

Seed Germination  
Biology of the  
Weedy Biennial  
*Alliaria petiolata*

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**ABSTRACT:** Seeds of *Alliaria petiolata* were dormant at maturity and required cold stratification to come out of dormancy. In an unheated greenhouse, the germination peak for seeds sown in June 1986 occurred during the period February 11–18, 1987, when mean daily maximum and minimum temperatures were 8.1 and -1.0°C, respectively. Buried seeds that overwintered in the unheated greenhouse were nondormant when they were exhumed on February 1; 96–100% germinated in a daily light/dark (12/12 h) thermoperiod of 15/6°C. There was 99 and 94% germination success after 18 weeks on moist soil at 1 and 5°C, respectively, whereas seeds on sand germinated to 17 and 3%, respectively. Seeds cold stratified in darkness at 1°C for 16 weeks on soil germinated to a maximum of 48% in light (at 20/10°C) and to 60% in darkness (at 15/6°C), while none of those stratified on sand germinated in light or darkness. In the unheated greenhouse, 21–88 seedlings/m<sup>2</sup> appeared in soil samples collected from population sites after the first germination season following dispersal, while no seeds germinated in samples collected after two germination seasons. Although seeds in the soil samples germinated only the first spring after collection, seeds sown on soil in the nonheated greenhouse germinated the following four springs. In the field, plants from seeds in the seed bank died when allowed to compete with established rosettes, but 3% survived and set seeds when rosettes were removed.

### INTRODUCTION

*Alliaria petiolata* (M. Bieb.) Cavara & Grande (= *A. officinalis* Andr.) is a strict (obligate) biennial (sensu Kelly 1985) member of the Brassicaceae that was introduced into North America from Europe (Cavers et al. 1979). In Canada it occurs in gardens in Vancouver, British Columbia; in moist, shady sites in southern Ontario and Quebec (Scoggan 1978, Cavers et al. 1979); and in alluvial woods in New Brunswick (Hinds 1986). In the United States it grows in moist woods, fields, roadsides, and gardens from Vermont, Connecticut, and Massachusetts (Seymour 1969) south to North Carolina, Tennessee, and Arkansas (Al-Shehbaz 1988) and west to Missouri (Yatskievych and Turner 1990), Kansas, and North Dakota (Great Plains Flora Association 1986).

This weedy mustard is of great concern to managers of forested natural areas because it invades woodlands and displaces native herbaceous species (Cavers et al. 1979; Schwegman n.d.). It is a threat to the survival of herbaceous woodland species. Typically, *Alliaria petiolata* is first seen in a forest along trails or next to streams (Schwegman n.d.). If plants are not eradicated, the species spreads by seeds, and within a few generations a dense population may occur throughout the forest. In some shaded and semishaded natural areas, *A. petiolata* has become one of the most important species in the herb layer (Yost et al. 1991).

*Alliaria petiolata*, or garlic mustard, has been the subject of a number of studies including ones on control methodology (Nuzzo 1991), ecological life history (Trimbur 1973, Byers 1988), floral biology and breeding system (Babonjo et al. 1990), allelopathic properties (Kelley and Anderson 1990), acclimatization to irradiance levels (Anderson and Dhillon 1991), and some aspects of seed biology (Lhotska 1975, Kelley et al. 1991). Although seeds are dormant at maturity and require cold stratification to become nondormant (Lhotska 1975), little is known about the seed germination ecology of *A. petiolata*. The purposes of our study were to monitor germination phenology, investigate dormancy breaking and germination requirements, and determine if persistent seed banks (sensu Grime 1981) are formed.

