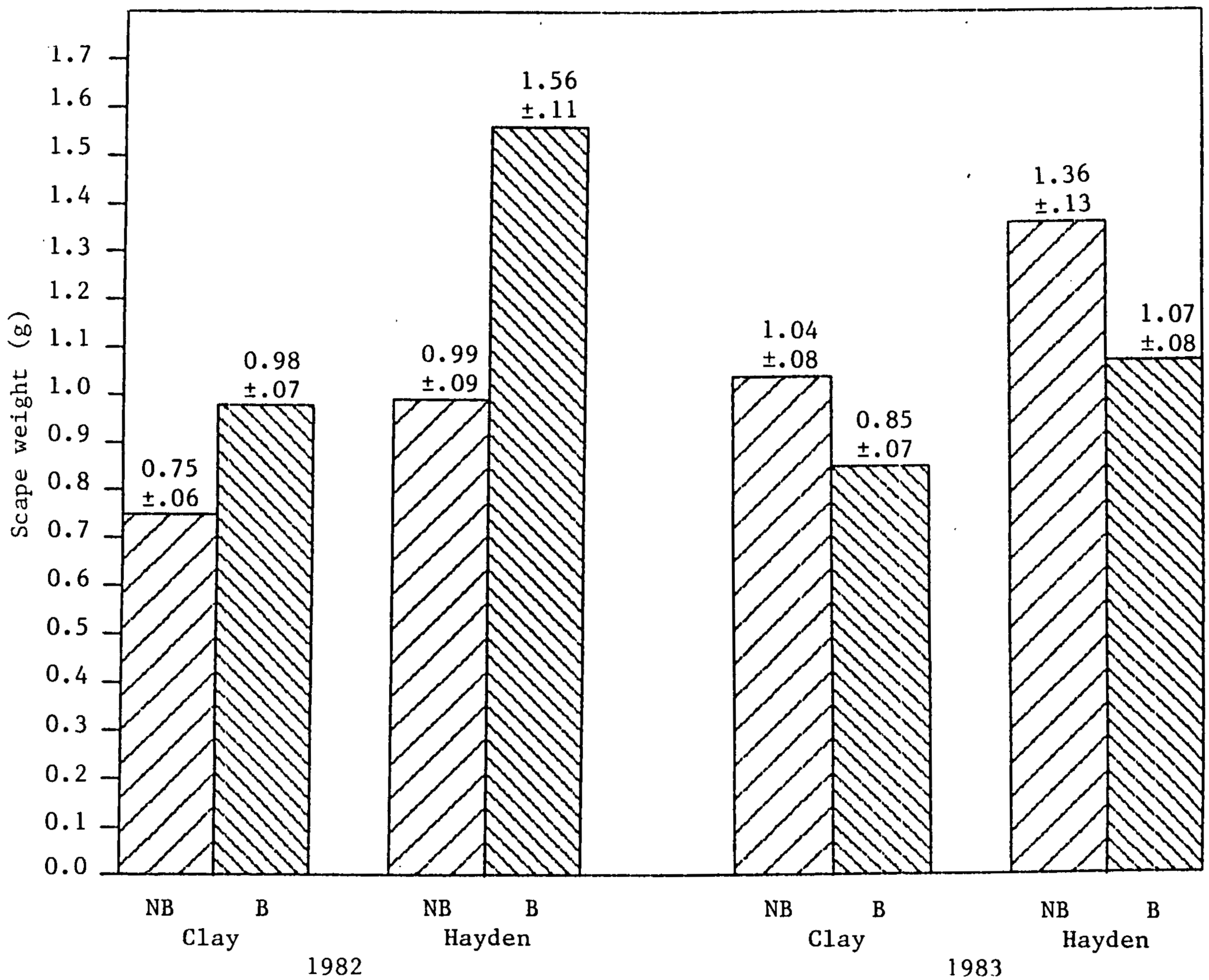



Fig. 4. Mean scape weight

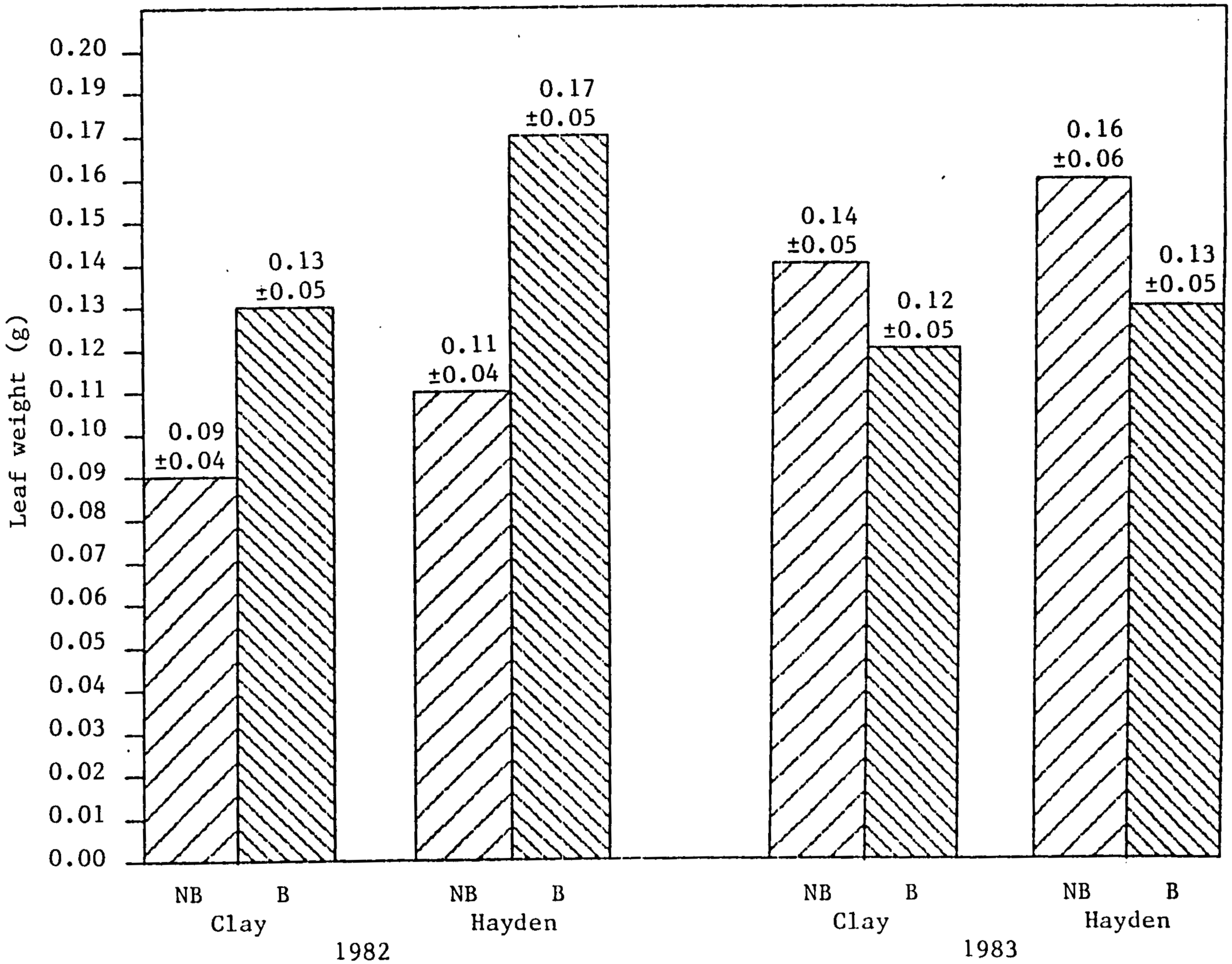



Fig. 5. Mean weight per leaf of flowering adult plants

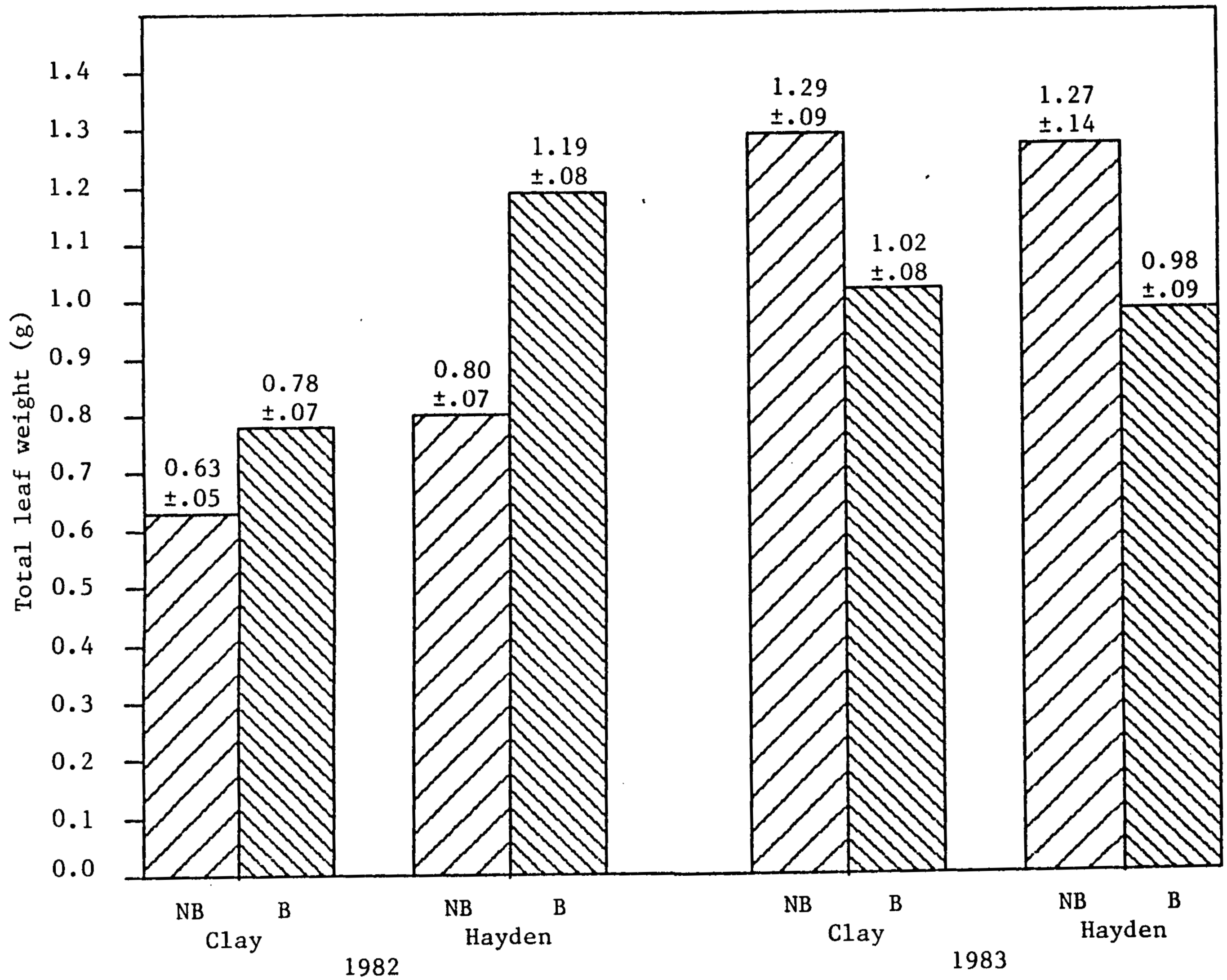



Fig. 6. Total leaf weight per flowering adult plant

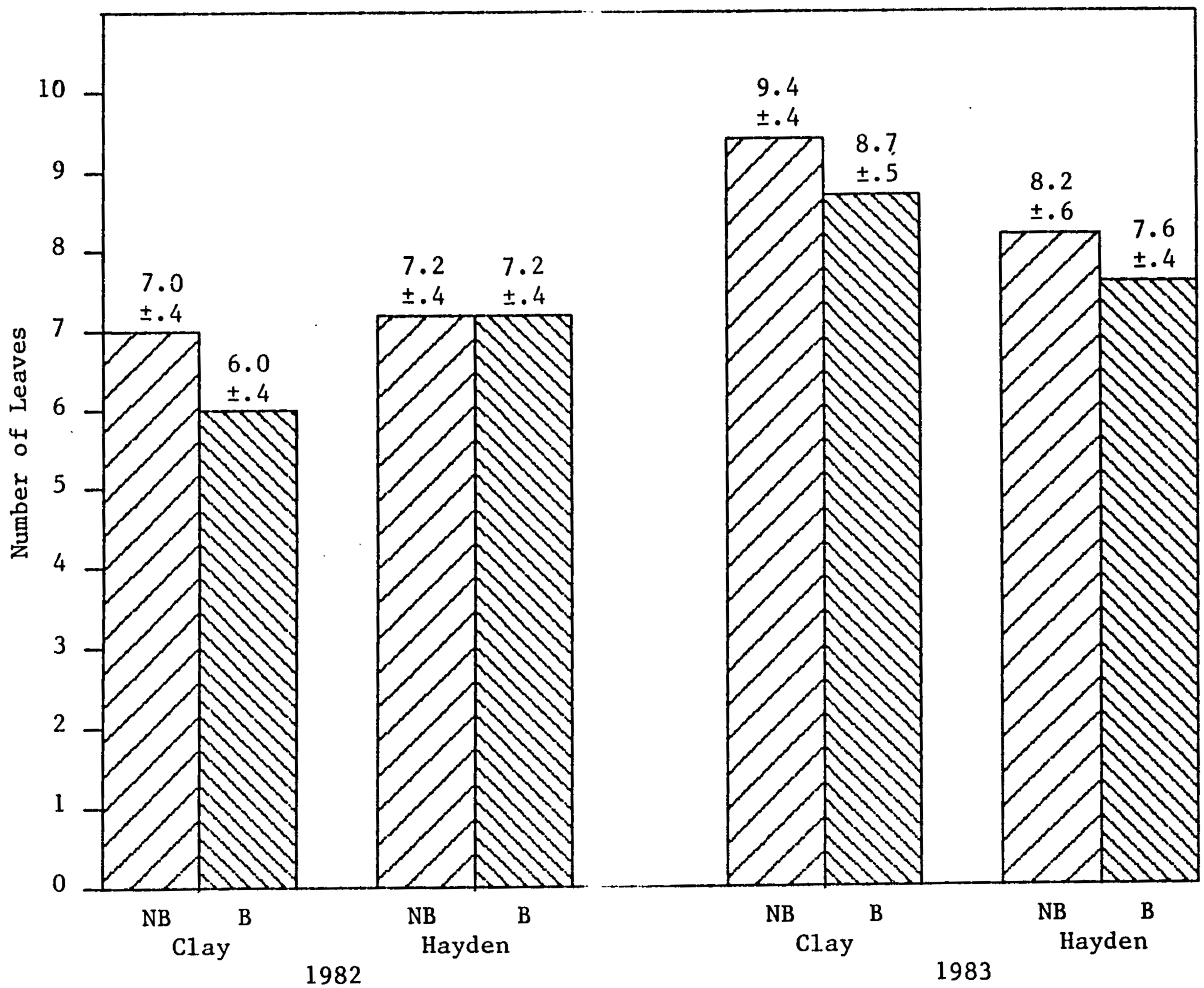



Fig. 7. Mean number of leaves per flowering adult plant.

following an early burn and a decrease with a later burn, like D. meadia in the present study. Sisyrinchium campestre and Valeriana ciliata showed no change in leaf number with either fire treatment. Lovell et al. (1983) did not distinguish between vegetative and flowering adult plants.

In three out of four burns, scape height decreased with fire (Fig. 8). Hayden South 1982 (burned) had a slight increase in scape height, while at Clay 1983 scape height was only slightly lower on the burn site than on the unburned site. A decrease in scape height may be a result of direct damage to the scape or a change in the allocation patterns of photosynthate by the plant. Lovell et al. (1983) noted that a late spring burn shortens flower stems on Gentiana puberula.

The average weight of vegetative adult plants tended to increase with an early burn (Fig. 9). With a late fire Clay had a smaller increase with burning, while the unburned Hayden site had a slightly higher value.

The average weight per leaf of a vegetative plant decreased with a late burn at both Clay and Hayden (Fig. 10). Hayden had a higher average weight per leaf on the burned site with an early burn, while Clay had a higher average on the unburned site. The later the burning, the more likely is a decrease in the average weight per leaf. Some damage occurs with an early burn, but the enhanced growing conditions generally compensate for this. With a late burn, however, more damage is done and the enhanced growing conditions come later in the brief growing season of the plant. This combination makes it more difficult for the plant to recover.

The average number of leaves per vegetative adult plant increased with burning (Fig. 11). The difference at Hayden in both years were smaller than those found at Clay. An increase in leaf number would tend to increase total plant weight. However, a late burn can lower the average weight per leaf and so counteract an increase in leaf number.

Fire tends to produce an increase in the number of leaves per vegetative plant, while a decrease occurs with flowering adults. This difference may be due to the fact that flowering adults provide photosynthate for a scape and extant leaves and may not have any to spare for new leaves. Vegetative adults have no scape and so may have additional

