JOURNAL OF THE TENNESSEE ACADEMY OF SCIENCE
VOLUME 52, NUMBER 4, OCTOBER, 1977

SEED AND SEEDLING ECOLOGY OF *OPUNTIA COMPRESSA* IN TENNESSEE CEDAR GLADES

JERRY M. BASKIN AND CAROL C. BASKIN
University of Kentucky
Lexington, Kentucky 40506

ABSTRACT

In the cedar glades of central Tennessee, germination of *Opuntia compressa* seeds occurs in early May. Stratification is required for optimal germination. Seedlings grow very slowly in the field; seedlings that germinated in May 1970 were only 2.5 cm tall in September 1973. Of 50 seedlings that germinated in May 1970, 26 were alive in June 1971, 13 in May 1972, 2 in May 1974 and none in September 1974. Cottontail rabbits eat many of the fertile fruits, but the seeds pass through the rabbits' digestive tracts unharmed. Fruits in which the larvae of *Asphondylia betheli* overwinter do not set viable seeds. Establishment of plants from seedlings does not appear to be an effective mechanism for propagation of this species in Tennessee cedar glades.

INTRODUCTION

Opuntia compressa (Salisb.) Macbr. is a member of the Cactaceae which, according to Weniger (1969), ranges ". . . over the entire United States except approximately the northwest third and the state of Maine." In a study of *O. compressa* habitats in New Jersey, Hanks and Fairbrothers (1969) found that the species grows in a variety of soil types ranging from organic detritus over parent rock to coastal beach sand. However, all the sites which they examined were open and xeric. In central Tennessee, *O. compressa* frequently occurs in the cedar (limestone) glades in habitats that are open and have shallow, rocky limestone soils which are subject to long periods of drought during summer.

Opuntia compressa occurs in cedar glades ranging in disturbance from relatively undisturbed to severely disturbed, but is more abundant in badly disturbed glades, such as those that have been pastured. In lightly disturbed glades, it is associated with *Croton monanthogynus, Erigeron strigosus, Galactia volubilis, Heliotropium tenellum* (Nutt.) Torr., *Isanthus brachiatus, Nothoscordum bivalve, Pleurochaete squarrosa* (Brid.) Lindb., *Ruellia humilis, Satureja glabella, Scutellaria parvula, Sporobolus vaginiflorus* and *Verbena simplex*. (Unless authorities are given, nomenclature follows Fernald, 1950.) In disturbed glades, the associates may include not only the previous species but also *Ambrosia artemisiifolia, Arenaria patula, Carduus nutans, Cassia marilandica, Chrysanthemum leucanthemum, Daucus carota, Diodia teres, Grindelia lanceolata, Gutierrezia dracunculoides, Helenium amarum* (Raf.) H. Rock, *Lespedeza stipulacea, Potentilla recta, Sedum pulchellum* and *Solanum carolinense*.

In cedar glades, plants of *O. compressa* produce new stem joints in late April and May. Flowering occurs in late May and early June, and immature fruits are present by late June. Fruits attain full size by mid-July, and they begin to ripen in early August. Fruits are ripe by late August and early September, but they do not fall from the plants until early winter. Fruit tissues decompose during winter, and by late February seeds may be seen on the soil surface. Germination occurs in early May, but little is known about germination or the seedling stage of the life cycle. The purpose of this paper is to report our studies on the seed and seedling stages of the life cycle of *O. compressa* in the middle Tennessee cedar glades.

METHODS AND RESULTS

SEEDLING GROWTH AND SURVIVAL IN THE FIELD

From October 1968 to September 1974, phenological observations were made on various populations of *O. compressa* in cedar glades in middle Tennessee. Studies of seedling growth and survival where carried out in a badly disturbed cedar glade near Lavergne, Tennessee, where there were about 55 large clumps of mature plants. On 11 May 1970, 70 *O. compressa* seedlings were found around the clumps of this population. The seedlings were marked by placing a small nail with a piece of colored wire on it beside each seedling. Fifty seedlings were used to study survival, and the others were collected and line drawings made at various stages of growth.