### METHODS

#### Germination phenology

To determine when seeds would germinate if exposed to natural seasonal temperature changes, ripe seeds were collected from about 50 plants of *A. petiolata* growing in a mesic forest in Jessamine County, Kentucky, on June 17, 1986. Nine days later three replications of 300 seeds each were sown on the soil (3:1 v/v mixture of limestone-derived topsoil and river sand) surface in metal flats (6 dm<sup>2</sup> in area and 1 dm deep) and covered with 5 cm of dead oak leaves. The flats were placed under a bench

in a greenhouse in Lexington, Kentucky. This greenhouse had no heating or air-conditioning, and windows were kept open all year. Temperatures in the greenhouse were recorded with an electric thermograph. During each summer (May 1–August 31) of the study, soil in the flats was watered to field capacity once each week, and during the remainder of the year it was watered daily, unless frozen in winter. The flats were kept in the greenhouse until July 22, 1991, and at weekly intervals they were checked for germinated seeds. To do this, leaves were lifted, and all seedlings were counted and removed. Germination percentages and standard errors were calculated.

### **Dormancy break in the unheated greenhouse**

To determine when seeds exposed to natural seasonal temperature changes would lose their dormancy, seeds were collected from about 50 plants of *A. petiolata* growing in a small woodlot in Fayette County, Kentucky, on July 8, 1984. Two days later about 3000 seeds were placed in each of 24 fine-mesh nylon bags. The number of seeds per bag was determined by counting 1000 seeds into a pile, then using measuring spoons to approximate 3000 seeds per bag. Each bag was buried to a depth of 7 cm in soil in a 15-cm clay pot with drainage holes, and the pots were kept under benches in the greenhouse and watered as described above. Germination tests were done on freshly matured seeds and on those in a bag exhumed on the first day of each month until March 1, 1985, by which time nearly 100% of the buried seeds had already germinated. The study was terminated on this date.

Germination tests were conducted in five temperature- and light-controlled incubators at a 14-hr daily photoperiod (ca. 20 mol/m<sup>2</sup>/s, 400–700 nm of cool white fluorescent light) and in constant darkness at alternating temperature regimes (12/12 hr) of 15/6, 20/10, 25/15, 30/15, and 35/20°C. These temperatures approximate mean daily maximum and minimum monthly air temperatures in central Kentucky during the growing season (Hill 1976): March and November, 15/6°C; April and October, 20/10°C; May, 25/15°C; June and September, 30/15°C; and July and August, 35/20°C. In

each incubator, the photoperiod extended from 1 hr before to 1 hr after the high temperature period.

Seeds were incubated on quartz sand moistened with distilled water in 5.5 cm plastic Petri dishes. Three replications of 50–75 seeds each were incubated in darkness at each thermoperiod, and the dishes were wrapped with plastic film and two layers of aluminum foil. All manipulations of dark-incubated seeds were done in a completely darkened room; therefore, seeds incubated in darkness were not exposed to any light from the time they were buried until the end of a germination test. Three replications of 50 seeds each were incubated in light at each thermoperiod, and the seeds were counted using fluorescent room light. The dishes were wrapped with plastic wrap. Final germination percentages were determined after 15 days of incubation, and protrusion of the radicle was the criterion for germination. Standard errors were calculated for all germination percentages.

This study was repeated with seeds collected in Fayette County, Kentucky, on June 28, 1985. Seeds were buried on June 29 and were exhumed and tested on November 1 and December 1, 1985 and on January 1 and February 1, 1986. Nearly 100% of the seeds exhumed on March 1, 1986 had germinated, at which time the study was ended.

### **Cold stratification requirements for germination**

To determine (1) how much cold stratification was required to break dormancy and (2) if light was required during cold stratification and/or the incubation period at the test temperatures for seeds to germinate, studies were done on seeds collected on July 28, 1985; June 17, 1986; June 21, 1987; and July 16, 1988.

Seeds were collected in Jessamine County, Kentucky, on July 28, 1985, and the following day they were used in cold stratification experiments. Seeds were placed on moist sand in 5.5 cm plastic Petri dishes, and three replications of 50 seeds each were used for each treatment. Seeds incubated in light received a 14-h daily photoperiod of ca. 20 mole/m<sup>2</sup>/s (cool white fluorescent light) and

those in darkness were kept in continuous darkness for the stated period of time. All dishes were wrapped with plastic film, and those to be incubated in darkness were wrapped with two additional layers of aluminum foil. Seeds were given 0, 2, 4, 8, 10, and 12 weeks of cold stratification at a constant temperature of 5°C in light or constant darkness and then incubated in light or darkness, respectively (LL and DD), at 15/6, 20/10, 25/15, 30/15, and 35/20°C. Also, seeds stratified at 5°C for 12 weeks in light were incubated in darkness (LD) at the five thermoperiods, and seeds cold stratified at 5°C in darkness were incubated in light (DL) at each temperature. Germination percentages were determined after two weeks, and protrusion of the radicle was the criterion of germination.