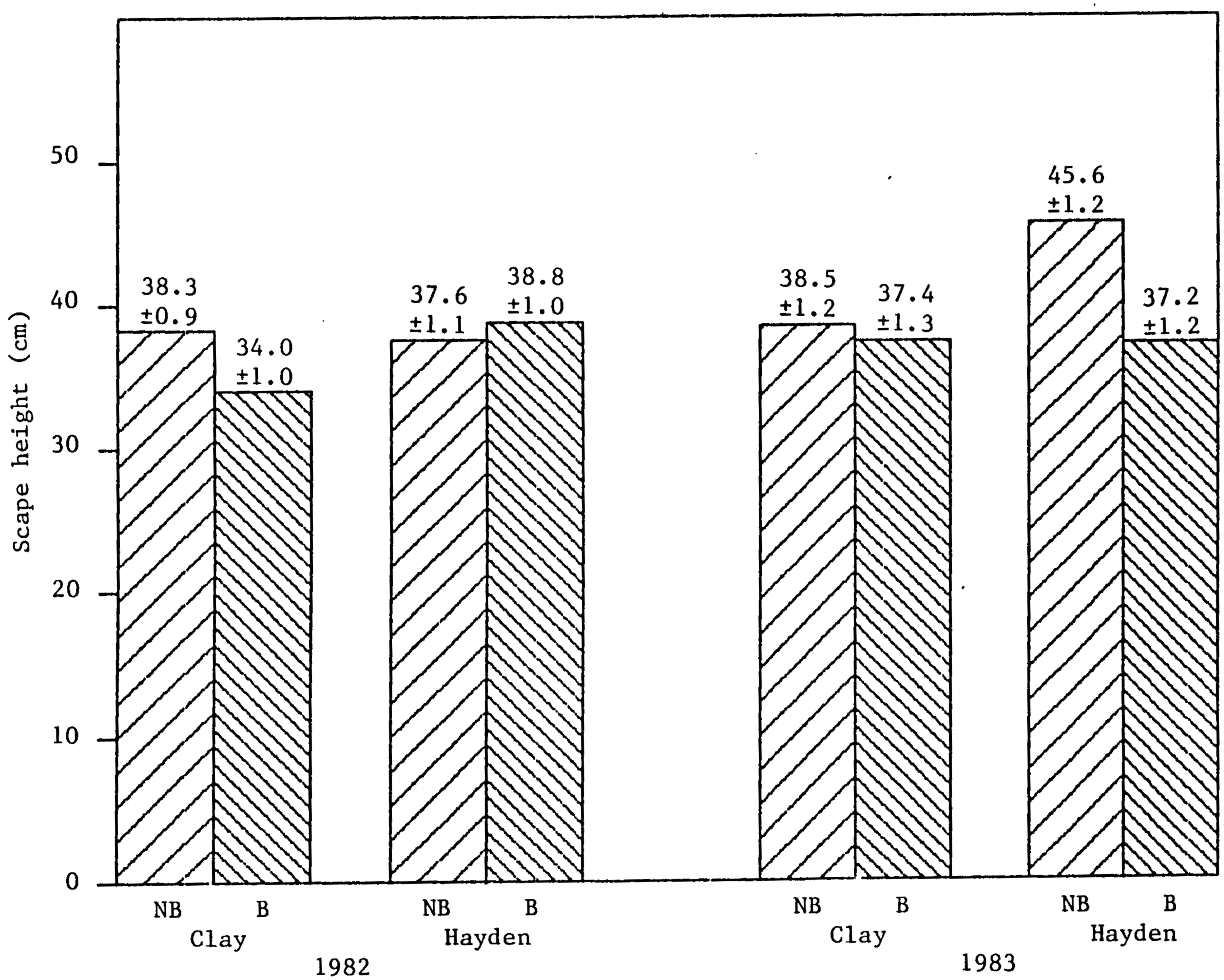



Fig. 8. Mean scape height for flowering adult plants

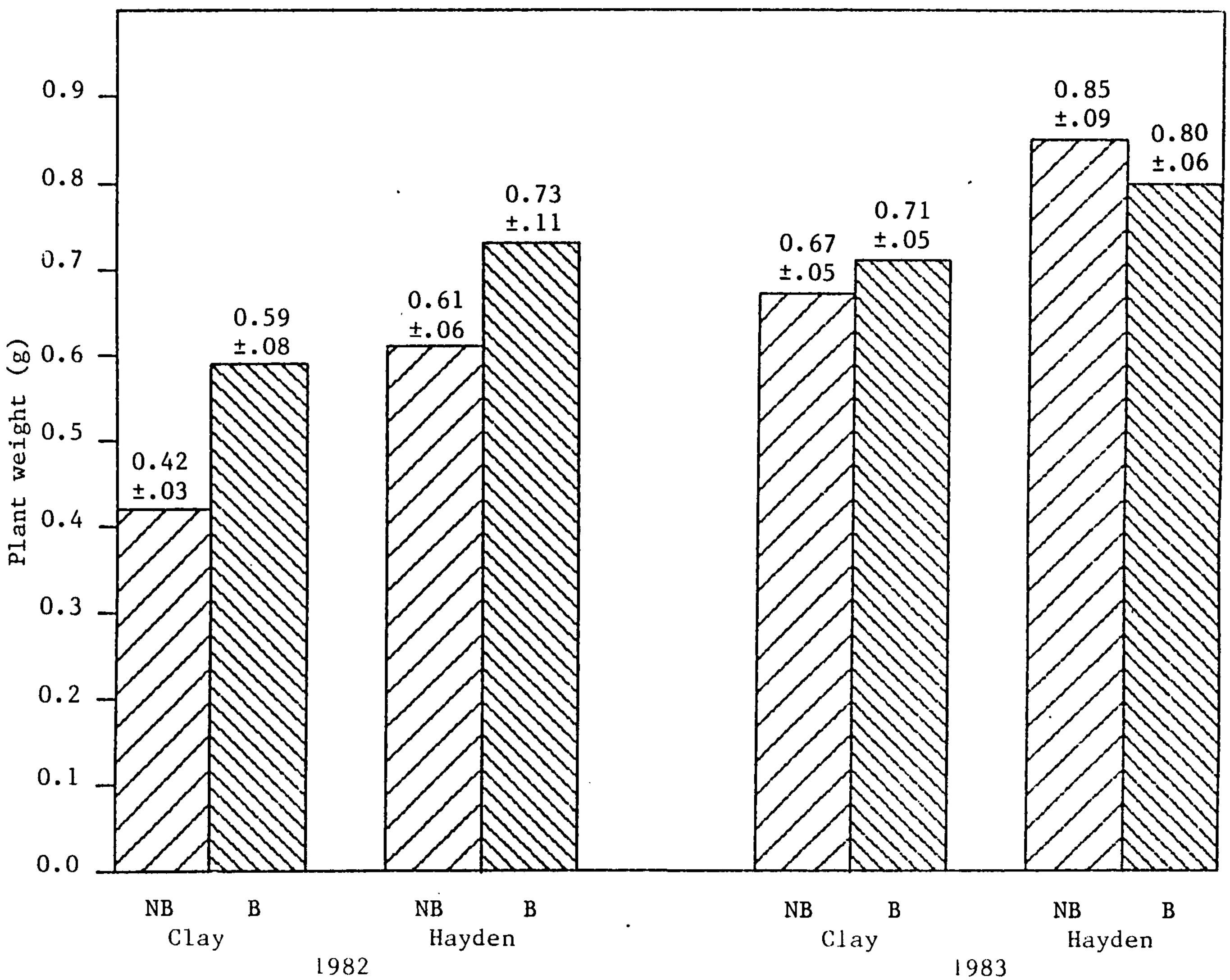