SEEDLING GROWTH. Seedling morphology was examined (Fig. 1) at about 1 month intervals during 1970 and in September 1971, 1972 and 1973. Observations ceased in 1974 because all the seedlings were dead. The seedlings were in the cotyledon stage when they were marked on 11 May, but by 23 May many of them had formed a small stem joint, with areoles, between the cotyledons. The cotyledons withered and died in late June and early July. June 1970 was the period of most rapid growth, and during this period stem joints increased from ca. 0.5 cm to 1.5 cm in length. The stem joints grew very slowly during July and August of 1970, and by September they were only about 2.0 cm long. Stems grew very little, if any, during the summers of 1971, 1972 and 1973, and on 29 September 1973 they were only about 2.5 cm long. Stem joints remained cylindrical on all seedlings, and none of them formed a second stem joint.

SEEDLING SURVIVAL. At intervals from 11 May 1970 until 20 September 1974 the *O. compressa* seedlings marked on 11 May 1970 were examined to determine how many were alive. Throughout the study, there was a steady decline in the number of living plants; none were alive on 20 September 1974 (Table 1). Seedlings died during all seasons, but more died during summer than during winter; 38 deaths occurred in summer (April to September) and 12 in winter (October to late March and early April).

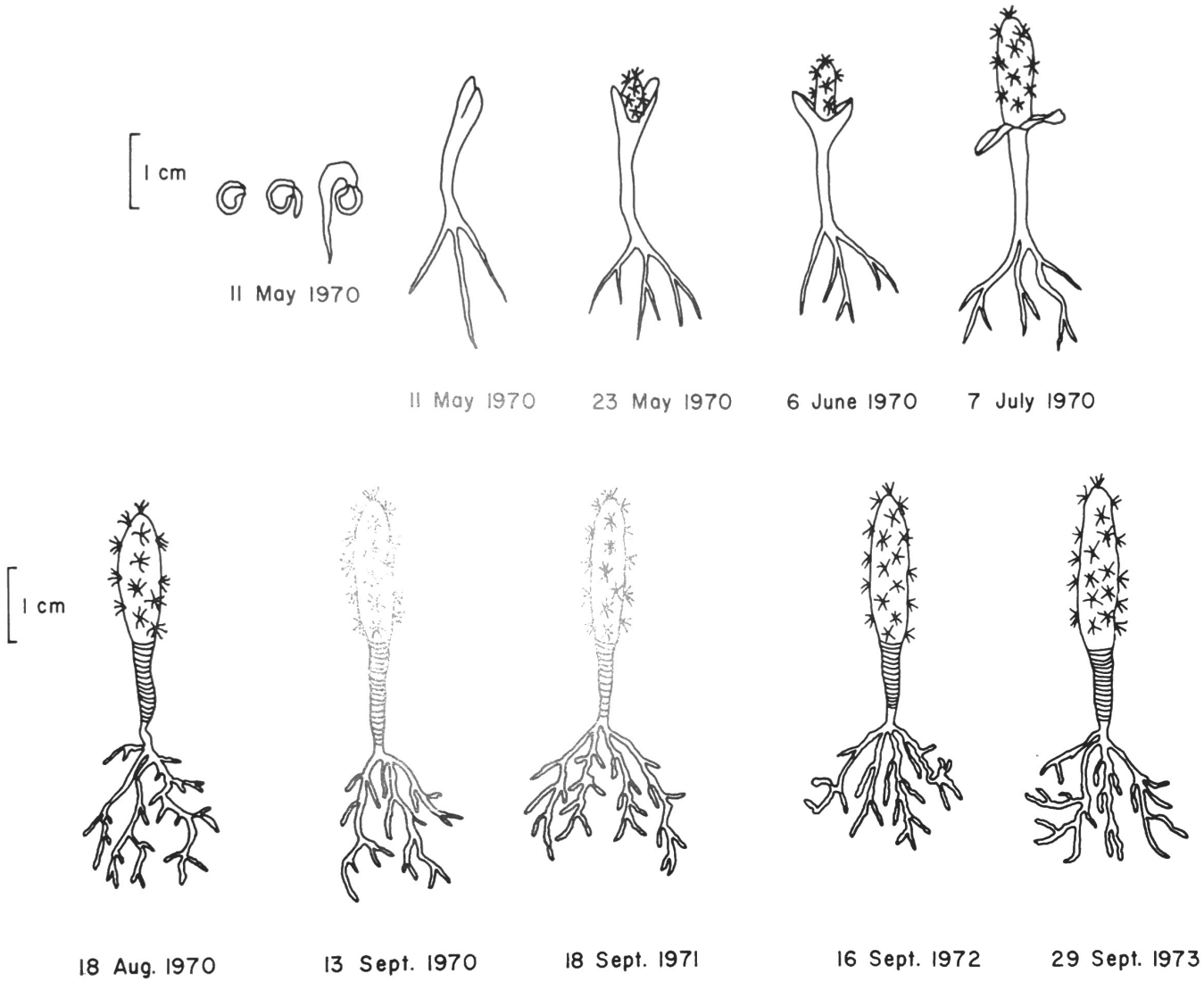

FIG. 1: *Morphology of germination and seedling growth of* O. compressa *in the field.*