Seeds were collected in Jessamine County, Kentucky, on June 17, 1986 and used three days later in stratification studies. They were placed on moist sand and stratified in darkness at 5 and at 1°C for 0, 4, 8, 12, and 16 weeks. After the stratification period, seeds were incubated in light at 15/6, 20/10, 25/15, 30/15, and 35/20°C (DL) for two weeks. Also, seeds were stratified in darkness at 5 and 1°C for 16 weeks and incubated in darkness (DD) at each of the five thermoperiods for two weeks.

Seeds were collected in Fayette County, Kentucky, on June 21, 1987 and used five days later. They were placed on moist sand and on moist soil at 5 and 1°C. At two-week intervals for 22 weeks, Petri dishes were opened and germinated seeds counted and removed. Seeds at 5°C received a 14-h daily photoperiod, and those at 1°C were in darkness. However, seeds at 1°C were exposed to fluorescent room light for about five minutes each time germination was checked.

Seeds were collected in Fayette County, Kentucky, on July 16, 1988 and used the following day. They were placed on moist sand and soil in darkness at 5 and 1°C for 0, 4, 8, 12, and 16 weeks and then incubated in light (DL) at 15/6, 20/10, 25/15, 30/15, and 35/20°C for 2 weeks. Also, seeds were stratified on both substrates at 5 and at 1°C in darkness for 16 weeks and then incubated in darkness (DD) at each thermoperiod for 2 weeks.

## Soil seed reserves at population sites

To determine if a species has a persistent seed bank, soil samples need to be collected in the field after the normal germination season has passed, but before freshly matured seeds are dispersed. However, the presence of viable seeds in the soil at the time of collection does not necessarily mean that they will live until the next germination season. Thus, we collected soil samples after germination and before seed dispersal, and they were kept in the unheated greenhouse through two springs.

Soil samples were collected from a woodlot population site of *A. petiolata* in Fayette County, Kentucky, on June 9, 1986 (12 samples); May 11, 1987 (6 samples); and May 9, 1988 (8 samples) and from a population site in Miami County, Ohio, on September 2, 1986 (9 samples). Samples collected on June 9, 1986; September 2, 1986; and May 9, 1988 were taken after one germination season had passed in the field but before additional seeds were produced. Samples collected on May 11, 1987 were taken after two germination seasons had passed but before additional seeds were produced. This was possible because no seeds of *A. petiolata* were observed to be produced at the Kentucky site in 1986. Each soil sample was 6 dm<sup>2</sup> (i.e., 2 x 3 dm) in area and 6 cm deep. Samples were lifted as intact as possible and fitted into flats and placed in the greenhouse, where they remained through two germination seasons. From May 1 to August 31 each year, the soil was watered to field capacity once each week, and from September 1 to April 30 it was watered daily, except when frozen in winter. Flats were examined weekly, and germinated seeds were counted and removed.

## Germination of reserve seeds in the field and survival of the plants

During a visit to an *A. petiolata* population in a woodlot on the University of Kentucky's Research Farm in Fayette County in March 1987, we observed that although the species did not produce seeds at this site in 1986, seedlings of *A. petiolata* were present. Also present were numerous second-year juveniles from seeds that germinated in 1986. Consequently, we (1) sampled this

Table 1. Cumulative germination percentages (mean  $\pm$  SE) of *Alliaria petiolata* seeds sown on soil in the unheated greenhouse on June 26, 1986. Mean daily maximum and minimum temperatures are given for each week during the germination seasons.