Fig. 9. Mean weight of vegetative adult plants

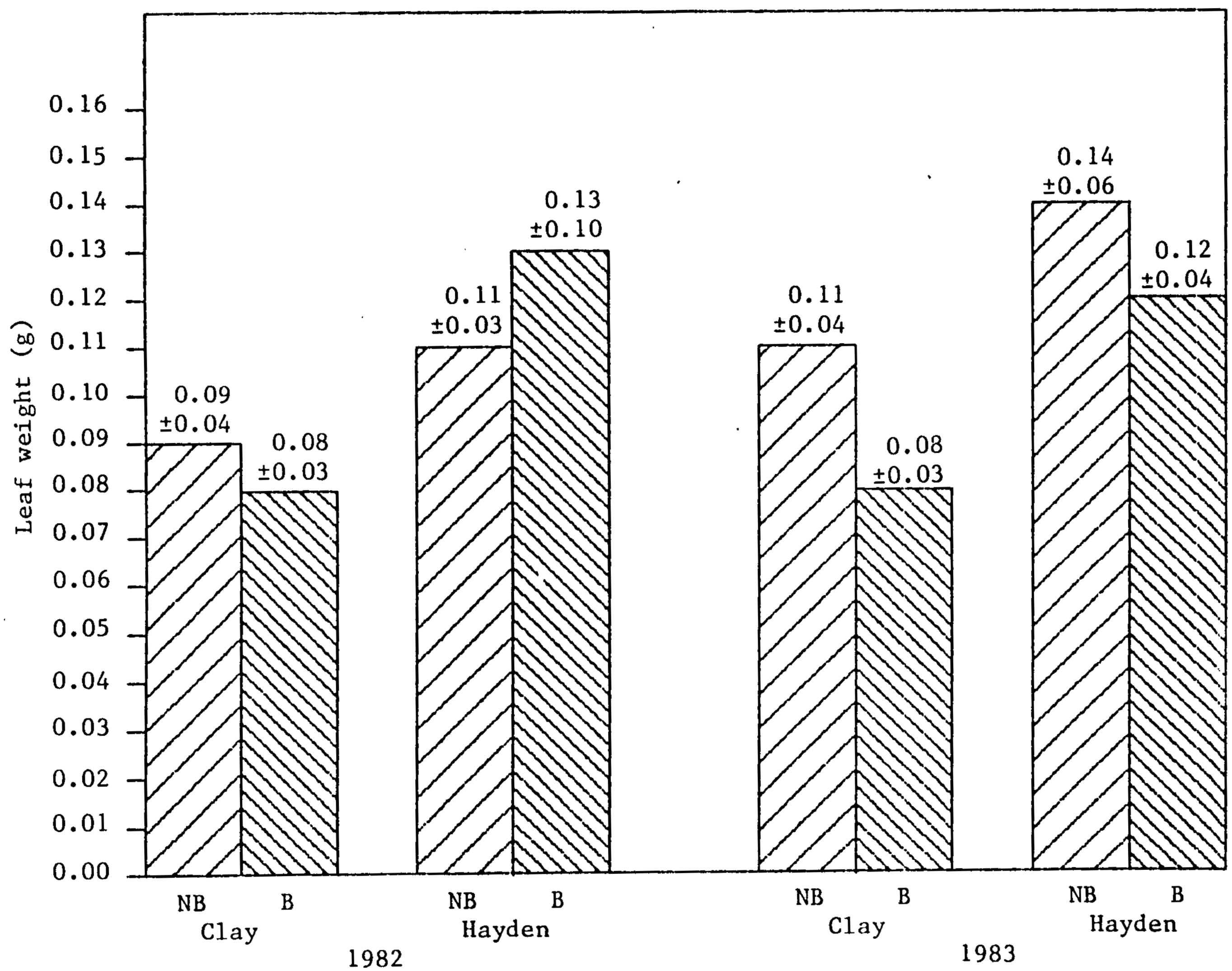



Fig. 10. Mean weight per leaf of vegetative adult plants.

