Demographic Variation in Alliaria petiolata (Brassicaceae) in Four Contrasting Habitats

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BYERS, D. L. AND J. A. QUINN (Department of Ecology, Evolution, and Natural Resources, Rutgers University, New Brunswick, NJ, USA 08903-0231). Demographic variation in *Alliaria petiolata* (Brassicaceae) in four contrasting habitats. J. Torrey Bot. Soc. 125:138–149. 1998—The expansion of *Alliaria petiolata* into a broad range of habitats in New Jersey was examined by comparing demographic and reproductive characteristics in four habitats that differed in availability of moisture and light. Plants behaved as strict biennials in all sites in all years. Survivorship, seed weight, and seed germination were lower in the drier habitats. The timing of flowering was later (1–2 weeks) in the drier habitats, although it did not appear to affect fruit maturation (as estimated by fruit abortion) which occurred during the drier months in all sites. Fecundity as measured by seeds/fruit and fruit production significantly differed among the populations although seeds/plant did not differ. Fruit abortion, which differed among the populations and among years, may be most influenced by environmental fluctuations rather than any characteristics intrinsic to the sites. The allocation of resources (biomass) to reproduction was greatest in the most disturbed site. A common garden experiment using seedlings from the two most contrasting sites suggested that variation in most traits (flowering phenology and resource allocation) was primarily a response to the environment. However, survivorship was more affected by seedling origin. This research suggests that *A. petiolata* responds to the broad range of habitats primarily by phenotypic plasticity. While *A. petiolata* had lower survivorship in the drier habitats, its phenotypic variation in demographic and reproductive characteristics may have allowed successful range expansion.

Key words: *Alliaria petiolata*, invasive species, demography, populations, phenotypic plasticity.

A significant proportion of the present flora in many locations of the world is not native to that location (Baker 1974; Loope and Mueller-Dombois 1989; MacDonald et al. 1989; Yost et al. 1991; Robinson et al. 1994). *Alliaria petiolata* (Bieb.) Cavara & Grande, a biennial of European origin, is an exotic of increasing concern because of its geographic expansion in the United States and the expanded range of habitats in which it has a demonstrated negative impact on the indigenous community (Nuzzo 1991; Yost et al. 1991; Schwegman n.d.; Baskin and Baskin 1992; Anderson et al. 1996; McCarthy 1997). *Alliaria petiolata* was first recorded in North America in 1868 on Long Island, New York. By the 1930s, it was found throughout the northeastern states, eastern Canada, and in a few areas

in the northern midwestern states (Nuzzo 1993). By the 1970s and 1990s it was found commonly throughout the northeastern states, eastern Canada, and the midwest, and also found in Oregon and Utah (Nuzzo 1993). *Alliaria petiolata* has historically been found mostly in shaded moist areas such as in or adjacent to floodplain forests, although more recently it can be found in drier sites, some with full sun, and in a range of sites associated with disturbance (Cavers et al. 1979; Nuzzo 1993). In the northeastern United States, *A. petiolata* most frequently occurs in floodplains while in the Midwest it most frequently occurs in upland woodlands (Nuzzo 1993). Until relatively recently in New Jersey, *A. petiolata* was primarily associated with shaded river floodplain sites along the Delaware and Raritan rivers (H. Buell pers. comm.). Most populations appear to be associated with some degree of disturbance (Byers per. obs.); therefore, the increase in numbers of populations of *A. petiolata* may be associated with the extensive and frequent disturbances in natural areas in northeastern United States (Robinson et al. 1994).

Non-native species often colonize habitats opened by human disturbance and may initially exhibit rapid population growth rates, having left behind their natural competitors, predators, parasites, and pathogens (Baker 1974; Mack 1985). Many non-native species that become in-

vasive have the characteristics associated with weeds. The definition of a weed can be very broad. For this paper we will focus on the characteristics associated with weeds that may facilitate the expansion of non-native species. Baker (1965) characterized the "ideal" weed as having broad germination requirements, generalized pollinators, and a wide environmental tolerance (see also Harper 1977; Barrett 1992). The "ideal" weed is also self-compatible, has a short lifespan, is highly plastic in growth, and can produce large numbers of seeds. In addition, seed banks are important for invasive species and may serve as a reservoir of genotypes (Templeton and Levin 1979). In some cases, non-native species compete more successfully for available resources than native species, thus changing the community's composition (e.g., Mack 1985; Vitousek and Walker 1989; Hester 1991; Nuzzo 1993).

Many invasive non-native species occur in a diverse range of habitats. Species which occur in a wide range of habitats have been found to have significant demographic differences among populations (Law et al. 1977; Angevine 1983; Van Der Aart 1985; Matlack 1987). For example, populations at the margins of a species' range may show a decrease in reproductive success compared to other populations (Antonovics 1976). Different selection pressures specific to each population may create populations with individualistic responses to their unique environments (Bradshaw 1972; Quinn 1987). The variation in selection pressure may lead to genetic differences and/or a plastic response among the habitat types (Bradshaw 1972; Via et al. 1995).

Variation in timing of reproduction in some monocarpic species has been found to be highly plastic in response to environmental variation (Werner 1975; Kelly 1985). In these species the size of the vegetative rosette rather than age was found to be a better predictor of probability of flowering (Werner 1975; Gross 1981), while in other species, age determined the timing of flowering (Kelly 1985). Flexibility in the timing of flowering may allow a species to colonize a wider range of habitats.