Week ending	Germination Percentage	Weekly Temperature ( $^{\circ}$ C)	
		Maximum	Minimum
11 Feb. 1987	0	6.8	-2.0
18 Feb. 1987	43 $\pm$ 2	8.1	-1.0
25 Feb. 1987	53 $\pm$ 5	12.5	2.1
4 Mar. 1987	60 $\pm$ 2	12.6	3.9
11 Mar. 1987	61 $\pm$ 2	16.0	2.8
18 Mar. 1987	61 $\pm$ 2	17.0	4.1
25 Mar. 1987	62 $\pm$ 2	21.4	6.4
11 Mar. 1988	62 $\pm$ 2	16.0	3.0
18 Mar. 1988	66 $\pm$ 2	8.5	1.0
25 Mar. 1988	66 $\pm$ 2	21.5	7.0
18 Mar. 1989	66 $\pm$ 2	19.6	5.7
25 Mar. 1989	66 $\pm$ 2	16.0	4.4
1 Apr. 1989	67 $\pm$ 2	22.0	12.7
4 Mar. 1990	67 $\pm$ 2	19.8	5.6
11 Mar. 1990	70 $\pm$ 2	12.5	2.3
18 Mar. 1990	70 $\pm$ 2	19.6	5.7
4 Mar. 1991	70 $\pm$ 2	12.7	6.5
11 Mar. 1991	70 $\pm$ 2	15.6	6.3
18 Mar. 1991	70 $\pm$ 2	16.0	9.3

small population to determine the density of newly germinated seedlings that were from seeds produced in 1985 or earlier and (2) studied the effects of the presence of second-year plants on survivorship of first-year plants.

One hundred and eleven 2-dm x 2-dm plots were marked off at 0.5-m intervals along 12 evenly spaced transects through the woodlot on March 20, 1987, and a loose wire ring was placed around each seedling. In 43 of the plots all second-year juveniles were removed, whereas in 68 of them second-year juveniles were not disturbed. All plots, except one, had 1-11 second-year juveniles; one plot had no juveniles. Juveniles were removed by gently pulling the roots out of the soil with one hand and holding the soil in place with the other hand. Thus, plants were removed with a minimum of soil disturbance. After juveniles were removed, no additional *A. petiolata* seeds

germinated. At about two-week intervals until May 19, 1988, survivorship of the 1987-germinated plants was determined in each plot.

## RESULTS

### Germination phenology

Seeds of *A. petiolata* sown on June 26, 1986 germinated only in February and March, and they germinated in the springs of 1987-1990 but not in 1991 (Table 1). The fate of ungerminated seeds in the flats was not determined. Most of the 626 (70%) seeds that germinated did so in 1987, but 43 (4%), 1 (0.1%), and 28 (3%) germinated in 1988, 1989, and 1990, respectively. In 1987 the peak of germination occurred between February 11 and 18, when mean maximum and minimum temperatures were 8.1 and -1.0 $^{\circ}$  C, respectively. In 1988, 1989, and 1990, germination occurred in March, and

Table 2. Germination percentages (mean  $\pm$  SE) of *Alliaria petiolata* seeds exhumed after various periods of burial in soil in the unheated greenhouse and incubated for 2 weeks in light (L) and darkness (D) over a range of thermoperiods.

	Date exhumed	Germ. in	Test Temperatures ( $^{\circ}$ C)				
			15/6	20/10	25/15	30/15	35/20
BURIED ON JULY 10, 1984	7-10-1984	L	0	0	0	1 $\pm$ 1	0
		D	0	0	0	0	0
	8-1-84	L	0	0	0	0	0
		D	0	0	0	0	0
	11-1-84	L	3 $\pm$ 1	0	0	0	0
		D	0	0	0	0	0
	12-1-84	L	0	0	0	0	0
		D	0	0	0	0	0
	1-1-85	L	0	0	0	0	0
		D	8 $\pm$ 4	2 $\pm$ 1	0	0	0
BURIED ON JULY 29, 1985	2-1-85	L	96 $\pm$ 0	47 $\pm$ 2	16 $\pm$ 6	20 $\pm$ 8	7 $\pm$ 2
		D	100	100	82 $\pm$ 4	57 $\pm$ 7	9 $\pm$ 2
	6-29-85	L	0	0	0	0	0
		D	0	0	0	0	0
	11-1-85	L	13 $\pm$ 5	2 $\pm$ 1	0	0	0
		D	0	0	0	0	0
	12-1-85	L	1 $\pm$ 1	0	0	0	0
		D	2 $\pm$ 1	1 $\pm$ 1	0	0	0
	1-1-86	L	1 $\pm$ 1	0	0	0	0
		D	1 $\pm$ 1	0	0	0	0
	2-1-86	L	100	82 $\pm$ 6	12 $\pm$ 8	9 $\pm$ 4	0
		D	99 $\pm$ 1	100	68 $\pm$ 11	23 $\pm$ 8	0

