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SEASONAL CHANGES IN THE GERMINATION RESPONSES OF BURIED SEEDS OF ARABIDOPSIS THALIANA AND ECOLOGICAL INTERPRETATION

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Buried seeds of *Arabidopsis thaliana* exposed to natural seasonal temperature changes exhibited an annual dormancy/nondormancy cycle. The majority of freshly matured seeds were dormant. During burial in summer, fresh seeds and those that had been buried for 1 and 2 yr afterripened. During afterripening, seeds first germinated at 15/6 C and then at progressively higher temperatures until they were nondormant by October, when they germinated to high percentages at all thermoperiods except 35/20 C. Light was required for germination of both conditionally dormant and nondormant seeds. During autumn and winter, seeds reentered dormancy, first losing the ability to germinate at high and then at low temperatures. Thus, seeds can germinate in the field only in autumn, and germination is restricted to those seeds on or near the soil surface where both light and moisture can be nonlimiting. In spring, seeds are dormant; in summer, temperatures are too high for germination, and in winter, they are too low. Consequently, *A. thaliana* behaves as a winter annual.

Introduction

Winter annuals are important weeds in temperate zones of the world, and many form large seed reserves (BRECHLEY 1918; BRECHLEY and WARRINGTON 1930; KROPÁČ 1966; ROBERTS and STOKES 1966; ROBERTS 1968). Seed reserves play an important role in the population dynamics of the species, and thus better weed-control measures in agroecosystems undoubtedly could be developed if we understood the regulation of the timing of germination.

The physiological responses of exhumed seeds that had been buried in soil and exposed to seasonal temperature changes have been studied for *Veronica hederifolia* L. (ROBERTS and LOCKETT 1978), *V. arvensis* L. (BASKIN and BASKIN 1983), *Lamium amplexicaule* L. (BASKIN and BASKIN 1981), and *Aphanes arvensis* L. (ROBERTS and NEILSON 1982a). Generally, seeds of these four species are dormant at maturity in late spring or early summer and give little or no germination at any temperature. However, during summer the seeds afterripen (become nondormant) and consequently germinate to high percentages over a wide range of temperatures in autumn. During the following autumn/winter cold season, seeds lose the ability to germinate at high (25/15, 30/15 C) but not at low (20/10, 15/6, and 10/4 C) temperatures, although percentages of germination at low temperatures are reduced. Since some seeds germinate at low temperatures, germination can occur in the field in early spring when other microenvironmental fac-

tors are nonlimiting. During summer, seeds become nondormant again, and the cycle of germination responses is repeated.

Since the seasonal changes in germination of exhumed seeds buried in soil for 1 yr or more have been studied in only a few species of winter annuals, the temporal, qualitative, and quantitative aspects of these changes have not been fully characterized. Thus, this study tests the temperature and light requirements for germination of exhumed seeds of *Arabidopsis thaliana* (L.) Heynh., buried in soil for 0-30 mo, and compares the pattern of seasonal changes in their germination responses to those reported for other weedy winter annuals.

Arabidopsis thaliana (Cruciferae) is a native of Europe and is now widely distributed in fields, roadsides, and waste places in the northern temperate regions of the world (RATCLIFFE 1961; GLEASON and CRONQUIST 1963). In central Tennessee and Kentucky, where we have observed the species, and in Great Britain where RATCLIFFE (1961) studied it, *A. thaliana* has a winter annual life cycle. However, both summer and winter annual races are reported in Europe (LAIBACH 1951). A high percentage of the freshly matured seeds of *A. thaliana* is dormant, and the seeds afterripen during summer in dry storage in the laboratory (RATCLIFFE 1961; BASKIN and BASKIN 1972a).

Methods

Mature, ripe seeds were collected from plants of *Arabidopsis thaliana* growing in cultivated fields in Fayette County, Kentucky (39°N, 84°30'W) on May 25, 1978, May 15, 1979, and May 21, 1980. Within 4-6 days after each collection, ca. 3,000 seeds were placed in each of 24, 29, and 22 fine-mesh nylon bags in 1978, 1979, and 1980, respectively. Each bag of seeds was buried 7 cm deep in

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soil in a 15-cm-diameter plastic pot with drainage holes, and the pots were placed in a non-temperature-controlled greenhouse (no heating or air conditioning and open windows all year). Mean daily maximum and minimum monthly greenhouse temperatures for the duration of the study were calculated from continuous thermograph records (table 1).

