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GERMINATION ECOLOGY OF WINTER ANNUALS: *Valerianella umbilicata*, *F. patellaria* AND *F. intermedia*

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ABSTRACT

The effect of age, temperature, light and darkness and soil moisture on germination of seeds of *Valerianella umbilicata*, f. *patellaria* and f. *intermedia* were investigated. In June freshly-matured seeds of both forms were dormant, but by early July a portion of the seed population had gained the ability to germinate at low but not at high temperatures. In late July and August a high percentage of the seeds could germinate on moist sand at simulated field temperatures; however, very few seeds germinate in the field during summer. Germination apparently does not occur because seeds germinate slowly at this stage of afterripening, and the periods of favorable soil moisture are too short. Seeds germinate in September and October after they have acquired the ability to germinate at their maximum rate. Afterripened seeds germinate better in light than in darkness and better at alternating than at constant temperatures. In autumn seeds of f. *intermedia* germinate to higher percentages than seeds of f. *patellaria* in both light and darkness. Differences in germination responses of the forms may be of survival value to the species in a given habitat.

INTRODUCTION

Valerianella umbilicata (Sull.) Wood (Valerianaceae) is a winter annual that grows in fallow fields, floodplains, open woodland borders and occasionally on roadsides in much of the eastern United States from New York, Ohio, Michigan and Illinois south to Alabama, Tennessee and North Carolina (Ware, 1969). In central Tennessee the species is frequent in floodplains, meadows, vacant lots and on moist roadsides and is commonly associated with *Allium vineale, Carex* spp., *Festuca elatior, Phleum pratense, Plantago lanceolata, Rumex crispus, Trifolium pratense, T. repens* and many species of winter annuals including *Arabidopsis thaliana, Bromus japonicus, Galium aparine, Geranium carolinianum, Hordeum pusillum, Lamium amplexicaule, Lithospermum arvense, Phacelia purshii, Valerianella olitoria, V. radiata, Veronica arvensis* and *Viola rafinesquii*. (Unless authorities are given nomenclature follows Fernald, 1950.)

Although we have seen a few *V. umbilicata* seedlings in the field in mid August, most of the germination in middle Tennessee occurs in mid to late September when soil moisture becomes continuously non-limiting for completion of the life cycle. In dry autumns germination may not occur until October. During autumn a rosette with 15-20 leaves is formed, and the plant overwinters in this condition. Flower bud initials are present by mid February, and by mid March flower buds are well developed. Bolting occurs during April, and plants are in full flower by early May. Seed maturation and dispersal are completed in late May and early June, just before many of the habitats are mowed. Seeds lie in or on the soil surface until the following autumn, when conditions become favorable for germination.

Since Ware (1969) described three forms of *V. umbilicata* (f. *umbilicata*, f. *intermedia* (Dyal) Eggers and f. *patellaria* (Sull. ex A. Gray) Eggers), it was of interest to know if the forms exhibit differences in their germination behavior. As a part of a broader investigation of the germination ecology of weedy winter annuals, we have investigated certain aspects of the germination characteristics of *V. umbilicata* f. *patellaria* and f. *intermedia* seeds: (1) the effect of age and temperature on germination in light and darkness and (2) the effect of age, temperature and soil moisture on germination.

METHODS

Mature, dry seeds (one-seeded, indehiscent fruits) of f. *patellaria* and f. *intermedia* were collected on May 26, 1970 from a mixed population of plants growing in a meadow in Davidson Co., Tennessee. Seeds were cleaned, allowed to dry 5 days, and then those that were not used in the first experiments were stored in a closed jar in the laboratory (25 ± 2°C). Germination experiments were started on June 1, 1970, and the seeds were considered to be 0 months old at that time.

Age, temperature and light and darkness

Germination responses of seeds to temperature were determined in light (14-h photoperiod) and constant darkness when the seeds were 0, 1, 2, 3 and 4 months old. Germination tests were carried out in temperature- and light-controlled incubators at five constant temperatures (5, 10, 15, 20 and 25°C) and two alternating temperature regimes (30/16 and 23/12°C). All temperatures were ± 1°C. The 30/16 and 23/12°C alternating temperature regimes simulate the mean daily maximum and minimum monthly air temperatures during September and October, respectively, in middle Tennessee (U.S.D.C., 1965). During June, July and August seeds were incubated at an additional alternating temperature regime that simulated the mean daily maximum and minimum monthly air temperatures of each respective month in middle Tennessee: 31/17°C, June; 33/21°C, July; 33/20°C, August (U.S.D.C., 1965).