TABLE 1: *Survival of 50* O. compressa *seedlings marked in a cedar glade near Lavergne, Tennessee on 11 May 1970.*

Date seedlings were checked (1970)	No. alive	Date seedlings were checked (1971)	No. alive	Date seedlings were checked (1972)	No. alive	Date seedlings were checked (1973)	No. alive	Date seedlings were checked (1974)	No. alive
11 May	50	26 February	31	21 March	16	11 April	6	20 May	2
6 June	46	3 April	29	28 May	13	29 September	4	20 September	0
7 July	46	5 June	26	23 July	11				
25 July	36	12 July	22	16 September	9				
18 August	33	18 September	21						
13 September	31	20 November	21						
10 October	31								
6 November	31								
29 December	31								

BIOTIC FACTORS

RABBITS. In mid-August 1970 the *O. compressa* plants growing in the Lavergne population had numerous fruits which were beginning to ripen and turn red. However, by mid-September most of the ripened fruits had disappeared, and there were hundreds of rabbit (*Sylvilagus floridanus Mallurus* (Thomas)) droppings (skats) on the ground in the vicinity of the *O. compressa* plants. A preliminary examination revealed that some of the skats contained *O. compressa* seeds. Therefore, all the skats that could be found near the 55 clumps of *O. compressa* plants were collected. A total of 1,310 skats was collected and 154 of them (11.8%) contained *O. compressa* seeds. Of the skats, 103 had one seed, 29 had two seeds, 15 had three seeds, three had four seeds, three had five seeds and one had six seeds. None of the 239 seeds recovered from the skats appeared to be damaged and 39.7% of them germinated the following spring after being exposed to winter weather on moist soil in a nonheated greenhouse. In a control set of seeds collected from fruits, 63.8% of the seeds germinated the following spring.

CECIDOMYIIDAE. During fruit ripening in August, some of the *O. compressa* fruits do not ripen. These green fruits contain undeveloped ovules (ovules that never mature) and larvae of *Asphondylia betheli* Cockerell (Cecidomyiidae). They remain attached to the plants all winter and in early May the adults of *A. betheli* emerge through holes they make in the fruit walls. Most of the unripened fruits fall from the plants soon after the flies have emerged. However, in some cases the fruits are not shed, and stem joints grow from the tops of the fruits.

GERMINATION STUDIES

Fully ripened fruits were collected from plants of *O. compressa* growing in the Lavergne population. The seeds were removed from the fruits, washed several times with tap water, dried for 5 days and then immediately used in germination experiments. Freshly matured seeds did not germinate when incubated at a 14 h photoperiod at alternating temperature regimes (12/12 h) of 20/10 and 30/15 C for 30 days. Mechanical and acid scarification were ineffective in promoting germination.

STRATIFICATION REQUIREMENT. To determine if moist chilling (stratification) is necessary to overcome dormancy, seeds were planted on soil in greenhouse flats and placed either in a heated greenhouse or in a nonheated greenhouse (with windows open, where they were subjected to low, winter temperatures). On 17 October 1968 three replications of 200 seeds collected on 12 October 1968 were placed in each greenhouse, and on 19 October 1970 two replications of 500 seeds collected on 14 October 1970 were placed in each greenhouse. The 1968 seeds were kept in the greenhouses until the end of two germination seasons and the 1970 seeds until the end of three germination seasons. From 1 September to 30 April of each year, the soil was watered daily to simulate the high soil moisture conditions in the cedar glades during winter. From 1 May to 31 August of each year, the soil was watered to saturation once each week to simulate the alternate wetting and drying that the surface layers of soil in the habitat undergo during summer. The flats were examined at about 1 week intervals, and germinated seeds were counted and removed.