During each year, the soil in the pots containing seeds buried in 1978 and 1979 was watered to field capacity weekly from May 1 to August 31 and daily (except when frozen) from September 1 to April 30. These watering regimes simulated soil moisture conditions that could occur in the field. For seeds buried in 1980, 11 pots were watered to field capacity each day from May 27, when they were buried, until the last seeds were exhumed on April 1, 1981. The other 11 pots of seeds were watered to field capacity weekly from May 27 to August 31, 1980, and then daily (except when frozen) until April 1, 1981.

For each collection of seeds, germination tests were performed on freshly matured seeds. At monthly intervals thereafter, buried seeds were exhumed and tested until the supply of buried seeds for each burial date was exhausted. With the exception of 1980, when seeds were exhumed on June 29 and August 11, rather than on July 1 and August 1, seeds were exhumed on the first day of each month. Germination tests were carried out in light- and temperature-controlled incubators at a 14-h daily photoperiod and in continuous darkness at (12/12 h) alternating temperature regimes of 15/6, 20/10, 25/15, 30/15, and 35/20 C. These thermoperiods approximate the mean daily maximum and minimum monthly temperatures 2.5 cm below bare soil in north central Kentucky in spring, summer, and autumn (J. HILL, unpublished data): March, 15/6; April, 20/10; May, 25/15; June, 30/15; July

and August, 35/20; September, 30/15; October, 20/10; and November, 15/6 C. At each thermoperiod, the photoperiod extended from 1 h before the beginning to 1 h after the ending of the high-temperature period. The light source was 20-W cool white fluorescent tubes, and photon flux density at seed level was ca. $20 \mu\text{mol m}^{-2} \text{s}^{-1}$.

Seeds were incubated in 5.5-cm plastic petri dishes on clean quartz sand moistened with distilled water. For dark-incubated seeds, three replications of 50–75 seeds each were placed at each thermoperiod, and for light-incubated seeds, three replications of 50 seeds each were used. All dishes were wrapped with plastic film, and those containing seeds to be incubated in darkness also were wrapped with two layers of aluminum foil. All manipulations of dark-incubated seeds were done in total darkness, and seeds were not exposed to any light after they were buried until the germination tests were concluded. Seeds incubated in light were plated in fluorescent room light. Final germination percentages were determined after 15 days of incubation, and protrusion of the radicle was the criterion of germination. Standard errors were determined for all germination percentages, and both values were rounded to the nearest whole number.

Results

Seed viability was high throughout the study, and only an occasional dead seed was found. On November 1, 1979 (seeds buried in 1979) and on October 1, 1980 (seeds buried in 1980), seedlings were found when the bags of exhumed seeds were opened, but less than 1% of the seeds had germinated.

Seeds required light for high percentages of germination. Of the 385 germination tests performed in darkness, seeds germinated only in 43 (11.2%). Germination was greater than 10% in six (1.6%)