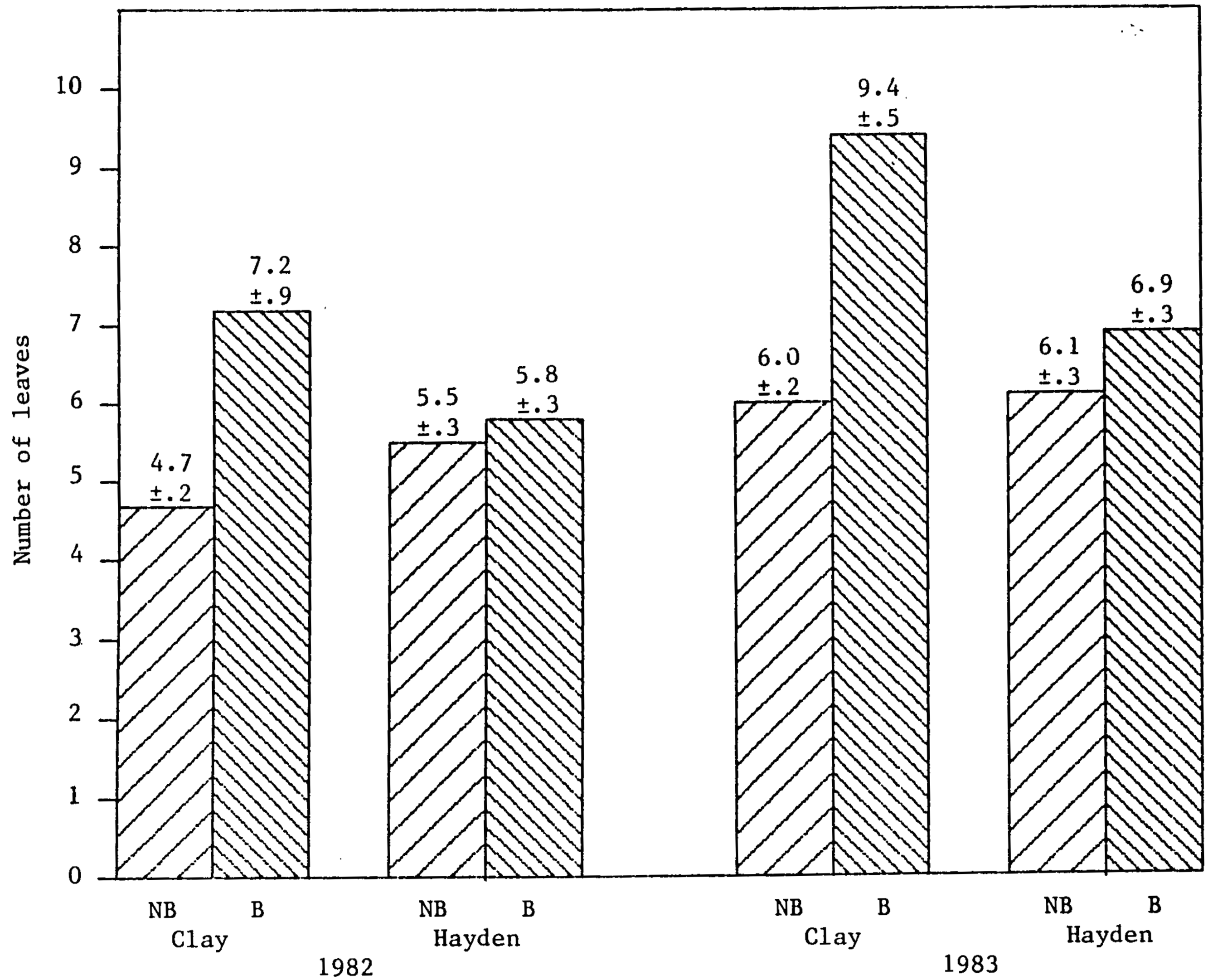



Fig. 11. Mean number of leaves per vegetative adult plant.

photosynthate to allocate to the production of new leaves.

Burning slightly decreased the percentage of vegetative reproduction in flowering adult plants (Table 5). The vegetative reproduction response of vegetative adults to burning was variable (Table 6). In 1981 a small decrease in the percentage of roots with buds was found, while in 1982 a small increase occurred on the burn site. The differences between burned and unburned were smaller for the vegetative adults than for the flowering adults.

The overall differences in vegetative reproduction within the two plant groups were relatively small. Fire probably has little, if any, direct affect on vegetative reproduction, as the soil above the roots insulates them from damaging heat. The leaves of a plant can certainly be damaged by fire and so indirectly influence vegetative reproduction via the amount of photosynthate produced. However, the differences between plants on burned and unburned sites indicates that the amount of photosynthate allocated to vegetative reproduction is only slightly affected by fire.

Vegetative and flowering adults cannot be directly compared in terms of vegetative reproduction. The vegetative adult category included the smallest possible size that a plant could have and still flower. (This was the only way to keep the selection of vegetative adults objective. Though plants can flower at this minimum size, most probably attain a larger size before flowering for the first time.) Most flowering adults were larger than this minimum size. Consequently, plants in the vegetative adult category were smaller on the average than flowering adults. Since larger plants tend to have more roots, flowering adults had more root buds than vegetative adults.

## Flowering

The percentage of adult plants that flowered was always higher on unburned areas (Table 2). This difference was due to the destruction of inflorescences by fire. The sensitivity of an inflorescence to fire is probably due in large part to its position. It is as tall or taller than

Table 5. Flowering adult asexual reproduction at Hayden 1981-1983. Values recorded are total number of roots per plant and number of budded roots per plant

| | 1981 | | 1982 | | 1983 | |
|---|---|---|---|---|---|---|
| | burned | unburned | burned | unburned | burned | unburned |
| Number of plants sampled | 17 | 11 | 13 | 23 | 16 | 10 |
| Roots with buds | | | | | | |
| Mean ± SE | 10.9±0.5 | 11.8±0.9 | 12.4±0.7 | 11.7±0.7 | 12.4±0.8 | 13.3±0.7 |
| Range | 8-22 | 7-16 | 8-16 | 6-17 | 8-18 | 10-17 |
| Total roots | | | | | | |
| Mean ± SE | 16.8±0.6 | 17.2±0.8 | 17.8±0.7 | 16.3±0.7 | 17.8±0.9 | 17.5±0.7 |
| Range | 13-22 | 13-21 | 15-22 | 12-23 | 13-25 | 13-20 |
| Percent roots with buds | 65.6 | 68.0 | 69.2 | 71.2 | 69.4 | 75.8 |

Table 6. Vegetative adult asexual reproduction at Hayden Prairie, 1981-1982. Values recorded are total number of roots per plant and number of budded roots per plant

| | 1981 | | 1982 | |
|---|---|---|---|---|
| | burned | unburned | burned | unburned |
| number of plants sampled | 14 | 7 | 11 | 18 |
| roots with buds | | | | |
| Average±SE | 8.3±.7 | 9.9±1.1 | 9.0±.7 | 8.4±.8 |
| Range | 4-13 | 5-13 | 5-12 | 2-16 |
| total roots | | | | |
| Average±SE | 13.6±.8 | 16.1±1.9 | 14.6±1.4 | 13.3±.8 |
| Range | 10-21 | 8-22 | 8-25 | 9-22 |
| % roots with buds | 60.6 | 61.8 | 63.2 | 62.5 |

the leaves and thus exposed to the hotter temperatures found above the soil surface.