Table 3. Germination percentages (mean  $\pm$  SE) of *Alliaria petiolata* seeds cold stratified at 1 and 5 $^{\circ}$ C on moist sand and soil for 12 and 16 weeks. Strat. = stratification; subst. = substrate; L = light, D = darkness.

Strat. temp. ( $^{\circ}$ C)	Strat. time (wks)	Strat. subst.	Strat. in	Tested in	Test temps. ( $^{\circ}$ C)				
					15/6	20/10	25/15	30/15	35/20
1	12	sand	L	L	0	0	0	0	0
5	12	sand	L	L	0	0	0	0	0
1	16	sand	D	L	0	0	0	0	0
5	16	sand	D	L	0	0	0	0	0
1	16	sand	D	D	0	0	0	0	0
5	16	sand	D	D	0	0	0	0	0
1	12	soil	L	L	20 $\pm$ 3	23 $\pm$ 4	0	0	0
5	12	soil	L	L	22 $\pm$ 7	0	0	0	0
1	16	soil	D	L	46 $\pm$ 4	48 $\pm$ 10	45 $\pm$ 5	27 $\pm$ 4	20 $\pm$ 5
5	16	soil	D	L	11 $\pm$ 3	1 $\pm$ 1	0	0	0
1	16	soil	D	D	60 $\pm$ 10	57 $\pm$ 3	51 $\pm$ 6	35 $\pm$ 4	27 $\pm$ 1
5	16	soil	D	D	1 $\pm$ 1	1 $\pm$ 1	0	0	0

temperatures were higher than they were during the peak of germination in 1987.

#### Dormancy break in the unheated greenhouse

Seeds of *A. petiolata* buried in the greenhouse in July 1984 and June 1985 became nondormant during the subsequent January (Table 2). The optimum temperature for germination of nondormant seeds exhumed on February 1, 1985 and 1986 was 15/6 $^{\circ}$ C (March temperature), and 96-100% germinated in light and darkness at this thermoperiod. Germination percentages declined progressively with an increase in temperature, and seeds germinated at higher percentages in constant darkness than at the 14-h photoperiod.

#### Cold stratification requirements for germination

No germination occurred in seeds collected on July 28, 1985 and stratified at 5 $^{\circ}$ C on moist sand for 12 weeks in light or darkness, nor did it occur in seeds collected on July 17, 1986 and stratified at 1 and 5 $^{\circ}$ C on moist sand for 16 weeks in light or darkness.

Seeds collected on June 21, 1987 and placed on both sand and soil at 1 and 5 $^{\circ}$ C for 22 weeks began to germinate the 14th week; the last ones germinated the 18th week. Seeds on moist soil at 1 and 5 $^{\circ}$ C germinated to 99 and 94%, respectively, while those incubated on moist sand germinated to only 17 and 3%, respectively.

Seeds collected on July 16, 1988 and stratified on moist sand at 1 and 5 $^{\circ}$ C for 16 weeks and then transferred to the five thermoperiods failed to germinate, whereas those stratified on moist soil at 1 and 5 $^{\circ}$ C for 16 weeks germinated to a maximum of 60 and 11%, respectively (Table 3). The optimum thermoperiods for germination were 15/6 and 20/10 $^{\circ}$ C.

