

Effect of Population Density on the Demography of an Invasive Plant (*Alliaria petiolata*, Brassicaceae) Population in a Southeastern Ohio Forest

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ABSTRACT.—As interest in invasive species management increases, new information with respect to invasive species abundance and distribution in invaded habitats is imperative. One essential type of information is demographic data. When invasive plants colonize a new habitat, their numbers may be low at first, but the population may undergo rapid expansion. We were interested in the effect of intraspecific density on the population dynamics and life history attributes of *Alliaria petiolata* a Eurasian biennial herb that has become an invasive pest in portions of North America. Thirty plots were established in a mesic second-growth deciduous forest in high, medium and low density patches of *A. petiolata* rosettes. Demographic data were collected for all *A. petiolata* cohorts present in the plots from 1996–1998. In June 1998 all first year rosette and second year mature individuals were harvested, dried and weighed. Stage-based population projection matrices were constructed in order to compare demography among plots and years, and models were used to predict trends in future population growth. There were significant differences among demographic parameters as a function of density and year. Survival to flowering in 1998 was greatest for plants in low density plots. These plants were also larger and produced more fruits than plants in either medium or high density plots. Initial differences among plots in plant density diminished and by 1998 there was no significant difference among density treatment plots in number of flowering plants or number of seeds produced. Seed bank formation ensures that, even under less favorable circumstances, *A. petiolata* can remain at a site for a number of years. Lambda values indicated that the number of plants in plots of each density is increasing, with the greatest increase in low density plots ($\lambda = 1.45$). As this study shows, due to abundant seed production, patches of low *A. petiolata* density in a newly colonized mesic forest can grow rapidly and in a few years form a dense stand.

INTRODUCTION

The prediction and elucidation of patterns of species abundance and distribution are important aims of ecological research (Bullock *et al.*, 1994). To meet these objectives researchers often adopt a population biology approach, since an organism's population dynamics, including natality and mortality, determine its abundance and dispersal within and among habitats (Bullock *et al.*, 1994). Plant populations respond to a combination of external and internal factors in a complex multivariate manner (Werner and Caswell, 1977). Mortality, germination rates, establishment, fecundity and biomass allocation patterns can vary among populations and years (*e.g.*, Matlack, 1987; Bullock *et al.*, 1994; Allphin and Harper, 1997; Byers and Meagher, 1997; Damman and Cain, 1998). Survival of a species often ultimately depends upon its life history characteristics (Silvertown and Lovett-Doust, 1993).

Demographic studies often focus on rare species management and conservation with the aim of predicting population dynamics on the basis of demographic data (*e.g.*, Menges, 1986; Silvertown *et al.*, 1996; Allphin and Harper, 1997; Menges and Dolan, 1998). However,

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these same demographic techniques can be used for the study of invasive species as well, and may reveal important aspects of plant performance that influence management decisions. In order to develop a successful site monitoring program, it is crucial to study invasive species behavior in relation to habitat characteristics (Luken and Mattimiro, 1991), including the demographic parameters of the organism under different environmental conditions, its reaction to habitat disturbance, ecological limitations, ability to proliferate and persist in a specific site and rate of spread (Luken and Mattimiro, 1991). Since invasive species can quickly enter and spread in a new habitat (Cronk and Fuller, 1995) and initial population density can vary widely, it is also especially important to understand population dynamics with respect to population size and density. By examining population demographics, it may be possible to predict the future behavior of the population in a particular site and to identify crucial stages of the life cycle which contribute to population growth and target those stages as part of a management strategy.

Intraspecific plant density can be important in the initial success of the colonization process for invasive plants (Bazzaz, 1986). Often large numbers of plant propagules must be introduced to a new site before a population becomes established. When seeds of *Trifolium hirtum* were sown in a natural environment, only 12% of the newly established colonies persisted for more than one season, and many of those subsequently died (Martins and Jain, 1979). As this experiment indicates, the probability that a recently established invasive plant population will be eliminated due to the effect of low population density is great (Bazzaz, 1986).