TABLE 1

MEAN DAILY MAXIMUM AND MINIMUM TEMPERATURES (C) IN THE NON-TEMPERATURE-CONTROLLED GREENHOUSE AT LEXINGTON, KENTUCKY

| MONTH | MAXIMUM | | | | MINIMUM | | | |
|-----------|---------|------|------|------|---------|------|------|------|
| | 1978 | 1979 | 1980 | 1981 | 1978 | 1979 | 1980 | 1981 |
| January | -.2 | .4 | 4.9 | 3.9 | -5.9 | -6.3 | -1.6 | -4.0 |
| February | 4.0 | 3.3 | 6.1 | 9.4 | -6.1 | -5.3 | -3.2 | .3 |
| March | 13.9 | 16.5 | 12.3 | 13.7 | 1.8 | 5.7 | 2.2 | 2.8 |
| April | 26.9 | 21.3 | 21.4 | 24.9 | 10.3 | 9.6 | 7.8 | 11.7 |
| May | 24.7 | 27.7 | 25.8 | 25.5 | 13.4 | 13.7 | 14.6 | 13.3 |
| June | 30.6 | 32.9 | 30.7 | 32.3 | 15.0 | 19.3 | 18.2 | 20.2 |
| July | 33.7 | 31.9 | 35.6 | 31.8 | 21.2 | 21.4 | 23.3 | 21.2 |
| August | 32.3 | 32.5 | 35.1 | 32.4 | 21.0 | 20.9 | 22.9 | 20.2 |
| September | 30.8 | 28.0 | 30.2 | 28.6 | 18.3 | 17.0 | 19.3 | 16.9 |
| October | 20.2 | 21.0 | 21.8 | 22.0 | 8.7 | 10.7 | 9.8 | 10.8 |
| November | 15.1 | 14.5 | 13.8 | 15.1 | 6.7 | 5.3 | 5.0 | 6.0 |
| December | 8.7 | 9.4 | 8.8 | 6.6 | 1.0 | .6 | 1.3 | -1.8 |

tests and greater than 15% in three (0.8%). The highest germination was 38% for seeds buried in 1979, exhumed on September 1, 1981, and tested at 20/10 C.

Data for seeds exhumed and tested in light show that, during each year of burial, seeds exhibited seasonal changes in their germination responses, passing from dormancy in spring to nondormancy by autumn and back into dormancy by late winter (figs. 1, 2). Whereas dormant seeds give little or no germination at any temperature, nondormant seeds germinate to high percentages over a wide range of temperatures. Most of the freshly matured seeds in 1978, 1979, and 1980 were dormant and germinated only at 15/6 C to 4%, 2%, and 28%, respectively.

During burial in summer, dormant seeds produced in the current year and those that had been buried for 1 and 2 yr afterripened. As this happened, seeds first germinated at 15/6 C and then at progressively higher temperatures until they germinated at 30/15 C. Seeds kept continuously wet during summer had the same afterripening pattern as those that were watered only once each week (fig. 2). Seeds were nondormant by autumn and

germinated to the highest percentages over the widest range of temperatures when exhumed in October (figs. 1, 2). During October and November, seeds lost the ability to germinate at 30/15 and 25/15 C, and during winter they first lost the ability to germinate at 20/10 and then at 15/6 C. In most cases, seeds were completely dormant when exhumed in January, but low percentages of those exhumed in February and March 1979 (fig. 1A) and February 1981 (fig. 2) germinated at 15/6 C. However, seeds in these lots were completely dormant and gave no germination when exhumed in April 1979 and March 1981, respectively.

Discussion

Seeds of *Arabidopsis thaliana* have been found with those of numerous other species of weeds in the buried seed pool of arable soils (ROBERTS 1968; JENSEN 1969; THOMPSON and GRIME 1979; ROBERTS and NEILSON 1981). Since exhumed seeds of *A. thaliana* required light to germinate, lack of germination during burial may be attributed to the continuous darkness of the burial environment. However, light is not the only requirement for germination of *A. thaliana* seeds, and whether an exhumed seed germinates on a moist, well-lighted soil surface depends on the dormancy state of the seed and habitat temperatures. Seeds exhumed in summer are in conditional dormancy and thus can germinate only at temperatures (15/6, 20/10 C) lower than those in the habitat. In autumn, seeds are nondormant and can germinate over a wide range of temperatures, including those in the field. Winter temperatures are too low for germination, and by spring, seeds have reentered dormancy.

The annual dormancy/nondormancy cycle of *A. thaliana* seeds is different from that of *Veronica hederifolia* (ROBERTS and LOCKETT 1978), *V. arvensis* (BASKIN and BASKIN 1983), *Lamium amplexicaule* (BASKIN and BASKIN 1981), and *Aphanes arvensis* (ROBERTS and NEILSON 1982a), in which seeds germinate in both autumn and spring. In these species, timing of germination determines type of life cycle: plants from seeds that germinate in autumn are winter annuals, and those from seeds that germinate in spring are summer annuals. Thus, *A. thaliana* behaves as a winter annual, whereas *V. hederifolia*, *V. arvensis*, *L. amplexicaule*, and *A. arvensis* behave as both winter and summer annuals.