Considering these aspects associated with invasive species, *A. petiolata* was studied to examine what traits may have contributed to its success. *Alliaria petiolata* is green through the winter and begins rapid growth very early in the spring (March in New Jersey). Therefore, it is a likely competitor with spring ephemerals and of concern for the preservation of native species

(Yost et al. 1991, Baskin and Baskin 1992; Schwegman n.d.; Anderson et al. 1996). The extent that *A. petiolata* can invade an undisturbed woodland and outcompete native vegetation is unclear since populations are usually associated with disturbance (Nuzzo 1991; Byers pers. obs.; but see Anderson et al. 1996; McCarthy 1997). However, in a wooded floodplain with a dense cover of *A. petiolata*, the diversity of herbaceous vegetation increased after removal of *A. petiolata* (McCarthy, 1997). *A. petiolata* is self-compatible and if the flowers are not visited by pollinators they will self upon wilting (Cruden et al. 1996); therefore one isolated individual can begin a population.

A. petiolata in other areas of its range in North America has been found to be a strict biennial (southern Ontario, Cavers et al. 1979; northern Illinois, Nuzzo 1991; Kentucky, Baskin and Baskin 1992; central Illinois, Anderson et al. 1996). However, life history can differ across a species' range or habitat types (Kelly 1985). In England, *A. petiolata* is a winter-annual or a monocarpic perennial (Grime et al. 1988).

In order to more fully understand the population dynamics of *A. petiolata* in differing habitats, a demographic study of *A. petiolata* was conducted in a representative range of habitats in New Jersey. The study was designed to address the following questions: 1) How unique are the different habitats for *A. petiolata* in terms of nutrients and soil characteristics? 2) Does the relative success of *A. petiolata* as determined by survivorship, resource allocation, and seed and reproductive traits differ among the habitats? 3) Does the size of the winter rosettes determine the timing or quantity of sexual reproduction? 4) Given possible demographic and reproductive differences among the populations, is there any evidence for genetic differences between the populations or is the variation environmentally induced? This information will add to our basic understanding of successful weeds as well as provide insights that may facilitate management or control of *A. petiolata*.

Materials and Methods. STUDY SITES. *Light, Water, and Flora.* This study was conducted in four sites which were chosen for their differences in the availability of light and moisture and are representative of the range of habitats for *Alliaria petiolata* in New Jersey. The Floodplain site (FLP) was located in Piscataway, along the Raritan River. The Floodplain site represents habitat typical of the initial sites colo-

nized by *A. petiolata* and is typical of its' European habitat. This area was flooded at least several times (often submersing the plants for days) in most years and had usually significantly more moisture available to the plants throughout the year as determined using the gravimetric method (Byers 1988). The canopy trees (*Acer saccharinum* and *Fraxinus* spp.) produced a dense shade after leafing out, which resulted in significantly less light than in the other sites (0.71% of full sunlight using a Li-cor Inc. photometer, Byers 1988). Percentage cover of *A. petiolata*, sampled in twelve 0.25 m² quadrats monthly, ranged from 15 to 75% over the year with a density up to 132 flowering plants/m². Other herbaceous species present included *Geum virginianum, Glechoma hederacea* and *Impatiens capensis.*

Two upland forest sites, Hutcheson Memorial Forest (HMF) in Franklin Township and Kilmer Woods (KW) in Piscataway were chosen to represent a drier habitat with a forest canopy. Hutcheson Memorial Forest was a mature upland forest, and the canopy trees (*Quercus alba, Q. rubra,* and *Carya* spp.) produced a moderate level of shade (3.7% of full sunlight) in relation to the other sites (Byers 1988). The moisture available at the Hutcheson Memorial Forest site was at times higher than the Floodplain site due to the higher organic matter in the soil (20.7%, see results below). *Alliaria petiolata* varied in cover from 5 to 65% throughout the year (Byers 1988). Additional herbaceous species and woody vines present included *Podophyllum peltatum, Smilacina racemosa,* and *Parthenocissus quinquefolia.* In the Kilmer Woods site there was a slightly greater availability of light (5 to 9% of full sunlight, Byers 1988). Moisture at the Kilmer Woods site was similar to Hutcheson Memorial Forest, but somewhat drier during the summer months. The vegetation cover of *A. petiolata* varied from 10 to 75% over the year. The herbaceous species and woody vines in this site present included *Podophyllum peltatum, Eupatorium rugosum,* and *Parthenocissus quinquefolia.*

The fourth site (RR) was an old railroad bed located on the Livingston Campus of Rutgers University. The canopy trees (*Ailanthus altissima*) cast significantly less shade (24.4% of full sunlight) than trees at the other sites (Byers 1988). This site also had significantly less available moisture (Byers 1988). The density of *A. petiolata* was greatest in this site with up to 500 flowering plants/m², and the cover ranged from 25 to 95% throughout the year. Woody vines present at the site included *Rhus radicans* and *Lonicera japonica.*

Soil Characteristics. Four randomly chosen soil samples from the top 5 cm were collected from each site and air dried. Analyses of nutrients, texture, and percentage organic matter were done by the Rutgers University Soils Lab. Analyses for Mg, P, K, and Ca were conducted by a dilute acid technique. Nitrogen was analyzed as the total percentage nitrogen. Texture analysis was done using the hydrometer method, and organic matter content was determined by a calculation of the weight lost during ignition. Principal component analysis (PCA) was used to determine if the sites were unique and what soil traits distinguished the sites.