#### Soil seed reserves at population sites

Seeds germinated in three of the four sets of soil samples collected in the field (Table 4), and germination occurred only in the first spring following collection of the samples. Seeds germinated in the samples collected

Table 4. Number (mean  $\pm$  SE) of *Alliaria petiolata* seeds that germinated in soil samples collected from population sites and kept in an unheated greenhouse through two germination seasons.

Most recent year of seed production	Collection date	Number Germinated/m <sup>2</sup>	
		1st year	2nd year
1985	June 9, 1986	87.5 $\pm$ 22	0
1985	Sept. 2, 1986	22.2 $\pm$ 10	0
1985	May 11, 1987	0	0
1987	May 9, 1988	20.8 $\pm$ 12	0

after one germination season had passed (June 9, 1986; September 2, 1986; and May 9, 1988) but not in the samples collected after two germination seasons had passed (May 11, 1987).

### Germination of reserve seeds in the field and survival of the plants

On March 20, 1987, 6.5 $\pm$ 0.8 (mean  $\pm$  SE) seedlings/0.04 m<sup>2</sup> were present at the population site. In the 68 plots where the second-year juveniles were not disturbed, all of the 362 plants from seeds that germinated in March 1987 died without flowering, and in the 43 plots where the second-year juveniles were removed 11 of 364 (3%) plants survived to reproduction.

## DISCUSSION

As in the studies of Lhotska (1975) in Czechoslovakia, seeds of *A. petiolata* from Kentucky were dormant at maturity and required cold stratification before they would germinate (Tables 2 and 3). Seeds came out of dormancy in the unheated greenhouse and at 1 and 5°C, which is not surprising since in Lhotska's (1975) studies dormancy was broken at 3–5°C and at 4–6°C. What we did not expect to find in *A. petiolata* was a substrate effect on after-ripening (dormancy loss) of the seeds. That is, at both 1 and 5°C, *A. petiolata* seeds after-ripened when placed on soil, but they failed to do so on sand. The fact that seeds buried in nylon bags in soil until February germinated on sand in the incubators (Table 2) indicates that the failure of seeds to germinate when stratified on sand is the result of a lack of after-ripening and not germination inhibition per se. Perhaps the seeds placed on moist sand were not ade-

quately hydrated for after-ripening to occur. Seeds of *Campanula americana* L. also after-ripened (and germinated) to higher percentages on soil than on sand (Baskin and Baskin 1984). Seeds of *A. petiolata* placed in nylon bags in a variety of natural habitats in Ontario from September until the following June did not after-ripen on sandy soil or while submerged in a river. However, about half the seeds placed on moist organic soil lost viability by June, indicating that they after-ripened, germinated, and then the seedlings died in the bag (Cavers et al. 1979). Interestingly, Byers (1988) obtained about 80% germination for *A. petiolata* seeds cold stratified at 4°C for 100 days on Rochester blue-gray seed germination blotter paper.

The stratification requirement for dormancy loss in seeds of *A. petiolata* is noteworthy because seeds of many species of Brassicaceae in eastern North America, including the genera *Alyssum*, *Arabidopsis*, *Draba*, *Leavenworthia*, *Lepidium*, *Lesquerella*, and *Thlaspi*, require high summer temperatures to come out of dormancy (Baskin and Baskin 1988). However, seeds of two other members of this family, *Dentaria laciniata* Muhl. ex Willd. (Baskin and Baskin unpubl. data) and *Arabis laevigata* (Muhl. ex Willd.) Poir. (Bloom et al. 1990) require cold stratification to come out of dormancy. In nature, seeds of *A. petiolata* are stratified during winter, and consequently they are nondormant in spring. By March 1 during the winters of 1984–85 and 1985–86, seeds in the unheated greenhouse received 1269 and 1452 hours, respectively, of exposure to temperatures between 0.5 and 10°C — the effective range for low temperature stratification of seeds (Crock-er and Barton 1957). Although stratifying

temperatures in the greenhouse in 1984–85 and 1985–86 were equal to only 7.5 and 8.6 weeks, respectively, of continuous stratification in the laboratory, seeds germinated to higher percentages (Table 1) over the range of thermoperiods than those stratified on soil at 1 and 5°C for 16 weeks (Table 3). The only explanation that we can offer for these differences is that seeds of *A. petiolata*, like those of a few other species, after-ripen better at fluctuating low than at constant low temperatures (Flemion 1933).