One of the most obvious environmental factors related to the yearly dormancy/nondormancy cycle in buried seeds of *A. thaliana* is the pattern of seasonal temperature changes, i.e., high temperatures in summer and low in winter. In some species of winter annuals, dormant seeds afterripen at high (25, 30, 30/15, and 35/20 C) but not at low (4, 5, and 15/6 C) temperatures (BASKIN and BASKIN 1972b, 1976; ROBERTS and NEILSON 1982b).

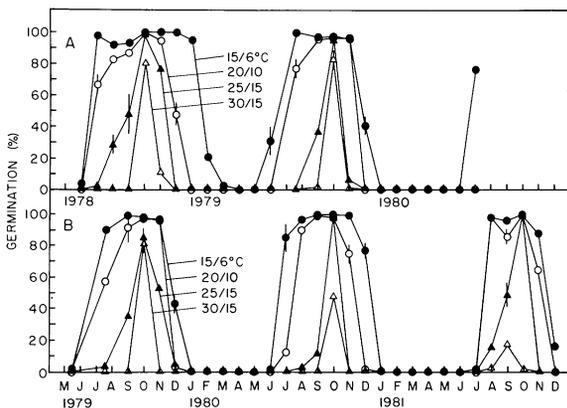


FIG. 1.—Germination percentages (\pm SE, when SE \geq 5%) of *Arabidopsis thaliana* seeds incubated at a 14-h photoperiod following 0–30 mo of burial. A, Seeds were buried on June 1, 1978. B, Seeds were buried on May 19, 1979.

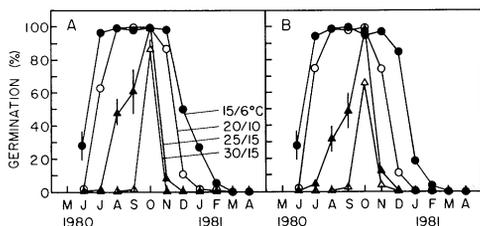


FIG. 2.—Germination percentages (\pm SE, when SE \geq 5%) of *Arabidopsis thaliana* seeds incubated at a 14-h photoperiod following 0–11 mo of burial. Seeds were buried on May 27, 1980. A, Soil was watered daily during summer. B, Soil was watered once each week during summer.

During burial, freshly matured seeds of *A. thaliana* and those that had been buried for 1 and 2 yr afterripened in summer when temperatures in the greenhouse were well within the range of those which promote afterripening in seeds of winter annuals (BASKIN and BASKIN 1972*b*, 1976; ROBERTS and NEILSON 1982*b*). In addition, nondormant seeds of some species of winter annuals reenter dormancy when they are exposed to natural low winter temperatures or to 4 or 5 C (BASKIN and BASKIN 1973, 1975, 1977, 1979; ROBERTS and NEILSON 1982*b*). In three of the six sets of data on autumn-winter induction of dormancy, seeds of *A. thaliana* gave no germination when exhumed in January, showing that they had entered dormancy between October and the end of December. In the other three sets of data, seeds were dormant by March or April. Temperatures in the greenhouse during autumn and winter were within the range of those (4, 5 C) that induce nondormant seeds of some species of winter annuals into dormancy

(BASKIN and BASKIN 1975, 1977, 1979; ROBERTS and NEILSON 1982*b*).

Although all seeds in our study eventually became completely dormant during the cold season, there may be field situations in which some seeds are not induced into dormancy and thus could germinate on the soil surface in spring. For example, seeds may not receive enough hours of exposure to the appropriate low temperatures for dormancy induction during mild winters or when buried deep in the soil. Further, we do not exclude the possibility that some populations of *A. thaliana* may exist in which some seeds are not induced into complete dormancy during the cold season, regardless of the number of hours they are exposed to low, inductive temperatures.

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