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ROLE OF TEMPERATURE IN THE REGULATION OF THE LIFE CYCLE OF THE WINTER ANNUAL *PHACELIA DUBIA* VAR. *DUBIA* IN TENNESSEE CEDAR GLADES

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ABSTRACT

Published and unpublished information on the ecological life cycle of the winter annual *Phacelia dubia* (L.) Trel. var. *dubia* McVaugh in the cedar glades of middle Tennessee is presented to show how temperature regulates the timing of the life cycle in nature. The complex time-temperature dependent changes in the seeds' physiological responses to temperature restricts germination to autumn, the only season of the year that is followed by a period that is favorable for completion of the life cycle. Vernalization is not a requirement for flowering, but in the field, flower buds are initiated during winter. Bolting and flowering are independent of photoperiod per se and occur with increases in temperature in early spring.

INTRODUCTION

Phacelia dubia (L.) Trel. var. *dubia* McVaugh (Hydrophyllaceae) is a winter annual plant species whose range of distribution includes westwardly disjunct populations in the cedar glades of middle Tennessee (Constance, 1949; Murdy, 1966). In the cedar glades *P. dubia* var. *dubia* grows mostly in open, well-lighted habitats where the soil is 10-12 cm deep. It occurs on relatively undistrubed glades as well as on glades that have been lightly to moderately disturbed. In relatively undisturbed glades it grows in soil-filled cracks, on soil surrounding limestone outcrops and at the edges of open glades near thickets (Baskin and Baskin, 1971). From mid-autumn to spring, soil moisture in these habitats generally is adequate for growth of non-drought tolerant species, but during summer these habitats are subject to varying periods of drought. In his studies of the plant communities of the middle Tennessee cedar glades, Freeman (1933) found that soil moisture was frequently below the wilting coefficient during summer. Non-drought tolerant species such as *P. dubia* var. *dubia* can grow in this habitat because they complete their life cycles during the cool, moist period between autumn and spring and are dormant during the usually hot, dry summer. Thus, timing of the life cycle is an important ecological adaptation to this seasonally variable environment. In this paper we pull together published and unpublished information on the ecological life cycle of *P. dubia* var. *dubia* and show how temperature regulates the timing of the life cycle in its natural habitat.

GENERALIZED LIFE CYCLE

Seed germination and annual population establishment of *P. dubia* var. *dubia* occur in early autumn. Germination was monitored in a population on a cedar glade near Murfreesboro, Tennessee, from May to November, 1969. During 1969 most of the germination occurred between 6 and 20 September (Baskin and Baskin, 1971). If September is a dry month, the peak germination season may be October or November. Usually, however, there will be (*a*) period(s) during September or October when soil moisture is adequate for germination. Although not all the seeds in the seed reserve at a population site germinate in autumn, germination does not occur at any other time of the year. In the springs of 1969, 1970 and 1971, freshly-matured seeds of *P. dubia* var. *dubia* were planted on soil in greenhouse flats and placed in a non-temperature controlled greenhouse (no heating or air conditioning and windows open all the time) at Lexington, Kentucky. Temperatures in the greenhouse were near air temperatures that occur in middle Tennessee. Watering regimes were given to simulate the soil moisture conditions that may occur in the cedar glade habitat during a given year. From 1 September to 1 May the soil was watered daily, and from 2 May to 31 August it was watered once each week. From the time of planting until late autumn of 1976 the flats were examined at approximately one-week intervals for seedlings of *P. dubia* var. *dubia;* if seedlings were present, they were counted and removed. In each year germination occurred in one or more of the flats and in all cases seeds germinated only in autumn, mostly in September and October. Germination of seeds planted in each year was spread over a number of years (Table 1). Some of the seeds planted in 1969 germinated in each of the following seven germination seasons, and some of the seeds planted in 1970 and 1971 germinated in each of the following six germination seasons.