The transects at Clay South 1983 provided a detailed look at the nature of burn damage (Table 7). In this case, 55.8% of the inflorescences were moderately damaged to destroyed. Serious damage (destroyed and unusually small) occurred in 39.2% of the inflorescences. Those scored as healthy inflorescences probably escaped damage by being located in moist litter. They may also have had an inflorescence that was shorter than the leaves at the time of burning, the leaves offering some protection.

Although more adult D. meadia flowered on unburned areas in this study, results from Wisconsin suggest that the response may depend on site specific conditions. Pauly (1984) found that shooting star only flowered on burned areas, even after a fire that burned basal leaves. Apparently, the litter accumulation after years without fire was so great that it suppressed flowering on unburned sites.

Rochester had a higher percentage of flowering than Clay, even though Rochester is a drier site than Clay. However, Rochester also had a much smaller stalk borer attack rate. If Rochester had Clay's unburned stalk borer attack rates, its flowering rate would have been as low or lower than Clay's rate.

Results from the permanent plots at Clay and Hayden are found in Table 8. The data presented here are not random, as they represent the original marked plants minus data lost to unlocatable plots, problems with relocating plants and the fact that plants were not remarked in 1982 (a 1983 field season had not been anticipated at that time.) Vegetative plants were underestimated, as most of the original marking was done in late summer. At this time, vegetative adults cannot be distinguished from flowering adults whose scapes had dried out and fallen over or been destroyed by fire.

Burn patterns and the timing of burning also varied from site to site. Since the data are not statistically representative and the burn timing further complicates interpretation, it seemed best to lump the data by

Table 7. Inflorescence burn damage at Clay Prairie South in 1983
N = 311

| Destroyed | Unusually Small | Moderately Damaged | Slightly Damaged | Healthy |
|---|---|---|---|---|
| 28.0% | 11.2% | 16.6% | 3.4% | 40.9% |

Table 8. Flowering patterns from permanent plots at Clay and Hayden Prairies. F = flowering adult V = vegetative adult

| Years | Flowering Pattern | Number |
|---|---|---|
| 1981/1982 | FF | 166 |
| | FV[a] | 134 |
| | VF | 65 |
| 1981/1982/1983 | FFF | 56 |
| | FVF | 36 |
| | FVV | 2 |
| | VFV | 8 |
| | VVF | 4 |
| | FFV | 13 |
| | VFF | 2 |
| 1980/1981/1982 | FFF | 14 |
| | FVF | 9 |
| | FFV | 3 |
| 1980/1981/1982/1983 | FFFF | 7 |
| | FFFV | 1 |
| | FVFF | 6 |
| | FFVF | 7 |
| | FVVF | 5 |

[a]Some vegetative adults are actually flowering adults that lost their scapes to fire.

flowering pattern and number of years observed in order to determine rough trends.

Patterns varied from plants that flowered one year out of three to those that flowered four years in a row (Table 8). Most plants appear to flower at least once every three years, with many flowering more frequently. Rainfall, fire and herbivory the previous growing season probably all play a role in the flowering patterns.

## Flower Number

Inflorescences showed an increase in flower number following fire (Figure 12). The species has an indeterminate inflorescence, so apparently flower buds that normally would not have become mature did so after a fire. However, the increase in flower number was affected by fire timing. After an early burn in 1982, flower number increased with burning at both sites (Figure 12). In 1983, the year of the late burn, there was a smaller increase in flower number with burning at Clay, and flower number actually decreased slightly after burning at Hayden. The later burn likely does more damage to the plants and there is less time in the plants' brief growing season to recover from this damage to activate more flower buds.

Lovell et al. (1983) found that the number of flowers per flowering individual of *Sisyrinchium campestre* and *Viola pedatifida* increased by as much as 85% with an early (late March or early April) fire. However, all flowers were destroyed by a late (mid-May) burn. Shooting star had a maximum increase of only 31% with a late April burn, when plants were aboveground (this study). The Lovell et al. (1983) data suggest that shooting star flower production might be enhanced even further by a fire that occurred before the plant appeared aboveground.

The pooled distribution of flower number per plant at Clay, Hayden, and Rochester from 1982 and 1983 is found in Fig. 13. Most plants had 6-10 flowers per inflorescence; 11-15 flowers was the second most abundant category.