Stratification was not essential in overcoming dormancy of all the seeds (Table 2). Seeds planted in 1968 and in 1970 that did not receive stratification germinated to 23.5 and 30.0% respectively. However, for both plantings final germination percentages were twice as great for stratified as for nonstratified seeds.

Among the seedlings resulting from seeds planted in 1968, there were a number of cases of polyembryony, but no counts were made. When seeds planted in 1970 started to germinate, a record was kept of the number of seeds that produced two embryos. Of the 949 seeds that germinated, 11 of them (1.2%) had two embryos. The origin of embryos was not investigated.

TABLE 2: *Germination of stratified (in nonheated greenhouse) and nonstratified (in heated greenhouse) seeds of* O. Compressa.

Year planted	Year germination	Cumulative germination %	
		Stratified	Nonstratified
1968	1969	48.7	13.3
	1970	68.2	23.5
1970	1971	64.8	24.9
	1972	64.9	28.7
	1973	64.9	30.0

GERMINATION TEMPERATURES. On 10 October 1969 two replications of 200 seeds collected on 4 October 1969 were planted on soil in greenhouse flats and placed in a nonheated greenhouse where temperatures were near those out-of-doors. Temperatures in the greenhouse were recorded with a thermograph until the experiment was terminated on 15 June 1971, at the conclusion of the second germination season. From 10 October 1969 to 30 April 1970 and from 1 September 1970 to 30 April 1971, the soil was watered daily; from 1 May to 31 August 1970 and 1971, the soil was watered to saturation once each week. The seeds were examined at about 1 week intervals and germinated seeds were counted and removed.

Spring was the only season in which germination occurred, and most of the seeds germinated in late April and May (Fig. 2). In 1970, 58.0% of the seeds germinated, and most of the

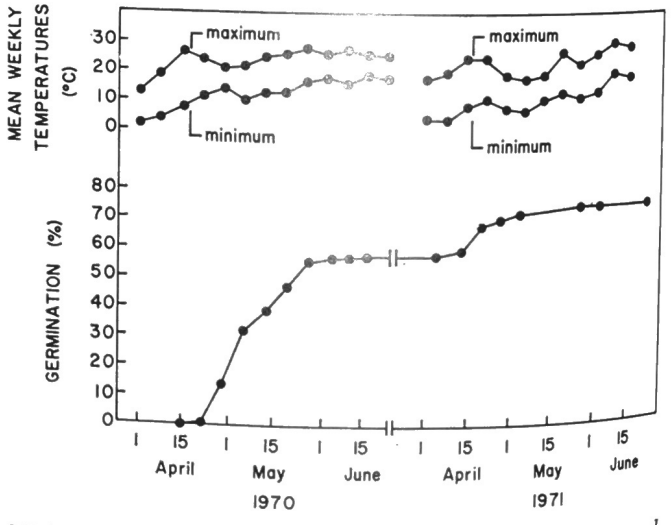

FIG. 2: *Germination of seeds of* O. compressa *planted in soil in a nonheated greenhouse 10 October 1969.*

germination occurred between 22 April and 27 May. During this period, mean weekly maximum temperatures ranged from 21.3 to 26.3 C and mean weekly minimum temperatures ranged from 10.7 to 14.6 C. In 1971 the germination percentage increased to 75.8, with most of the seeds germinating the last two weeks of April. Mean weekly maximum temperatures for these two weeks were 25.7 and 19.8 C, and mean weekly minimum temperatures were 11.7 and 8.9 C.

Discussion

The large number (70) of *O. compressa* seedlings in the Lavergne population in May 1970 is not indicative of the number that usually can be found in *O. compressa* populations—rarely can so many seedlings be found in a population. In most years, seedlings are infrequent; in some years, there are no seedlings. In the Lavergne population there were 70 seedlings in 1970, 19 in 1971, 5 in 1972, 8 in 1973 and 5 in 1974. Survival of seedlings marked in 1970, however, seems to be representative of seedling survival in general. Of the 19 seedlings found in 1971, only two were alive in September 1974; of the five seedlings found in 1972, only one was alive in September 1974 (Baskin & Baskin, unpub.).