At the alternating temperature regimes, the high and low temperatures were maintained for 12 h each day. The photoperiod at all temperatures was 14 h, and at the alternating temperature regimes it extended from 1 h before the beginning of the high temperature period to 1 h after the beginning of the low temperature period. The light source was 20-W "cool white" fluorescent tubes, and light intensity at seed level was about 2,100 lux. To test seeds for germination

in constant darkness, Petri dishes containing the seeds were wrapped with Saran wrap to retard loss of water and then with aluminum foil to provide darkness.

Germination tests were performed in 10-cm Petri dishes on two sheets of Whatman No. 1 filter paper moistened initially with 5 ml of distilled water; more water was added as needed during an experiment to keep the filter paper and seeds moist. Three replications of 50 seeds each were used for each treatment, and seeds were considered to be germinated when the radicle emerged from the seed coat. At the 14-h photoperiod the seeds were examined at 5-day intervals for 30 days, and if any seeds had germinated they were counted and removed from the Petri dishes. Seeds that germinated in constant darkness were counted only at the end of 30 days.

Age, temperature and soil moisture

On June 1, 1970 four lots of 200 seeds each of f. *patellaria* and f. *intermedia* were planted on greenhouse potting soil in small flats in a non-temperature-controlled greenhouse. Soil in two flats of seeds of each form was watered daily and, thus, remained at or near field capacity during the experiment (wet soil). Soil in the other two flats of each form was watered to field capacity once each week (wet-dry soil) until September 1, 1970, after which time it was watered daily. The wet-dry treatments were given to simulate the wetting and drying that the surface layers of soil in the habitat undergo during summer. The flats were examined at approximately 1-week intervals, and if any seeds had germinated they were counted and removed. The experiment was terminated on December 19, 1970. Mean maximum and minimum weekly temperatures were calculated from continuous thermograph records in the greenhouse.

RESULTS

Age, temperature and light and darkness

Most of the freshly-harvested seeds (0 months old) of both forms were dormant, and there was little or no germination at any temperature in either light or darkness (Tables 1 and 2). During the summer seeds of both forms afterripened, and by September and October 62% or more of the seeds germinated when they were placed at September and October temperature regimes at the 14-h photoperiod (Table 1). As the seeds afterripened, there was an increase in rate of germination. When seeds were placed in light at the June, July, August, September and October temperature regimes at the beginning of each respective month there was a decrease in the number of days before germination began. In June, July and August 25, 10 and 5 days, respectively, elapsed before any seeds germinated, but in September and October some seeds already had germinated by the fifth day. The rate of germination each month was the same for seeds of both forms.

Constant temperatures inhibited germination, and the best germination at a constant temperature was in light at 15°C where 46.7% of the f. *intermedia* seeds germinated in October (Table 1). With the exception of 4-month old seeds of f. *intermedia*, constant darkness also greatly inhibited germination of afterripened seeds. Four-month old seeds of f. *intermedia* germinated to 68.7 and 40.0% at the September and October temperature regimes, respectively (Table 2).

Seeds of *V. umbilicata* germinate in the field in August, September and October; therefore, differences in germination responses of f. *intermedia* and f. *patellaria* seeds must occur during this period if they are to have any ecological meaning. When seeds were incubated at a 14-h photoperiod at the August, September and October temperatures in August, September and October, respectively, seeds of f. *intermedia* germinated to higher percentages than seeds of f. *patellaria* (Table 1). Germination of f. *intermedia* seeds was 8.0% higher than germination of f. *patellaria* seeds in August, 18.0% in September and 21.3% in October. When seeds were placed in darkness there was no germination at the August temperature regime in August, and at the September temperature regime in September only 4.0% of the f. *intermedia* and 0.7% of the f. *patellaria* seeds germinated (Table 2). In darkness at the October temperature regime in October, however, 40.0% of the f. *intermedia* seeds germinated but only 5.3% of the f. *patellaria* seeds germinated.

Age, temperature and soil moisture

The purpose of this experiment was to determine the role of temperature and soil moisture in controlling germination during summer. In June almost 100% of the seeds were innately dormant (Tables 1, 2), and none of the seeds germinated on either wet or wet-dry soil (Fig. 1). During the first 2 weeks of July, temperature was the most important factor controlling germination of afterripened seeds. That is, although some of the seeds were nondormant, only a very low percentage of them germinated even on wet soil. During the remainder of the summer, soil moisture was the most important factor controlling germination because seeds had afterripened and gained the ability to germinate at summer temperatures. By August 28, 30.5% of the f. *intermedia* and 41.8% of the f. *patellaria* seeds had germinated on wet soil while less than 2% of the seeds receiving wet-dry treatments had germinated.