DEMOGRAPHIC CHARACTERISTICS. In February 1985, in each of the four sites, 12 randomly chosen 0.25 m² quadrats were established, and all rosettes were marked with plastic toothpicks. Seedlings were marked in March–April 1985 and 1986 by inserting small pieces of plastic coated wire next to each individual. The seedlings were easily identified by the persistence of cotyledons. Due to the high rate of mortality among the seedlings in the spring of 1986, an additional three quadrats per site were established to increase the sample size of flowering individuals. Survivorship in the quadrats was followed biweekly until all marked plants died in the summer of 1987. During the 1986–1987 census only the overall winter (November–February) mortality rate was recorded as opposed to the biweekly sampling. Kolmogorov Smirnov analysis was used to determine if survivorship differed among the sites (Sokal and Rohlf 1981).

To quantify flowering phenology, the number of receptive flowers was counted weekly at each site. In 1986, 20 randomly chosen plants per population were used for the flowering phenology; in 1987, 50 randomly chosen plants per population were used, except in the Railroad site where 20 randomly chosen plants were used (due to the destruction of most of the site—see below). These plants were also used for quantifying fruit abortion by counting the number of initiated fruits and matured fruits. The number of fruits and number of seeds/fruit (10 randomly chosen fruits/individual) were counted for all flowering plants in the quadrats in 1985 and 1986. Repeated measures analysis and profile comparison were used to determine if the timing of flowering differed among the populations

(SAS 1992). An analysis of variance (ANOVA) and a Duncan's multiple comparison test were used for comparing fruit and seed production and fruit abortion among the sites and rosette sizes (Sokal and Rolf 1981). A subset of these seeds was utilized for seed weight analysis and germination tests (see below).

The allocation of resources was determined by biomass measurement. After the seeds matured, but before the fruits opened in June 1985, plants were randomly chosen from each population (40 plants from KW, 60 from FLP, and 50 from each of HMF and RR). The plants were divided into the following three components: inflorescences (racemes) with fruits and seeds, stems and leaves, and roots. All parts were oven-dried at 80°C. Variation in resource allocation was analyzed using multivariate analysis of variance (MANOVA; SAS 1992).

Seed quality was determined by both weight and germination. In 1985 and 1986, the seeds were collected by maternal sibship families (seeds from one plant) from 20 randomly chosen plants in each population. In 1985 seeds were weighed in lots of ten; in 1986, seeds were weighed separately. Preliminary studies (Byers 1988) indicated the following methods to be optimal for germination of *A. petiolata*. The seeds were rinsed with a 1% sodium hydrochloride solution (for sterilization) and then rinsed several times with distilled water. After moist cold treatments of 100 days, the seeds were placed in a Model G-30 germinator (Controlled Environments, Inc.) at 10/20°C with a 12/12 hour dark/light cycle for 2 wk. A seed was considered to be germinated when the radical and both cotyledons had emerged from the seed coat. Seeds which did not germinate during the 2-wk period were tested with tetrazolium chloride for viability. For both seed weight and germination, seeds were identified by family for analysis by ANOVA and Duncan's multiple comparison tests (Sokal and Rolf 1981).

In order to quantify seed availability in each site before germination and seeds remaining in the seed bank, 25 soil samples of 5.5 cm diameter and 10 cm depth were collected from all of the field sites before (early February) and after (early May) germination in 1986. Germination in these sites began in late February and continued until late March. Each sample was divided into an upper and a lower 5 cm. Samples were washed sequentially through 2.38 and 0.59 mm mesh sieves, and the remaining material was carefully examined for seeds. The variation in seed bank was analyzed using ANOVA and Duncan tests (Sokal and Rolf 1981).

To determine if *Alliaria petiolata* behaved as a winter annual, a strict biennial, and/or a facultative biennial (monocarpic perennial) in New Jersey, survivorship and reproduction in relation to size or age of the plants were examined in the different sites. This was accomplished by classifying all rosettes as to size in February 1985 using the sum of the width of all leaves (small < 10 cm, medium 10 to 20 cm, large > 20 cm). Earlier work determined that width of the leaves in the winter was significantly correlated with both leaf area ($R^2 = 0.73$, $P < 0.0001$) and aboveground biomass ($R^2 = 0.53$, $P < 0.0001$) in the winter (Byers 1988). These size categories were chosen from natural breaks in the data from 100 plants from another floodplain (Byers 1988). In 1987, to more precisely examine the relationship between size and reproduction, the size (leaf width in February) was measured using 50 randomly chosen plants per site (within the demography quadrats) without putting individuals into size categories. To quantify the effect of rosette size on number of flowering days, seeds/fruit, fruit maturation, and fruit abortion, a multiple regression analysis was used. Population was included in this analysis as a dummy variable with the comparison to the Floodplain population (Neter et al. 1989).

COMMON GARDEN. To determine if life history variation was due to genetic differences between the populations or to environmentally-induced variation, the two most contrasting sites in terms of moisture and light availability, the Floodplain and the Railroad, were used. Seedlings with only cotyledons at the Floodplain and Railroad sites were dug up in April 1986 and placed in flats of vermiculite. The next day these plants were transplanted to both the Floodplain and Railroad sites in four 0.25 m² quadrats of 81 evenly spaced plants, where the existing vegetation was disturbed as little as possible. Each quadrat had 40 plants from each population plus an extra one from one population. Plants were randomly located within each quadrat. These plants were monitored for survivorship, flower phenology, fruit and seed production, fruit abortion, and resource allocation (measured as dry weight). A Kolmogorov-Smirnov test was used to compare survivorship between seedling source populations (Sokal and Rolf 1981). Flower phenology was compared using a repeated measures analysis with profile comparisons (SAS 1992). Fruit

Table 1. Soil nutrients, pH, soil texture, and percentage organic matter (% OM) in the four field sites. Nitrogen was measured as the total percentage nitrogen. All other nutrients were measured in parts per million. The field sites are Floodplain (FLP), Hutcheson Memorial Forest (HMF), Kilmer Woods (KW), and Railroad (RR).