TABLE I. *Percent (Cumulative) Germination of* Phacelia dubia *var.* dubia *Seeds on Soil in a Nontemperature-controlled Greenhouse. In 1969 and 1970 Two Replications of 200 Seeds Were Planted and in 1971 Two Replications of 1,000 Seeds Were Planted.*

Autumn in Which Seeds Germinated	Year Seeds Were Planted 1969	1970	1971
1969	59.3		
1970	71.5	31.5	
1971	82.5	47.0	25.4
1972	85.8	57.3	48.4
1973	86.5	60.5	70.2
1974	86.8	62.3	76.5
1975	87.0	62.5	82.2
1976	87.0	62.5	83.0

After germination each plant produces an overwintering rosette of leaves, and these rosettes grow slowly during thew inter. At any given time during winter and spring, rosettes of various sizes can be found in a population. The rosettes shown in Fig. 1 illustrate two sizes of rosettes collected from a population on 27 February 1971. Differences in sizes of rosettes probably are caused by differences in germination date and/or differences in the plants' microenvironment. Flower bud production occurs in late winter. In 1970 flower buds were not present on plants collected on 31 January, but flower bud initials were present on plants collected on 28 February. Rosettes were again checked for date of flower bud initiation during the 1970-71 growing season. No flower buds or initials were found on plants collected on 29 December 1970, whereas flower buds were present on plants collected on 26 February 1971. By mid to late March flower buds are well developed. Stem elongation begins in late March, and flowering (anthesis) occurs from early April to early May. The peak of flowering is from mid to late April. Seeds are mature by mid May to early June, and they are released from the capsules shortly after maturity.