Seedlings of *O. compressa* grow slowly, even when grown in a greenhouse where soil moisture and light are not limiting. Stem joints of plants grown from seeds in the nonheated greenhouse were only 5-6 cm long at the end of the first growing season. The stems became flattened during the first summer, but a second stem joint was not formed until the beginning of the second growing season (Baskin & Baskin, unpub.). In the cedar glade habitat, soil moisture and, to some degree, light are limiting during the growing season. The shallow, rocky soils of the *O. compressa* habitat are subject to long periods of drought from May to September or October, and seedlings are shaded by adult *O. compressa* plants and other species. Thus, seedlings grow much more slowly in the field than in the greenhouse. Slow growth is probably largely responsible for low percentages of seedling survival. Plants are unable to produce large root systems or to accumulate reserves of photosynthate which would enable them to tolerate periods of unfavorable environmental conditions such as drought.

Seedling growth in Plains pricklypear (*Opuntia polyacantha* Haw.) is also very slow. Turner and Costello (1942) studied growth and survival in 22 locations in northeastern Colorado over a three-year period. During the first summer, seedlings formed a single stem joint between the cotyledons, and the average total height of plants was less than 2.5 cm. At the end of the second summer, the plants had two stem joints and ranged from 2.0 to 3.5 cm in height. In the third summer, the plants produced one to two additional stem joints, and the height increased to 6-8 cm. Based on number of original seedlings, mortality during the first, second and third summers was 5, 12 and 31%, respectively.

The cedar glade habitat is unfavorable for survival and eventual maturation of large numbers of *O. compressa* seedlings. Since *O. compressa* is characteristically found in dry habitats and seedlings grow very slowly, sexual reproduction probably is not a very efficient mechanism for propagation of this species. The most effective means of propagation of the species is vegetative reproduction. Stem joints that become detached from the plants develop new roots from the areoles and new plants are formed.

Vegetative reproduction is an important means of propagation in many species of *Opuntia*. Although rootsprouts are formed in some species, e.g. *O. polyacantha* (Harvey, 1936), rooting of detached stem joints is the most common mechanism. In the Cylindropuntiae (round stem joints), the terminal joints are easily detached by a slight disturbance of the plant—usually by animals, wind or rain (Anthony, 1954). These joints have long spines that aid in dissemination by becoming attached to any animal that disturbs the plant (Toumey, 1895). In *O. compressa* and other Platyopuntiae (flat stem joints), the joints are more firmly attached than in the Cylindropuntiae; but fragmentation occurs when cattle, deer, rabbits and other animals browse upon the joints (Anthony, 1954), cattle trample the plants (Schaffner, 1938) and people gather the fruits (Phillips, 1940). Fragmentation also occurs when old joints of mature plants die, separating the original plants into several new individuals (Turner & Costello, 1942).

Though many animals eat the fleshy fruits of *Opuntia* spp., most of the seeds are unharmed by the digestive processes. Thus, animals are very important dispersal agents of the seeds. There are reports that seeds of *Opuntia* spp. have been eaten and disseminated by (1) birds, baboons, monkeys and goats in South Africa (Phillips, 1940); (2) cattle, deer, peccaries, rabbits and gophers in the Big Bend region of Texas (Anthony, 1954); (3) iguanas and tortoises in the Galapagos Islands (Raccine & Downhower, 1974); (4) emus, black magpies, cattle and rabbits in Australia (Darnell-Smith, 1919) and (5) jack rabbits in the Great Plains of the United States (Timmons & Wenger, 1940; Riegel, 1941; Cook, 1942; Timmons, 1942). Seed dispersal by jack rabbits is considered to be one of the reasons for the great increase of cacti in grazing lands of the central Great Plains during the drought years of 1930-1940 (Timmons & Wenger, 1940; Riegel, 1941; Cook, 1942; Timmons, 1942).

Following stratification, *O. compressa* seeds collected from skats germinated to 39.7%; seeds collected from fruits germinated to 63.8%. After stratification, *Opuntia macrorhiza* seeds collected from jack rabbit skats germinated to 62%; seeds collected from dried fruits germinated to 44%. In the nonstratified control (in a heated greenhouse), 7% of the seeds from skats and 0.3% of the seeds from fruits germinated (Timmons, 1942).

In *O. compressa,* lack of seed set apparently was caused by the presence of *Asphondylia betheli* larvae in the fruits; in some cases these sterile fruits produced new stem joints. In his studies of the abnormalities in the fruiting habits of *Opuntia* spp., Griffiths (1906) found that "a very peculiar set of fruit modifications is