Site	Mg	P	K	Ca	N	pH	% sand	% silt	% clay	% OM
FLP	247	36	245	1920	0.111	5.9	34.5	46.5	19.0	8.62
HMF	81	23	121	1106	0.416	5.5	45.5	41.0	13.5	20.67
KW	98	37	163	910	0.109	5.3	48.5	37.0	14.5	18.46
RR	247	158	245	1920	0.045	6.5	64.5	21.5	14.0	7.54

and seed traits were analyzed with ANOVA and resource allocation with MANOVA (SAS 1992). Influence of rosette size on reproduction was analyzed using a multiple regression (SAS 1992). Unfortunately, before substantial data could be collected from the Railroad site the study area was destroyed by a bulldozer; therefore only data from the Floodplain site are presented.

Results. SOIL CHARACTERISTICS. Soil nutrients, texture, pH, and organic matter clearly distinguished the FLP and RR sites from each other and from the two upland forest sites (HMF and KW) as shown by the PCA (Table 1 and Fig. 1).

All of the soil characteristics significantly contributed to the first and/or second principal component. The first and second components explain 52.7% and 26.2% of the variation among the samples respectively. For the first component phosphorus (Pearson correlation coefficient $= 0.96$, $P < 0.0001$), pH ($r = 0.89$, $P < 0.0001$), calcium ($r = 0.84$, $P < 0.0001$), % silt ($r = -0.79$, $P < 0.0003$), potassium ($r = 0.78$, $P < 0.0004$), magnesium ($r = 0.74$, $P < 0.001$), % sand ($r = 0.69$, $P < 0.0029$), and % organic matter ($r = -0.64$, $P < 0.0077$) were significant, while for the second component % clay ($r = -0.83$, $P < 0.0001$), % sand ($r = 0.69$, $P <$
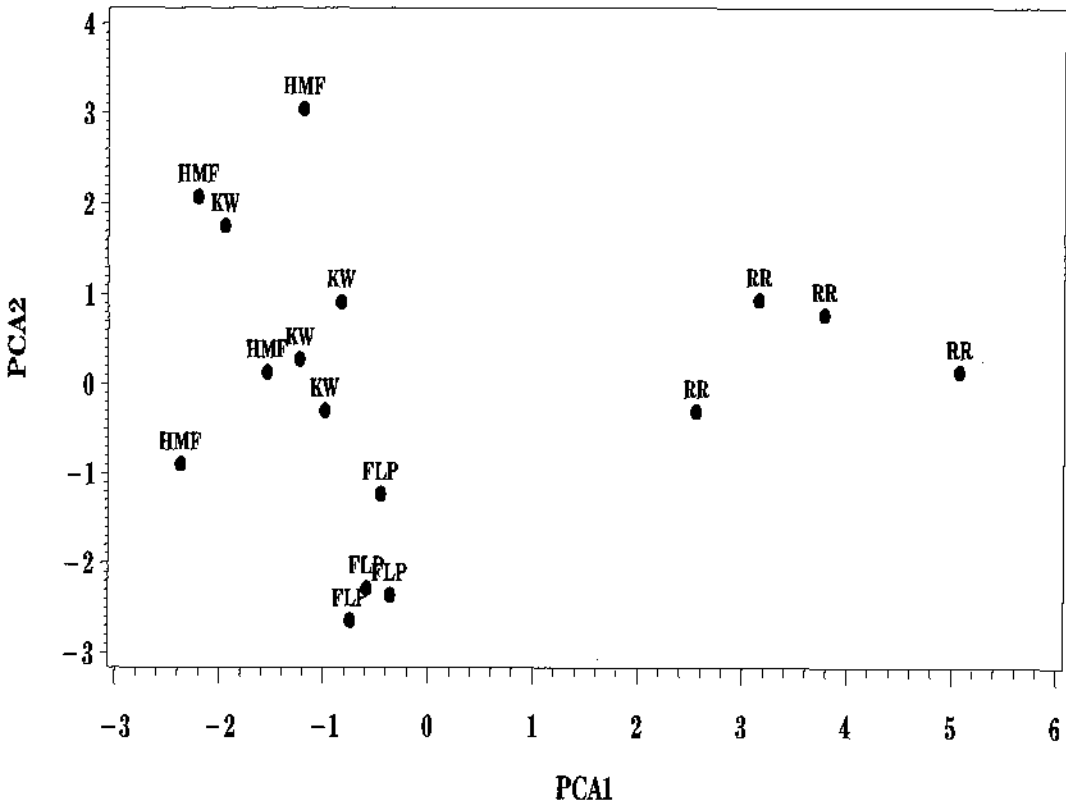

Fig. 1. Plot of the first and second principal component scores for four soil samples within each site. FLP = Floodplain, KW = Kilmer Woods, HMF = Hutcheson Memorial Forest, and RR = Railroad.

0.0032), nitrogen ($r = 0.59$, $P < 0.0169$), and % silt ($r = -.50$, $P < 0.0482$) were significant.

The floodplain soil was a loam and had less organic matter (8.6%) than the other two forest sites, probably due to removal of litter during flooding (Table 1). The soil at both upland forest sites (HMF and KW) had a loam texture with a high percentage of organic matter. The railroad site was classified as a sandy loam, and contained many fine and coarse pieces of red shale and limited organic matter which contributed to its lower water holding capacity.