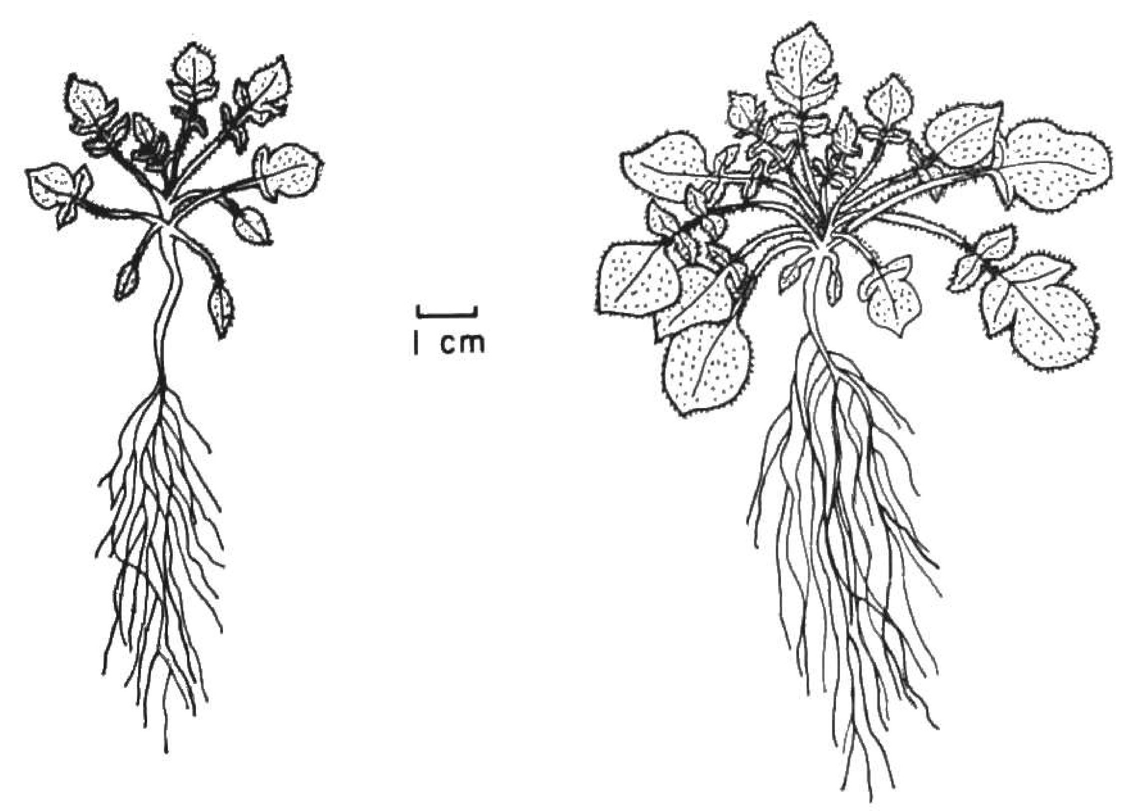

FIG. 1: Rosettes of *Phacelia dubia* var. *dubia* collected on a cedar glade near Murfreesboro, Tennessee on 27 February, 1971.

SEED STAGE

At maturity and dispersal the seeds are conditionally or innately dormant (Baskin and Baskin, 1971). Conditionally dormant seeds will germinate over a narrow range of temperatures, and over this range of temperatures germination is better in light than in darkness. Conditionally dormant seeds do not germinate immediately after dispersal because temperatures in the habitat are above those required for germination. Innately dormant seeds will not germinate at any temperature in light or darkness. During summer both conditionally and innately dormant seeds may afterripen. By July and August many of the innately dormant seeds have become conditionally dormant and the range of germination temperatures has widened for many of the conditionally dormant seeds. However, even though the seeds' ability to respond to higher temperatures has increased, the temperatures of the environment remain above those required for germination. Thus, during summer high temperature is the overriding factor preventing germination of conditionally dormant seeds (Baskin and Baskin, 1971).

Although high summer temperatures prevent germination of conditionally dormant seeds of *P. dubia* var. *dubia* in the field during summer, these high temperatures probably are a requirement for afterripening of the seeds. In *Viola rafinesquii* Greene (Baskin and Baskin, 1972) and three other species of winter annuals (Baskin and Baskin, 1976a) simulated summer habitat temperatures promoted and simulated winter habitat temperatures inhibited afterripening of freshly matured seeds. Thus, although the seed dormancy stage of the life cycle is an adaptation of winter annuals to the hot, dry summer season, the high temperatures during summer actually are required to break seed dormancy.

By autumn a portion of the seeds of *P. dubia* var. *dubia* are fully afterripened and will germinate over a wide range of temperatures, although some seeds still have a light requirement for germination (Baskin and Baskin, 1971). With a decrease in temperatures in the habitat in autumn, temperatures come within the range of those required for germination of afterripened seeds, and germination occurs if other external factors are not limiting. During the germination season in autumn when temperatures of the environment generally are within the range of those required for germination, soil moisture and light are probably the most important environmental factors controlling germination.

During a given germination season in autumn, many of the seeds at the population site will not germinate, and at the end of the germination season a reserve of ungerminated seeds remains in or on the soil. This seed reserve is composed of seeds produced in the current year as well as seeds produced in previous year(s); some of them are non-dormant, some are conditionally dormant and some are innately dormant. Low winter temperatures force the non-dormant and *i.e* dormant conditionally dormant seeds into a state of deep secondary dormancy and prevent afterripening of innately dormant seeds. By spring when temperatures are within the range of those required for germination of nondormant and/or conditionally dormant seeds, none of the seeds will germinate at any temperature, (Baskin and Baskin, 1973). In the two winter annuals *Torilis japonica* (Houtt.) DC. (Baskin and Baskin, 1975) and *Sedum pulchellum* Michx. (Baskin and Baskin, unpub.) low winter temperatures also have been shown to induce non-dormant and conditionally dormant seeds into secondary dormancy and to prevent afterripening of innately dormant seeds. The response of seeds of *P. dubia* var. *dubia* and other winter annuals to low winter temperatures insures that germination will not occur in spring. If seeds germinate in spring the plants probably could not complete their life cycle before the onset of drought conditions, to which the plants are not adapted. In