After seeds become nondormant, they can germinate at low temperatures. The peak of germination in the unheated greenhouse in 1987 occurred when mean daily maximum temperatures were 8.1 and -1.0°C, respectively, and the seeds kept at 1 and 5°C germinated to 99 and 94%, respectively, after 18 weeks. The ecological implication of nondormant seeds germinating at low temperatures is that germination occurs in the field in late winter and/or early spring. Consequently, seedlings become established before canopy closure and onset of summer drought. Seeds of *A. petiolata* germinated in January to March in England (Roberts and Boddrell 1983), in February to March in south-central Illinois (Kelley et al. 1991), in March to April in Czechoslovakia (Lhotska 1975), and in late-March to mid-April in southern Ontario (Cavers et al. 1979).

When soil samples were collected from *A. petiolata* population sites one year after seed dispersal, germination occurred the first but not the second spring in the greenhouse (Table 4). Further, when samples were collected two years (May 11, 1987) after seed dispersal (and before any 1987 seeds were dispersed), no seeds germinated the first spring in the greenhouse. In a study by Roberts and Boddrell (1983), 19.5–55.4% of the *A. petiolata* seeds sown in summer or autumn germinated the following (first) spring; 1.4–24.1% germinated the second spring; and only 0.1–1.5% germinated the third, fourth, and fifth springs. Similarly, most of the seeds sown in the unheated greenhouse that germinated did so the following spring, and only a few germinated the second, third, and fourth years (Table 1). Thus, *A. petiolata* has the ability to form small seed banks, but a reserve of seeds does not persist for long





Figure 1. *Alliaria petiolata* population in a woodlot on the University of Kentucky's Research Farm in Fayette County, Kentucky. (a) Photograph taken on June 9, 1986, in a year when no plants in the population flowered. (b) Photograph taken on May 11, 1987, in a year when all plants flowered.

periods of time. In view of the high germination percentages of nondormant seeds in darkness at 15/6°C (Table 2) and in pots of soil in the greenhouse, it is not surprising that *A. petiolata* does not form large, long-lived persistent seed banks. Presumably, seeds that fail to germinate the first spring following dispersal did not after-ripen during winter. Substrate, temperature, and light/dark conditions in mesic woodlands should

not inhibit germination of nondormant seeds of this species.

The significance of *A. petiolata* seed banks depends on what is happening at a population site. In the woodlot on the University of Kentucky's Research Farm, where we have observed the species for a number of years, it has flowered only in alternate years (Figure 1). Our data from seedling survival

studies show that the plants from seeds that germinate the second spring after dispersal (i.e., seed bank seeds), when second-year rosettes are present, have little, or no, chance for survival. Of course, little, or no seedling survival in years when rosette density is high helps to explain how a population could develop a two-year flowering cycle. However, at sites where populations are becoming established or where management techniques have removed juveniles and/or adults, plants from seeds in the seed bank would have little or no competition from already established plants of *A. petiolata*. Consequently, they would be able to survive, flower, produce seeds, and perpetuate the population. Thus, even a few seeds left in the soil have the potential to result in a reinfestation of a natural area.

There is no known way to kill seeds of *A. petiolata* in the soil at a site without killing those of other species. Thus, the only method to safely remove *A. petiolata* from a site is to kill the plants after the seeds have germinated. The formation of seed banks by *A. petiolata* makes management of the species a more difficult job than it would be if all seeds either germinated or died the first spring following dispersal. The eradication of *A. petiolata* from a site requires the removal of plants prior to seed set for a period of at least three to four years. However, there may be sites where removal for three to four years may not be sufficient to completely eradicate the species. It seems possible that seeds could live in the soil for longer than three to four years, and seeds may be brought in from other contaminated areas. Thus, control of *A. petiolata* in some natural areas may require search and destroy operations every year into the foreseeable future.

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