Competition can also have an important impact on an invasive species' ability to colonize and persist in a new site. This competition may be interspecific involving antagonism between the invasive plant and one or more of the resident plant species of the invaded habitat, or it may be intraspecific involving interactions within an established population of the invader (Barbour *et al.*, 1999). In a competitive situation, one resource (*e.g.*, sunlight, carbon dioxide, water, mineral nutrients and space) is in demand by two organisms (Begon *et al.*, 1996). Since individuals of the same species are more likely to need the same resources, one might conclude that intraspecific competition will be stronger than interspecific competition (Barbour *et al.*, 1999), but this is often not true (*see* Gurevitch *et al.*, 1990).

Increasing plant density within a population may affect mortality and therefore the number of plants surviving to reproduce, or density may instead affect individual plant size and therefore seed production per plant (Palmlblad, 1968; Ford, 1975). A plastic response to density in terms of adjustments in plant size, instead of increased mortality, may allow more plants to survive and therefore maintain a larger number of genotypes in the population (Harper, 1961; Palmlblad, 1968). Plant size varies even within populations, and some individuals can grow significantly larger than others as they acquire more resources, and therefore have a greater negative impact on neighbors (Gurevitch *et al.*, 1990). Size hierarchies of this nature with many small individuals and a few large ones become apparent during the seedling stage of plant development and often become more pronounced over time (Watkinson, 1985). Interactions among individuals in a dense stand may lead to an exaggeration of the size differences among them, and over time mortality within the population may increase (*e.g.*, Aikman and Watkinson, 1980; Cannell *et al.*, 1984). These density-dependent effects can serve to regulate population size (Begon *et al.*, 1996).

We conducted a 3-y demographic study of the invasive herb *Alliaria petiolata* (M. Bieb.) Cavara and Grande (Gleason and Cronquist, 1991) in response to population density. The primary goal of our study was to document demographic variability within a newly established population of *A. petiolata* in a forested habitat over time in response to variation in

intraspecific plant density. In addition, we wanted to: (1) Compare demographic parameters among cohorts from different years and (2) Determine the effect of density on population decline, growth or maintenance assuming a stable age distribution.

METHODS

Species.—*Alliaria petiolata* (garlic mustard) is an obligate biennial dicot, producing a basal rosette of leaves during the first year's growth which overwinters and bears flowers and fruits in the spring of the second year (Cavers *et al.*, 1979; Nuzzo, 1991; Byers and Quinn, 1998). Fruiting is followed by plant senescence. In the northern United States, *A. petiolata* seeds typically germinate from late February through April, depending on the year and habitat (Trimbur, 1973; Baskin and Baskin, 1992; Anderson *et al.*, 1996). True leaves form about 2 wk after germination (Trimbur, 1973) and eventually produce a rosette of coarsely toothed, kidney-shaped, notched leaves with deep venation and long slender petioles (Cavers *et al.*, 1979; Byers, 1988). First-year rosettes grow slowly at first, then more rapidly during the warm, moist spring months (Cavers *et al.*, 1979). Growth declines again during the typically drier summer months and rosette mortality can be high (Byers, 1988; Byers and Quinn, 1998). As fall approaches, plant growth increases until temperatures descend below a certain threshold (usually in late autumn), then growth slows and rosettes remain green until spring.

In March and April rosettes grow rapidly, producing tall inflorescences. Mature plants grow up to 1.25 m in height and usually exhibit little cauline branching (Cavers *et al.*, 1979; Byers, 1988; Anderson *et al.*, 1996). Numerous, small white flowers form racemes at the stem apex and occasionally in leaf axils (Cavers *et al.*, 1979; Susko and Lovett-Doust, 1998, 1999). Plants can be autogamous (Anderson *et al.*, 1996) or facultatively xenogamous (Cruden *et al.*, 1996). Flowers typically open from April through June, by which time mature fruits have formed (Cavers *et al.*, 1979; Byers, 1988; Anderson *et al.*, 1996). Fruits are slender siliques, usually containing 1–30 seeds (Byers, 1988; Susko and Lovett-Doust, 1999) which are protected by a tough, grooved seed coat (Cavers *et al.*, 1979).