DEMOGRAPHIC CHARACTERISTICS. Survivorship of seedlings to reproduction in 1985 and 1986 was significantly different at all four sites ($P < 0.05$; Fig. 2). In the 1985–86 census, 5% of the plants in the Floodplain population survived to reproduce, while less than 2% survived to reproduce in the other populations. The greatest mortality occurred during the dry summer months, and mortality was higher in 1985–86 than in 1986–87 in all populations. In 1986–87, 16% of the plants in the Floodplain survived to flowering, in contrast to less than 10% in the other populations (Fig. 2).

In 1986 and 1987, plants in the Floodplain population flowered significantly earlier than in the other populations (Fig. 3). A significant date by population interaction from the repeated measures analysis indicated that the number of receptive flowers over time differed significantly among the populations (1986 Wilk's Lambda$_{12,191}$ = 0.3602, $P < 0.0001$, 1987 Wilk's Lambda$_{21,448}$ = 0.2862, $P < 0.0001$). The profile analysis showed that for most dates in 1986 (all but May 1) and all dates in 1987 the pattern of receptive flowers in relation to time differed significantly among the populations (Floodplain earliest).

The fecundity of *A. petiolata* in the different habitats was measured by fruit and seed production and fruit abortion. The number of seeds per fruit (1985 $F_{3,3309}$ = 12.80, $P < 0.0001$; 1986 $F_{3,486}$ = 7.10, $P < 0.0001$) and the number of fruits per plant (1985 $F_{3,494}$ = 2.78, $P < 0.0406$; 1986 $F_{3,486}$ = 2.49, $P < 0.0456$; 1987 $F_{3,159}$ = 4.35 $P < 0.0056$) but not the number of seeds per plant (1985 $F_{3,494}$ = 1.43, $P < 0.2338$; 1986 $F_{3,486}$ = 1.20, $P < 0.3079$) differed among the populations (Table 2). In both years the Railroad population produced the greatest numbers of seeds/fruit, while the Kilmer Woods population produced the most fruits/plant. Fruit abortion differed significantly among the populations

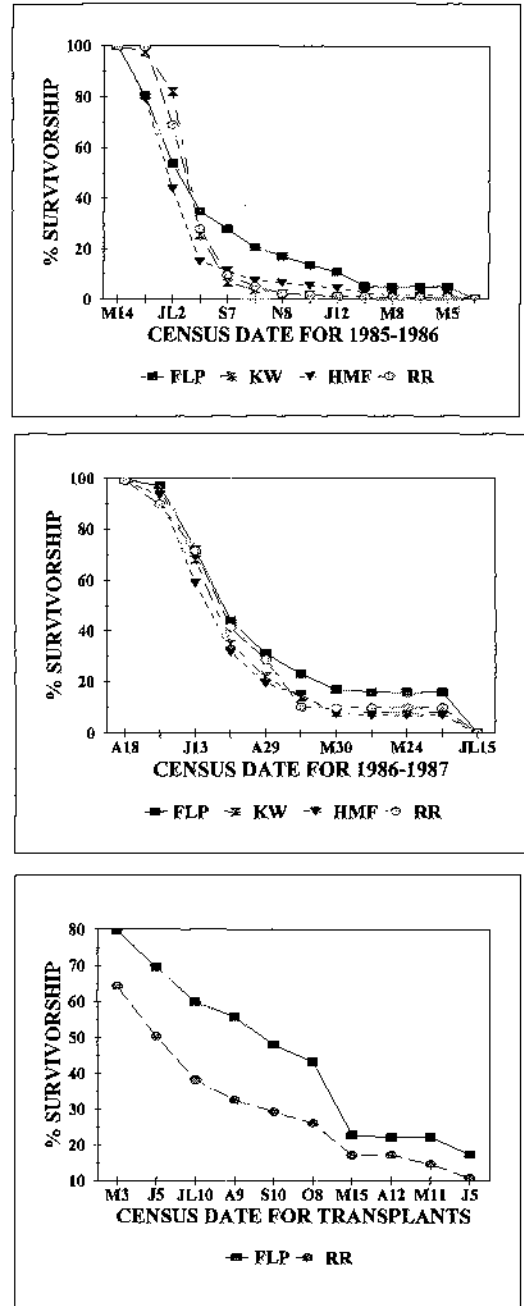Fig. 2. Survivorship of the natural populations and the transplanted seedlings. Census dates for 1985 to 1986 are May 14 to June 28. For 1986, cohort census is from April 18 to July 15. The transplants were censussed from May 3 until June 5 of the following year.

with Hutcheson Memorial Forest having the greatest percentage aborted although it was not significantly higher than all of the populations
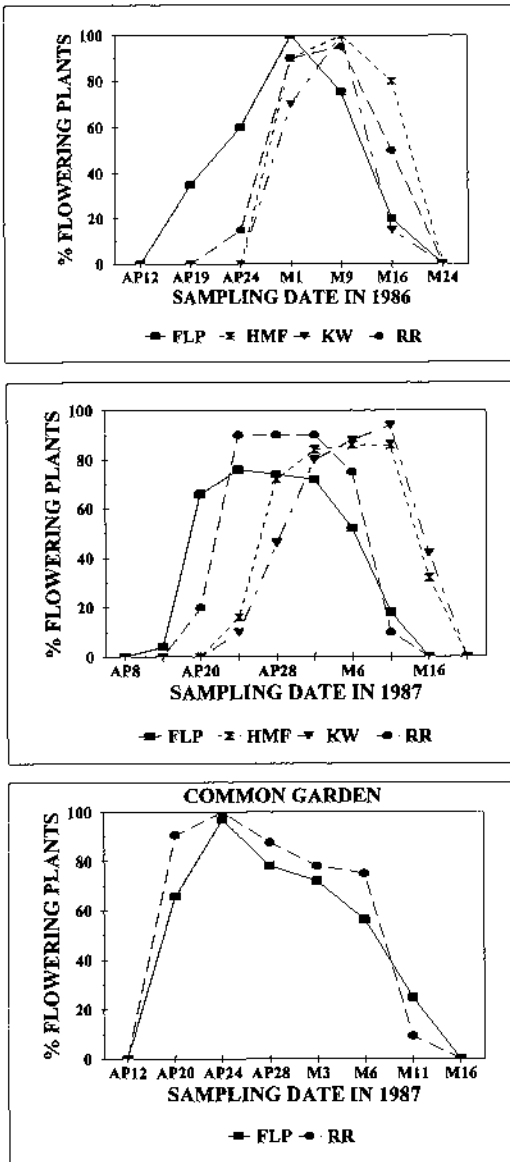
Fig. 3. The percentage of flowering plants in the populations and the transplanted seedlings. Sampling dates in 1986 were from April 12 to May 24, and in 1987 from April 8 to May 16.

