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Published and unpublished information on the ecological life cycle of the winter annual Phacelia dubia (L.) Trel.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 needed for flowering, but in the field, flower buds are initiated during winter. Bolting and flowering are independent of photoperiod 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 westward 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 undisturbed sites as well as on glades that have been lightly to moderately disturbed. In relatively undisturbed glades it grows in soil-filled cracks, on standing 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 low, creating a non-drought tolerant species, but during summer these habitats are subject to varying periods of drought. In his studies of the plant communities in the middle Tennessee cedar glades, Freeman (1933) found that soil moisture was frequently below the wilting coefficient during summer. Non-drought tolerant species like 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. This study was designed to evaluate the effects of temperature on the ecological life cycle of Phacelia 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 fall rain occurred between 26 September and 20 December (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. Temperature 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 October the soil was kept wet, 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 maintained at approximately 5°C for 16 hours, 10°C for 8 hours for seedlings of P. dubia var. dubia; if seedlings were present, they were counted and removed. In each 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 the field has spread over a number of years (Table I). Some of the seeds planted in 1969 germinated in each of the five following seasons, germination of the same batch germinated in each of the following six germination seasons.


| Year | Seeds Planted | Germinated
|------|---------------|-------------
| 1969 | 200           | 59.3        |
| 1970 | 200           | 71.5        |
| 1971 | 200           | 81.2        |
| 1972 | 200           | 85.8        | 48.4
| 1973 | 200           | 86.5        | 70.2
| 1974 | 200           | 86.5        | 76.5
| 1975 | 1,000         | 87.0        | 82.2
| 1976 | 1,000         | 87.0        | 83.0

SEED STAGE
At maturity and dispersal the seeds are conditionally or inherently dormant, (Baskin, 1971). Some of the seeds germinate conditionally dormant seeds will germinate over a narrow range of temperatures, and over this range of temperature 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. Incompetent dormant seeds will not germinate at any temperature in light or darkness. During summer both conditionally and inherently dormant seeds may germinate. By July and August many of the inherently 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. Viteri rafinescens seeds (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 is 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. Light, temperature, and water factors are not limiting. During the germination season in autumn when temperatures of the environment generally are within the range required for germination and 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 in each year certain portions of the population of ungerminated seeds remains in or on the soil. This seed reserve is composed of seeds produced in the previous year, those produced in the current year, and seeds that are non-dormant, some of them are conditionally dormant and some are inherently dormant. Low winter temperatures forces the seeds to become non-dormant and in dormancy conditionally dormant seeds into a state of deep secondary dormancy and prevent afterripening of inherently dormant seeds. By spring when temperatures are within the range of those required for germination of non-dormant and/or conditionally dormant seeds, most of the seeds germinate at any temperature, (Baskin and Baskin, 1973). In the two winter annuals Torilis japonica (Hook.) Ohwi and Sisymbrium officinale (L.) phelcheum Michx. (Baskin and Baskin, unpub.) low winter temperatures also have been shown to induce non-dormancy and alter dormancy conditionally dormant seeds into secondary dormancy and to prevent afterripening of inherently dormant seeds. The response of seeds of P. dubia var. dubia to ethylene and other gaseous compounds at low winter temperatures insures that germination will not occur in spring. If seed germination in the spring plants probably could not complete their life cycles under the onset of drought conditions, to which the plants are not adapted. In