Regardless of the summer soil moisture regime, final germination percentages of f. *intermedia* seeds were higher than those of f. *patellaria* seeds (Fig. 1). Since seeds on the soil surface in the natural habitat receive wet-dry treatments during summer, the most meaningful comparison of the forms is for seeds that also received wet-dry cycles during summer. For seeds receiving wet-dry treatments during summer, 81.5% of f. *intermedia* and 49.3% of the f. *patellaria* seeds germinated by the end of the germination season.

DISCUSSION

With the exception of a few winter annuals, such as *Helenium amarum* (Raf.) H. Rock, *Lactuca scariola* and *Gutierrezia dracunculoides*, that do not produce seeds until late summer or early autumn, winter annuals are in the drought resistant seed stage during summer. Summer dormancy in seeds of winter annuals is interpreted as an adaptation that allows the species to persist in habitats where soil moisture is insufficient for growth and survival of the plants during summer (e.g., Ratcliffe, 1961; Newman, 1963; Thompson, 1970; Baskin and Baskin, 1971; Hájková and Krekule, 1972; Janssen, 1974). Thus, to understand the life cycle strategy of winter annuals it is important to know why seeds do not germinate in summer, and why they do germinate in autumn.

Seeds of *V. umbilicata* do not germinate in June because they are dormant. As the seeds afterripen in June and early July they acquire the ability to germinate at low but not at high temperatures such as those that occur in the habitat in early July. Therefore, germination in the field in early July is prevented by high temperatures. With additional afterripening, the seeds gain the ability to germinate at normal field temperatures in late July and August, but very little, if any, germination occurs in the habitat. Germination appears to be prevented because seeds respond slowly to soil moisture and the soil surface in the habitat may stay wet for only 1-3 days following a shower. Seeds incubated at the July temperature regime during July did not begin to germinate until they had been moist for 10 days. Similarly, germination did not begin in August until the seeds had been moist for 5 days. In the greenhouse during late July and August seeds did not germinate in response to the 1-3 day period of apparently favorable soil moisture conditions for germination that followed each weekly watering. In other words, during late July and August the periods of favorable soil moisture are too short for seeds to germinate in the field. Germination occurs in the field in September and October because the periods of soil moisture favorable for germination become longer and the seeds have acquired the ability to germinate at their maximum rate.

In many species of winter annuals, such as *Silene secundiflora* Otth. (Thompson, 1970), *Arabidopsis thaliana* (Baskin and Baskin, 1972) and *Holosteum umbellatum* (Baskin and Baskin, 1973), the seeds never gain the ability to germinate at normal field temperaures in summer, although they will germinate at lower temperatures (e.g., 10 and 15°C). In these species temperature is the most important factor controlling germination, and germination is delayed until autumn when temperatures are no longer above those required for germination. By the time temperatures become nonlimiting, there is sufficient soil moisture and the seeds germinate. Newman (1963) found that seeds of the winter annuals *Aira praecox* L. and *Teesdalia nudicaulis* R. Br. could germinate at simulated field temperatures in summer, if they were kept moist for long periods of time. However, in the natural habitat essentially all of the germination in both species occurred in autumn, probably because the soil did not remain moist for long enough periods of time in the summer for germination to occur. In the winter annual *Alyssum alyssoides* germination in the field and at simulated summer field temperatures begins 2-3 days after the seeds are moistened (Baskin and Baskin, 1974). Rapid germination at field temperatures allows some seeds to germinate in the field when the soil is moist for brief periods in July and August. However, plants from summer-germinating seeds are killed by droughts during July and August, and all plants that survive to maturity are from autumn-germinating seeds.

The three forms of *V. umbilicata* can be distinguished on the basis of morphological characteristics of the fruits (Ware, 1969). The differences in germination responses of f. *intermedia* and f. *patellaria* seeds observed in this study indicate that the forms also may be distinguished on the basis of their physiological responses to environmental factors.