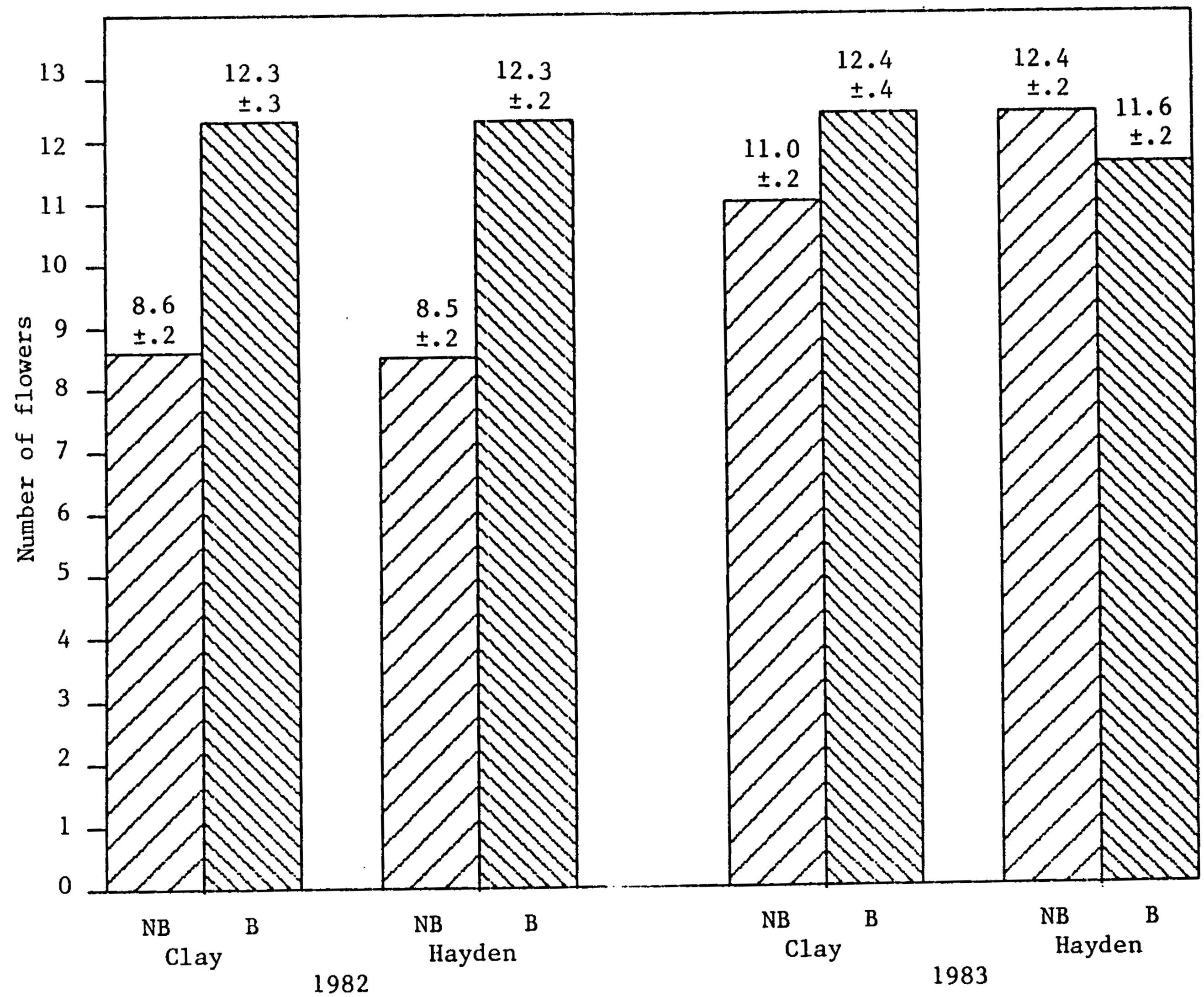



Fig. 12. Mean number of flowers per flowering adult plant

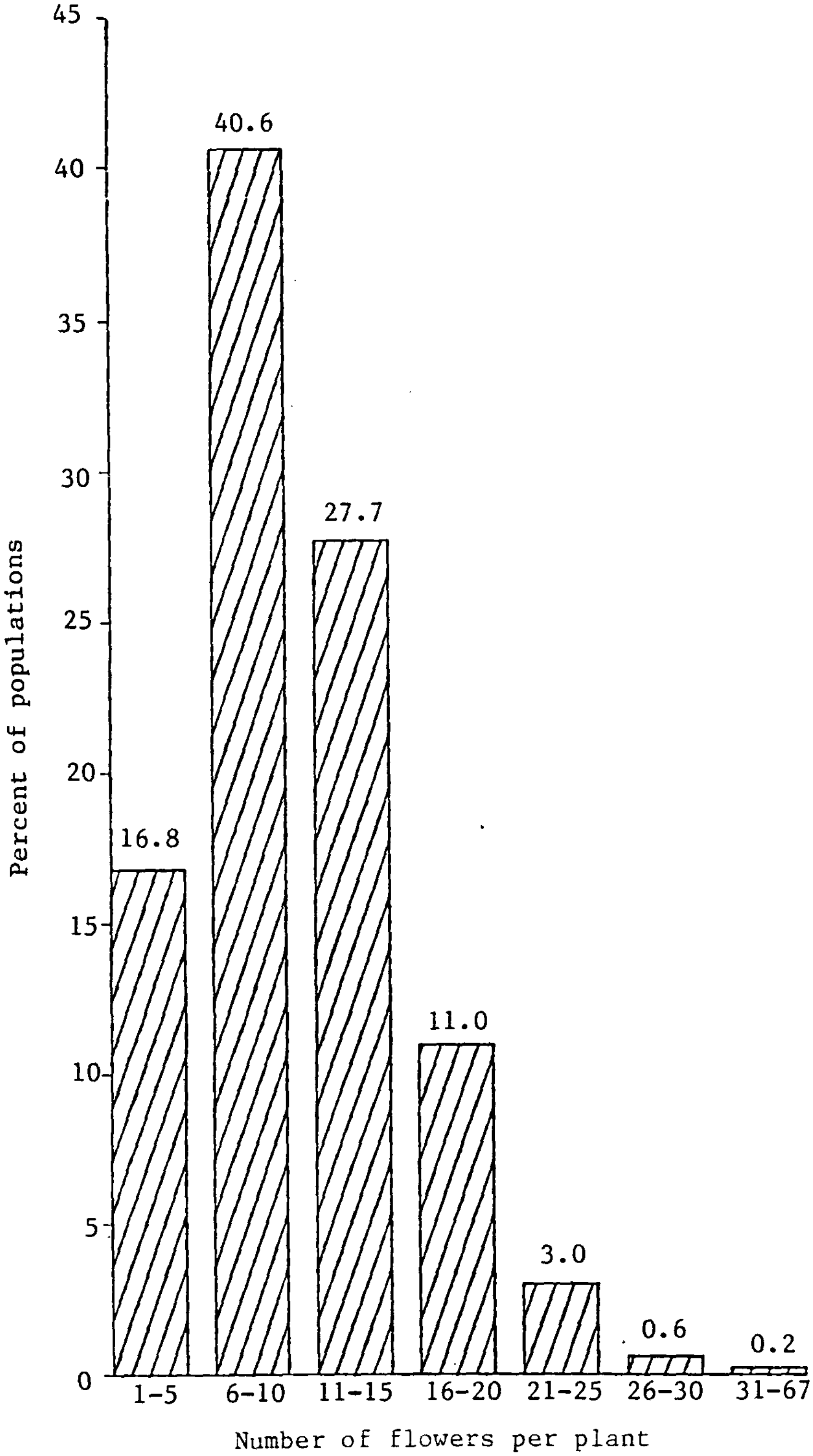



**Fig. 13. Frequency of flower number per plant**

## Seed Production

Seed counts were made on 323 capsules from 40 infructescences from Rochester 1982. A subsample of capsules from Clay South 1983 (burned) and Clay North 1983 (unburned) was also used for seed counts (Table 9). Both Clay 1983 areas had more mature and total seeds than Rochester. Clay North 1983 produced the highest percentage of viable seed, while Rochester had the lowest. Clay's greater number of mature and total seeds may be due to the fact that Clay has more soil moisture than Rochester, although this may also be a year effect.

Seed counts by plant and capsule from a study in Tennessee (Turner, 1969) are shown in Table 10. Plants in the cedar glade habitat had more mature seeds per plant than either a deciduous forest site or Rochester Prairie (compare Tables 9 and 10), and cedar glade plants had more capsules as well. Rochester had substantially more aborted and total seeds per plant than either Tennessee site.

The two Iowa sites had more mature, aborted, and total seeds per capsule than either Tennessee site. However, both Tennessee sites had a greater percentage of viable seeds per capsule than the three Iowa sites. In sum, the Iowa plants produced more seeds per capsule, but the Tennessee plants produced more seeds per plant because the Tennessee plants had both more capsules and a higher percentage of viable seeds.