(1986 $F_{3,75}$ = 9.76, $P < 0.0001$; 1987 $F_{3,156}$ = 4.7, $P < 0.0038$; Table 3).

Populations allocated their resources (biomass) in significantly different proportions in the different habitats (Table 4). Due to the problem of a lack of normality of these data (after arcsine and square root transformation) a nonparametric test (Kruskal-Wallis) was also used (Sokal and Rohlf 1981). Both tests showed highly significant differences ($P < 0.0001$) among popula-

Table 2. Fecundity in the different populations. Means (standard error) are presented with letters that indicate significant differences for a trait among the populations by Duncan's multiple comparison.

Population	1985		1986				1987	Transplants
	Seeds/fruit	Fruits/plant	Seeds/plant	Seeds/fruit	Fruits/plant	Seeds/plant	Fruits/plant	Fruits/plant
FLP	13.2^C (0.12)	13.7^A (0.94)	195 (16.7)	12.7^{AB} (0.30)	13.7^{AB} (0.95)	195 (17.0)	6.8^A (0.86)	7.7^A (0.96)
HMF	13.4^B (0.12)	10.8^B (0.83)	153 (13.9)	12.4^B (0.29)	10.9^B (0.84)	154 (14.1)	8.7^A (1.10)	—
KW	12.2^D (0.10)	14.7^A (1.23)	186 (18.1)	11.5^C (0.27)	14.7^A (1.24)	186 (18.3)	9.3^A (1.07)	—
RR	14.0^A (0.12)	13.0^{AB} (0.97)^A	191 (15.7)	13.4^A (0.31)	12.6^{AB} (0.95)	184 (15.6)	3.5^B (0.47)	6.9^A (1.19)

Table 3. The mean fruit abortion (standard error) as measured by aborted fruits/total initiated fruits × 100 for each population for 1986 and 1987. Different letters for means represent significant population differences as determined by Duncan's multiple comparison tests.

| Population | Mean % fruit abortion | | |
	1986	1987	Transplants
Floodplain	59.3^A (2.63)	51.6^A (2.41)	55.1^A (2.72)
HM Forest	64.6^A (3.14)	55.6^A (2.10)	—
Kilmer Woods	43.2^B (4.11)	42.5^B (3.23)	—
Railroad	42.4^B (4.40)	54.6^A (4.23)	57.2^A (4.80)

Table 5. Means (standard error) for seed weights in 1985 and 1986 and seed germination of the four populations. Different letters indicate that populations are significantly different by Duncan's multiple comparison tests. In 1985, seeds were weighed in lots of ten.

| Population | Mean seed weight (mg) | | % germination |
	1985	1986	
Floodplain	2.03^B (0.009)	2.02^A (0.016)	53.9^A (2.9)
HM Forest	1.84^A (0.017)	1.76^C (0.009)	43.9^B (6.4)
Kilmer Woods	2.02^B (0.016)	1.67^D (0.011)	28.3^C (4.6)
Railroad	2.21^A (0.015)	1.88^B (0.009)	39.6^B (3.9)

tions. The similarity in the results indicated that the lack of normality did not bias the results from the MANOVA. Only the results from the MANOVA are presented because it is the more appropriate analysis with correlated data. The multivariate test indicated that the populations allocated their resources differently (Wilk's Lambda$_{9,436}$ = 0.7035, P < 0.0001). The univariate analysis of the proportion of the total biomass (grams dry weight) allocated to reproduction showed that plants in the Railroad population allocated significantly more biomass to reproduction than the other populations ($F_{3,181}$ = 19.5, P < 0.001; Table 4). The Kilmer Woods population allocated the least to reproduction and the most to the leaves and stems ($F_{3,181}$ = 10.0, P < 0.0001) and roots ($F_{3,181}$ = 10.5, P < 0.0001).

Seed quality as measured by seed weight significantly differed both among populations (1985 $F_{3,76}$ = 887, P < 0.0001; 1986 $F_{3,91}$ = 258, P < 0.0001) and among individual plants (families; 1985 $F_{76,2321}$ = 108, P < 0.0001; 1986 $F_{91,8870}$ = 5 100, P < 0.0001) with the Railroad population (in 1985) and the Floodplain population (in 1986) having the heaviest seeds (Table 5). The analysis of seed germination showed that there were significant differences among populations ($F_{3,76}$ = 36.0, P < 0.0001) and among

plants within populations ($F_{76,160}$ = 19.7, P < 0.0001; Table 5). The Floodplain population had a significantly higher percentage germination.