Valerianella umbilicata grows in habitats that are subjected to mowing and other forms of disturbance that could prevent development of a seed crop. In order for *V. umbilicata*, or any other winter annual, to persist in a given habitat, seeds have to germinate in that habitat each autumn. Differences in the germination responses of f. *intermedia* and f. *patellaria* seeds may play a role in the long-term persistence of *V. umbilicata* in a given area. Seeds of f. *patellaria* do not germinate as well as seeds of f. *intermedia* in either light or darkness in autumn (Tables 1, 2; Fig. 1), so there probably is a reserve of seeds in the soil at the end of each germination season. If there was a seed crop failure,some seeds would be present in the habitat the next autumn and seedlings could become established without immigration of seeds from another area. Since competition from other species of winter annuals is a factor that influences persistence in a habitat, success or failure in a habitat may depend partly on how many of the microsites suitable for winter annuals are filled with seedlings of *V. umbilicata*. The high percentages of germination of f. *intermedia* seeds in both light and darkness in autumn may help to assure a competitive position for the species in a habitat.

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TABLE 1: *Germination percentages of* Valerianella umbilicata, *f.* intermedia *and f.* patellaria *seeds after 30 days at a 14-hr. photoperiod.*

	0 months old (June)		1 month old (July)		2 months old (Aug.)		3 months old (Sept.)		4 months old (Oct.)	
Temp. (°C)	inter.	pat.	inter.	pat.	inter.	pat.	inter.	pat.	inter.	pat.
5	0.0	0.0	0.7	0.0	0.0	0.0	0.7	0.0	0.7	0.0
10	0.0	0.0	28.8	23.3	31.3	26.0	29.3	32.7	28.7	21.3
15	0.0	0.0	14.0	6.7	20.7	19.3	36.7	26.0	46.7	36.0
20	0.0	0.0	0.7	6.7	7.3	8.0	21.3	17.3	30.7	32.7
25	0.0	0.0	0.0	0.0	0.0	0.7	0.7	1.3	2.0	5.3
31/17 (June)	4.7	2.7								
33/21 (July)			15.3	20.0						
33/20 (Aug.)					70.7	62.7				
30/16 (Sept.)	0.7	0.0	8.0	24.0	56.7	59.3	94.0	76.0	90.0	86.0
23/12 (Oct.)	0.7	0.0	34.0	36.0	72.7	58.0	77.3	62.7	88.0	66.7

TABLE 2: *Germination percentages of* Valerianella umbilicata *f.* intermedia *and f.* patellaria *seeds after 30 days in constant darkness.*

	0 months old (June)		1 month old (July)		2 months old (Aug.)		3 months old (Sept.)		4 months old (Oct.)	
Temp. (°C)	inter.	pat.	inter.	pat.	inter.	pat.	inter.	pat.	inter.	pat.
5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0
10	0.0	0.0	6.7	4.0	3.3	1.3	6.0	3.3	18.0	0.0
15	0.0	0.0	2.0	3.3	0.0	0.0	16.0	1.3	8.7	0.7
20	0.0	0.0	0.7	0.0	5.3	0.7	1.3	0.7	6.0	2.0
25	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	2.7	0.0
31/17 (June)	0.0	0.0								
33/21 (July)			0.0	0.0						
33/20 (Aug.)					0.0	0.0				
30/16 (Sept.)	0.0	0.0	2.0	2.0	12.7	19.3	4.0	0.7	68.7	8.7
23/12 (Oct.)	0.0	0.0	1.3	4.0	17.3	4.7	6.7	1.3	40.0	5.3

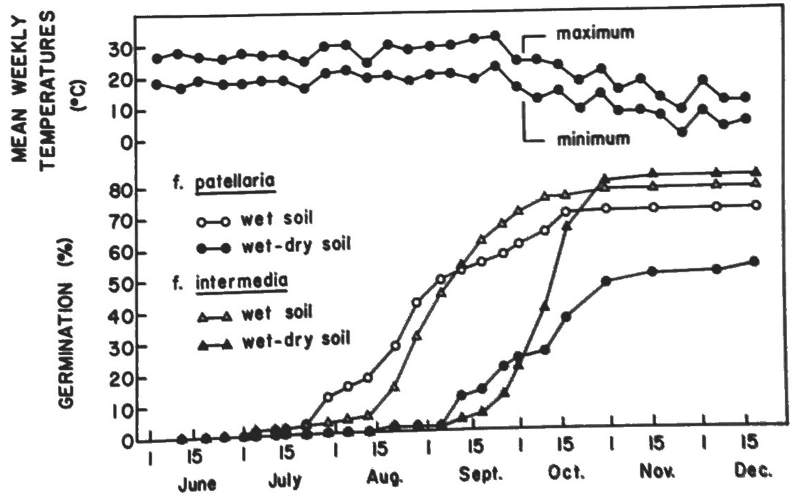

FIG. 1: *Germination of* V. umbilicata *f.* intermedia *and f.* patellaria *seeds in a non-temperature-controlled greenhouse during the summer and autumn of 1970.*