GERMINATION ECOLOGY OF WINTER ANNUALS: Valerianella umbilicata, F. patellaria AND F. intermedia
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ABSTRACT
The effect of age, temperature, light, 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 soil at simulated field temperatures, whereas 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 of both forms of F. intermedia germinate 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 and occasionally on roadsides in much of the eastern United States from New York to Ohio, Michigan and Illinois south to Alabama, Tennessee (Wilson, 1969). In central Tennessee the species is frequent in floodplains, although very few seeds are found in moist roadides and is commonly associated with Alliaceae/Compositae spp., Festuca elatior, Phleum pratense, Plantago lanceolate, Rumex crispus, Urtica dioica, Polygonum reptans and many species of winter annuals including Elytrigia repens, Arabidopsis thaliana, Bromus inermis, Galium aparine, Geranium carolinianum, G. spathulatum, Veronica anagallis-aquatica, Lithospermum arvense, Phacelia purshii, Valerianella locusta, radiata, Veronica arvensis and Viola rufaefolius. (Unidentified are given nomenclature follows Fernald, 1950.)

Germination experiments have been run with a few F. umbilicata seedlings in the field in mid August. Consistent with the germination in middle Tennessee occurs in mid to late September when soil moisture conditions are not limiting for completion of the life cycle. In dry autumns germination may occur but will not. This is because seeds germinate in early June-Mid July in field and laboratory. In the laboratory, seeds were started at temperatures higher than 25°C and were observed up to 12 months. Seeds which did not germinate were stored at -1°C for 2 months. Seeds which did not germinate were stored at -1°C for 2 months.

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 in either light or darkness (Tables 1 and 2). During the summer the seeds of both forms afterripened, and by September and October 65% 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 the rate of germination increased in rate of germination. When seeds were placed in light at the June, July, August and September temperature regimes at the beginning of each month there was a decrease in the number of days before germination began to decrease in September. The rate of germination in each month was the same for both forms of seeds. Constant temperatures inhibited germination, and the best temperature for germination was light at 15°C where 47.6% of the F. intermedia seeds germinated in October (Table 1). With the exception of the 4-h photoperiod, darkness also greatly inhibited germination of afterripened seeds. Four-month old seeds of F. intermedia germinated to 18.7% at 35°C, 47°C, 50°C, 55°C and 60°C in August and September temperature regimes, respectively (Table 2).

Germination of F. umbilicata germinate in the field in August and September. Therefore, differences in germination responses of F. umbilicata and F. patellaria seeds must occur during this period of the year. 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 those 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 21.0% 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 0.1% of the f. intermedia and 0.7% of the f. patellaria seeds germinated (Table 2). In darkness at the October temperature regime, 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 age, temperature and soil moisture in controlling germination during summer. In June almost 100% of the seeds were intact and not germinated. No seeds were germinated in either wet or 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 winter, soil moisture was the most important factor controlling germination because seeds stored 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 treatments had germinated.

DISCUSSION
With the exception of a few winter annuals, such as Helianthemum arenarium (Raf.), H. Rock, Lactuca scariola and Gutierrezia dracunculoides, that do not produce seeds until the autumn, the majority are in the drought resistant seed stage during summer. Summer dormancy in seeds of winter annuals is thought of 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., Ralston, 1963; Thompson, 1970; Baskin and Baskin, 1971; Häckel and Krecule, 1972; Jansen, 1974). Thus, to understand the process by which seeds do or do not germinate in summer, and why they do or do not germinate.
Seeds of *V. umbilicata* do not germinate in June because they are dormant. As the seeds afferiplen 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 afferiplen, the seeds gain the ability to germinate at normal field temperatures. In the field, 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* Orth. (Thompson, 1970), *Arabidopsis thaliana* (Baskin and Baskin, 1972) and *Holsotum umbellatum* (Baskin and Baskin, 1973), the seeds never gain the ability to germinate in normal field temperatures 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 non-limiting, there is sufficient soil moisture and the seeds germinate. Newman (1963) found that seeds of the winter annuals *Arca procer* L. and *Tecasaludicola* 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 *Alysum alpaeoides* 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 response of *L. intermedia* and *f. patellaris* seeds observed in this study indicate that the forms are also distinguished on the basis of their physiological responses to environmental factors.

**V. umbilicata** grows in habitats that are subjected to moving 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 *L. intermedia* and *f. patellaris* seeds may play a role in the long-term persistence of *V. umbilicata* in a given area. Seeds of *V. umbilicata* do not germinate as well as seeds of *L. 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 *L. intermedia* seeds in both light and darkness in autumn may help to assure a competitive position for the species in a habitat.

**LITERATURE CITED**