The seed bank data showed the Railroad site to have the greatest number of viable seeds per sample at all times and at all depths in the soil (Table 6). Before germination, the Railroad and Floodplain sites had more seeds in the top sample (upper 5 cm) than the Hutcheson Memorial Forest and Kilmer Woods sites. After germination, the Railroad site had the greatest number of seeds in the top samples and no seeds were found in the Floodplain site. At each site, there were more viable seeds in the upper samples.

While size had no effect on the probability of flowering (all plants flowered in their second year), it affected fecundity (Tables 7 and 8). Large overwintering rosettes produced significantly more seeds/fruit and fruits/plant (Table 7), but size did not significantly influence percentage fruit abortion (Table 8).

COMMON GARDEN. Seedlings transplanted to the Railroad site were destroyed by a bulldozer before any significant data could be collected. At the Floodplain site, survivorship was significantly higher for the Floodplain transplants than for the Railroad transplants (Fig. 2), but the percentage of flowering plants and the number of receptive flowers per sampling date were not

Table 4. The mean percentage of biomass (standard error) allocated to reproductive and vegetative structures at the population sites in 1985 and in the transplant experiment in 1987. Different letters indicate that populations are significantly different by Duncan's multiple comparison test.

| Population | Reproduction | Leaves and stems | Roots | Transplant experiment | | |
				Reproduction	Leaves and stems	Roots
Floodplain	28.3^B (1.33)	57.3^{AB} (1.21)	14.4^B (0.87)	35.2^A (2.94)	50.1^A (2.25)	14.7^A (1.15)
HM Forest	31.0^B (0.83)	56.2^B (0.66)	12.8^B (0.47)	—	—	—
Kilmer Woods	22.4^C (1.33)	59.3^A (0.84)	18.4^A (0.80)	—	—	—
Railroad	34.6^A (0.89)	52.0^C (0.79)	13.5^B (0.57)	35.9^A (1.81)	48.1^A (2.01)	16.1^A (1.14)

Table 6. The number of seeds found in 0.059 m^2 of soil at different depths before and after germination. ANOVA results are presented below.

Population	Before germination		After germination	
	1–5 cm	5–10 cm	1–5 cm	5–10 cm
Floodplain	50	6	0	0
HM Forest	40	2	2	2
Kilmer Woods	12	6	1	1
Railroad	92	13	12	2

Source	df	MS	F	$P > F$
Population	3	20	10.03	0.0001
Location	1	91	45.10	0.0001
Time	1	119	58.68	0.0001
Pop × Loc	3	14	6.92	0.0002
Pop × Time	3	12	5.77	0.0007
Loc × Time	1	72	35.41	0.0001
P × L × T	3	9	4.25	0.0057
Error	382	773		

significantly different between the source populations (Wilk's Lambda$_{6,48}$ = 0.8708, $P <$ 0.3295; Fig. 3). Fecundity as measured by fruits/plant ($F_{1,48}$ = 0.26, $P < 0.6124$) or the percentage fruit abortion ($F_{1,48}$ = 0.16, $P < 0.6930$) was not significantly different between the source populations (Tables 2 and 3). The transplants from the Floodplain and the Railroad were not significantly different in their pattern of biomass allocation (Wilk's Lambda$_{3,34}$ = 0.9113, $P >$ 0.3613; Table 4). While size differed among the plants in the populations and influenced fruit production, it did not vary between the source populations (Table 8).

Discussion. *Alliaria petiolata* populations in this New Jersey study were found in sites that differed significantly in light and water availability (Byers 1988) and are uniquely characterized by soil nutrients and texture. Possibly in response to these abotic differences, the populations were found to vary in their demographic characteristics. Overall, *A. petiolata* was most successful on the Floodplain as exhibited through greater survivorship and a higher percentage of germination. Plants in the Railroad population, the driest site, allocated the largest proportion of their biomass to fruits and had high mortality rates. A woodland population in Illinois of *A. petiolata* allocated less biomass to reproduction (20%, Anderson et al. 1996) than the populations in this New Jersey study. The Illinois population also produced fewer seeds/m^2 (15,000) than the populations of our study, especially the Floodplain (30,689) or the Railroad (45,018) populations.

As found in the Railroad population, investigators have found that plants in more open and earlier successional sites allocated a greater proportion of biomass to reproduction than plants in later successional habitats (e.g., Harper 1977; Roos and Quinn 1977; Newell and Tramer 1978). Likewise, the more extensively colonizing varieties of *Echinochloa crusgalli* allocated a greater proportion of their biomass to reproduction (Barrett and Wilson 1981).

While other traits differed among the populations there is no clear pattern among the sites

Table 7. Means (standard error) of seeds/fruit and fruits/plant for the different rosette size categories for the four populations. Duncan's multiple comparison tests comparing seeds/fruit indicated that Hutcheson Memorial Forest differed from the other populations. All rosette sizes differed in seeds/fruits produced. Duncan's analyses of fruits/plant indicated differences among all of the populations and all of the rosette sizes. The ANOVAs for seeds/fruit and fruits/plant are presented below.