The two longest capsules from Clay 1983 infructescences were used to compare seed production for burned and unburned sites (Table 9). While Clay South (burned) had more mature seeds per capsule, it also had more aborted seeds per capsule. Consequently, Clay South had a smaller percentage of mature seeds per capsule than Clay North (unburned). A late burn, such as occurred at Clay South, delays flowering (See Results -- Phenology). Perhaps the later flowering occurs, the greater the chance for warm, sunny days in spring conducive to bumblebee pollination. This may account for the greater number of mature seeds at Clay South. However, the greater number of aborted seeds (and so a lower percentage of mature seeds than Clay North) indicates there was a shortage of photosynthate for seed filling. The damage to the leaves caused by a late fire reduces the leaf area and so directly affects the amount of photosynthate burned flowering

Table 9. Seed production at two Iowa prairie sites. Only capsules that had not been attacked by fungi or larvae were used for seed counts

| | Rochester 1982 unburned | | Clay South 1983 burned | | Clay North 1983 unburned | |
|---|---|---|---|---|---|---|
| | $\bar{x}\pm SE$ | range | $\bar{x}\pm SE$ | range | $\bar{x}\pm SE$ | range |
| number of capsules sampled | 323 | | 59 | | 52 | |
| capsules/plant | 7.6±0.63 | 2-21 | ----- | ----- | ----- | ------ |
| mature seeds/plant | 475.2±66.5 | 36-2369 | ----- | ----- | ----- | ------ |
| aborted seeds/plant | 1432±134.1 | 331-4075 | ----- | ----- | ----- | ------ |
| total seeds/plant | 1907±183 | 507-6444 | ----- | ----- | ----- | ------ |
| mature seeds/capsule | 62.3±2.8 | 0-264 | 120.7±8.8 | 0-335 | 119.7±7.8 | 15-219 |
| aborted seeds/capsule | 187.8±3.7 | 52-385 | 192.0±12.9 | 66-471 | 166.4±9.4 | 65-345 |
| total seeds/capsule | 250.1±3.4 | 126-403 | 313.5±13.0 | 173-601 | 286.1±9.0 | 119-445 |
| percent viable seeds | 24.9 | ----- | 38.5 | ----- | 41.8 | ------ |

Table 10. Seed production at two Tennessee sites (Turner 1969), based on 15 plants per site

| | Deciduous Forest | | Cedar Glade | |
|---|---|---|---|---|
| | mean | range | mean | range |
| capsules/plant | 10 | 6-20 | 12 | 5-23 |
| mature seeds/plant | 177 | 0-414 | 589 | 24-2013 |
| aborted seeds/plant | 217 | 66-456 | 476 | 109-1287 |
| total # seeds/plant | 394 | 79-870 | 1065 | 293-2650 |
| mature seeds/capsule | 18 | 0-35 | 49 | 2-88 |
| aborted seeds/capsule | 22 | 5-97 | 40 | 12-129 |
| total # seeds/capsule | 39 | 12-132 | 89 | 47-121 |
| % viable seed | 46.2 | ______ | 44.9 | ______ |

adults could produce. A very early fire, with its subsequent advancement of flowering, might reduce the chance for pollination. However, it may enhance conditions for photosynthesis and so provide more photosynthate for seed filling.

## Fruit Production

Fruit success, defined as the percentage of flowers on an inflorescence that produced fruit, varied from a high of 95.1% at Hayden South 1982 to a low of 80.0% at Clay South 1982 (Table 11). The burned sites consistently had higher fruit success compared to their nonburned counterpart in the same year. The high fruit success at Rochester, however, indicates that fire alone does not account for higher fruit success. Most of the increase in fruit success on burned sites probably comes from the destruction of the eggs and larvae of shooting star's lepidopteran herbivores.

The fruit success of *D. meadia* is similar to that found in other members of the genus. Macior (1968) reports that in Wisconsin 93.7% of the *D. amethystinum* flowers produced fruit. He also notes that *D. pulchellum* had fruit successes of 82% and 100% at two sites in the Front Range of the Colorado Rocky Mountains (Macior, 1974).

Table 11. Fruit success at three Iowa prairies

| Site and Year | Number of Flowers | % Fruiting |
|---|---|---|
| Clay South 1982 | 3118 | 80.0 |
| Clay North 1982 (burned) | 1523 | 89.6 |
| Hayden North 1982 | 2216 | 87.6 |
| Hayden South 1982 (burned) | 2723 | 95.1 |
| Clay North 1983 | 4354 | 81.5 |
| Clay South 1983 (burned) | 1288 | 88.4 |
| Hayden South 1983 | 6895 | 82.9 |
| Hayden North 1983 (burned) | 1048 | 92.0 |
| Rochester 1982 | 2350 | 91.8 |
| Rochester 1983 | 1430 | 94.6 |

# SUMMARY

1. The life history and spring fire response of shooting star, *Dodecatheon meadia*, a perennial spring-flowering forb, was examined in this study.
2. The study took place at three prairies: Clay, Hayden and Rochester Cemetery. A pair of burned and unburned sites was examined at Clay and Hayden. Permanent plots and transects were used to gather information on flowering, fruiting, seed production, plant biomass, and population structure. A small number of vegetative and flowering adults were dug up to determine the amount of vegetative reproduction.
3. The greatest percentage of plants in three of four sites was in the category "small juvenile". The second largest category varied from site to site; these classes included large juveniles, vegetative adults and flowering adults.
4. Hayden Prairie had 71% seedling survival from 1981 to 1982. This is higher than those typically reported for other herbaceous species. This indicates that seedling recruitment may be pulsed — certain years may contribute more seedlings to the population than other years.
5. Phenology varied from year to year within prairies, depending on spring weather. Southern sites had flowering shooting star proportionately earlier than northern sites, probably due to earlier accumulation of growing degree days. Fire dramatically affected phenology. An early burn advanced phenology by approximately one week, while a late burn delayed the phenology by about one week.
6. Stalk borer larvae destroyed up to 21% of the scapes at a site. Stalk borer attack rates were always smaller on burned sites than on a nearby unburned site.
7. Geometrid larvae attacked 13.8% of the shooting star capsules in a sample. Fire reduced their attack rate to zero. Tortricid larvae also attacked shooting star capsules.

8. Fruit success was always higher on burned sites, due to destruction of moth larvae.

9. Total plant weight, average total leaf weight, average weight per leaf, and average scape weight of adult flowering plants increased with an earlier fire and decreased with a late fire. Number of leaves per plant and scape height decreased with burning.

10. The average weight and number of leaves of vegetative adults increased with burning. The average weight per leaf of vegetative adults decreased with burning.

11. Only small differences were noted in the asexual reproduction of both vegetative and flowering adults on burned and unburned sites.

12. The number of scapes was always higher on an unburned sites.

13. The number of flowers per inflorescence increased with an early burn but decreased with a late burn.

14. Capsules produced more seeds on burned sites, but also had more aborted seeds.

15. Flowering adults produced scapes one year out of four to four years out of four.

## FIRE MANAGEMENT RECOMMENDATIONS

The most important positive effects of burning on D. meadia come with an early burn. Flowering and vegetative adult plant weights and flower number increase with burning. Burning before plants appear aboveground would probably have the same effects, reduce attacks by lepidopteran larvae, and also eliminate the scape damage that occurs in later burns. Consequently, I would recommend that burns that are planned to benefit D. meadia should be conducted before the plant appears above the soil.

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