Population	Winter rosette size					
	Seeds/fruit			Fruits/plant		
	Small	Medium	Large	Small	Medium	Large
Floodplain	4.7 (0.44)	12.9 (0.65)	29.9 (2.99)	9.8 (0.29)	13.0 (0.13)	16.0 (0.20)
HM Forest	3.7 (0.28)	12.3 (0.82)	27.4 (2.77)	9.5 (0.23)	13.9 (0.12)	16.5 (0.21)
Kilmer Woods	6.2 (0.59)	17.8 (1.17)	38.0 (6.01)	10.8 (0.19)	12.6 (0.12)	13.6 (0.24)
Railroad	5.0 (0.98)	14.5 (0.92)	33.5 (4.23)	10.5 (0.28)	14.5 (0.12)	16.5 (0.24)

Source	ANOVA for seeds/fruit				ANOVA for fruits/plant			
	df	MS	F	$P > F$	df	MS	F	$P > F$
Population	3	568	112.78	0.0001	3	593	9.94	0.0001
Rosette size	2	4914	976.27	0.0001	2	15,359	257.47	0.0001
Pop × size	6	190	37.67	0.0001	6	80	1.34	0.2366
Plant (pop)	486	40	7.92	0.0001	—	—	—	—
Error	3307	5			486	59		

Table 8.   Regressions of rosette size and reproductive traits for 1987 of the four populations and the transplants.

Source	1987				Transplants			
	df	MS	F	$P > F$	df	MS	F	$P > F$
Fruits/plant								
Population	3	354	10.29	0.0001	1	6	0.20	0.6537
Rosette size	1	1607	46.67	0.0001	1	47	1.71	0.1972
Error	156	34				46	27.2	
Fruit abortion								
Population	3	1761	5.10	0.0021	1	98	0.29	0.5910
Rosette size	1	775	2.24	0.1361	1	125	0.08	0.7846
Error	156	345			46	334		

associated with the abiotic characteristics. For example, the Floodplain population has the earliest flowering date which may be considered advantageous because it would allow earlier maturation of fruits before the drier summer months. Varieties of the *Echinochloa crusgalli* complex which are found in a greater range of habitats flowered earlier, thus avoiding summer drought (Barrett and Wilson 1981). However, the Floodplain population does not have a lower percentage of fruit aborted, and fruit abortion was higher in all populations of this New Jersey study than in populations in Iowa (Cruden et al. 1996). Our populations differed in their packaging of seeds (seeds/fruit and fruit/plant), but remarkably they did not differ in seed production per plant (i.e., a similar response was achieved through different allocation and developmental tactics).

A seed bank was maintained after germination in the New Jersey populations (except in the Floodplain) and was greatest in the Railroad site. The existence of the seed bank is advantageous for the species and will need to be considered in its management/control. The lack of a seed bank in the Floodplain site may be due to flooding and scouring of the surface which could remove the seed bank or make it very patchy and therefore difficult to sample. In Kentucky, *A. petiolata* was found to form a small and short-lived seed bank (Baskin and Baskin 1992).

In general, *A. petiolata* exhibited considerable plasticity in its response to the different light and moisture availabilities among the sites. However, considering the extent of the variation in soil and availability of light and water, the many traits of *A. petiolata* were more similar than might be expected. In all of the sites the plants were strict biennials, and the timing of flowering differed only slightly among populations. These results indicate that many of the characteristics

of *A. petiolata* are of an "ideal" weed (Baker 1965), for example, having a wide environmental tolerance (soil, light, and moisture) in growth and reproduction.

Alliaria petiolata was found to be a strict biennial in all of the New Jersey sites, as reported for other locations in the United States (Nuzzo 1991; Baskin and Baskin 1992; Anderson et al. 1996). While size was not a predictor of the timing of reproduction, size did significantly influence the quantity of seeds and fruits produced. The Floodplain population had the highest frequency of large rosettes (16%) while the Railroad population had the lowest (8%).

Our research has established that the populations in the four New Jersey sites differed in many life history characteristics. The observed phenotypic variation may be due to genetic differences and/or to plastic responses to the environment. Characteristics, such as survivorship, that continued to differ in the transplant experiment may be due to genetic differences between the populations. Alternatively, population characteristics which did not differ in the transplant experiment may have been due to environmental effects. Survivorship of the Railroad population transplants was significantly lower than survivorship of the Floodplain population transplants at the Floodplain site. This was the same pattern of survivorship observed in the source populations. This consistency suggests that their differences in survivorship are possibly due to genetic variation, but an equally likely possibility is that the survivorship of Railroad plants was lower in both sites because the Railroad site is less favorable environmentally and because the Floodplain affected the Railroad transplants unfavorably.

The flowering phenology, fruit abortion, and biomass allocation of the transplanted seedlings from the two populations did not differ at the

Floodplain site. Since all of these characteristics differed significantly (fruit abortion only in 1986) when the plants were in their own habitats, these differences may be interpreted as plastic responses to the environment. Year to year variation in moisture availability or other environmental factors may affect fruit abortion more than either genetic or intrinsic habitat differences. For example, in *Bromus tectorum*, variation in demographic characteristics between three habitats was more influenced by year to year variation in weather conditions than by environmental differences intrinsic to the habitats (Mack and Pyke 1983). Variation in biomass allocation in another species, *Plantago lanceolata*, which occupies a range of successional habitats, was found to be mostly environmental (Primack and Antonovics 1981).

From the common garden experiment and the habitat data it can be concluded that *A. petiolata* has responded to the broad range of habitats through phenotypic variation in demographic and reproductive characteristics. While the mortality of *A. petiolata* is higher outside of the Floodplain habitat, this may be offset by increased seed production, thereby allowing for colonization of a wider range of habitats. In the Railroad site we found the greatest density of flowering plants resulting in the highest seed production per m². In addition, the Railroad population plants allocated the greatest proportion of their biomass to reproduction. The life history of *A. petiolata*, as suggested by Anderson et al. (1996), with its rapid early spring growth in its second year as well as very early seed germination (starting late February in New Jersey), may be advantageous for competing with spring ephemerals. However, *A. petiolata* is not always successful, as demonstrated by Drayton and Primack (1996) where deliberately started populations were not viable.

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