Seeds are released from July through October (Trimbur, 1973; Cavers *et al.*, 1979). These seeds are often passively dispersed by water (Byers, 1988), animals or humans (Lhotská, 1975; Cavers *et al.*, 1979). Seeds exhibit innate physiological dormancy at maturity and require cold stratification before initiation of germination (Lhotská, 1975; Baskin and Baskin, 1992). Dormancy may persist from 8 mo in warmer habitats (Baskin and Baskin, 1992; Anderson *et al.*, 1996) to 20 mo in colder habitats (Lhotská, 1975; Cavers *et al.*, 1979). In some locations seed banks are formed, but they are typically small and short-lived (Baskin and Baskin, 1992; Anderson *et al.*, 1996; Byers and Quinn, 1998). Plants are not clonal and all reproduction is by seed production (Cavers *et al.*, 1979). Rosettes and mature plants possess a taproot system.

Alliaria petiolata is a Eurasian native that commonly inhabits mesic shaded areas (Grime *et al.*, 1988). It is also found in well-drained sunny sites and forested areas with varying levels of canopy closure (Cavers *et al.*, 1979; Grime *et al.*, 1988). In addition, it has the ability to survive in areas that are inundated with water for up to 4 mo per year. As is typical of many invasive species, *A. petiolata* can also thrive in disturbed or waste areas (Cavers *et al.*, 1979) and is often correlated with moderately to highly exposed bare soil (Grime *et al.*, 1988). Besides its ability to survive under various natural light and hydrologic regimes, *A. petiolata* can also persist on several soil types ranging from clay to sand and rich loam (Cavers *et al.*, 1979), but it is rarely found on extremely acidic soils (Grime *et al.*, 1988). There is a high degree of genetic structuring within this species, with low genetic diversity within populations compared with diversity among populations (Meekins and McCarthy,

2001). In contrast, *A. petiolata* shows a high degree of phenotypic plasticity within populations subjected to different environmental conditions (Byers and Quinn, 1998; Meekins and McCarthy, 2000).

The first recorded appearance of *Alliaria petiolata* in North America was in 1868 in New York (Nuzzo, 1993). It is theorized to have been introduced to North America by early colonists who prized both its medicinal and its edible qualities (Grieve, 1985). Since its introduction, it has rapidly spread across the northern United States and southern Canada. *Alliaria petiolata* can form dense, virtually monotypic stands (Cavers *et al.*, 1979; Nuzzo, 1991; Yost *et al.*, 1991) that cover hundreds of square meters (Cavers *et al.*, 1979) and displace native species in invaded habitats (Nuzzo, 1991; McCarthy, 1997; Meekins and McCarthy, 1999). For these reasons, *A. petiolata* is considered to be a serious threat to understory communities in natural areas in North America (McCarthy, 1997). The ability of *A. petiolata* to grow under a wide range of habitat conditions has likely facilitated its rapid spread throughout Canada and the United States.

Study site.—This experiment was conducted within the Ridges Land Laboratory (39°19'13"N, 82°07'10"W; USGS, 1995), a 68 ha parcel of land in Athens, Ohio owned by Ohio University and used as a teaching and research resource (Kline, 1994). Athens is located within the unglaciated Allegheny Plateau region (Peacefull, 1996). This area consists of rolling hills dissected by small drainageways. The climate is continental with an average precipitation of 96.5 cm evenly distributed throughout the year (Lucht *et al.*, 1985). On average, 52.5 cm of precipitation falls during the growing season (April–September). In the winter the average temperature is 0 C (minimum of –6.1 C) and in the summer the average temperature is 21.7 C (maximum of 29.4 C).

Experimental plots were located within a second growth hardwood forest bordered on one side by a small stream that contains running water even during the driest months. The overstory dominants in the plot area were *Fraxinus americana* and *Quercus* spp. The woody understory dominants were *Acer saccharum* and *Asimina triloba*. Soils were Westmoreland-Guernsey silt loams with 15–25% slopes (Lucht *et al.*, 1985). These soils are well drained to moderately well drained, often acidic, with a deep root zone and moderate fertility. They are formed in residuum and colluvium from sandstone, siltstone, shale and limestone underlain by siltstone bedrock. Elevations in the experimental site ranged from ca. 225–235 m (USGS, 1995).

Experimental design.—In March 1996, a recently established population of *Alliaria petiolata* (covering an area approximately 320 m²) was surveyed within the Ridges Land Laboratory. A majority of the *A. petiolata* plants present were in the second year rosette growth stage. Isolated patches of high, medium and low rosette density were identified. A total of thirty 0.5 × 0.5 m plots were established in different density patches within the population. Ten plots of each density were chosen from the available patches. Plots were separated from each other by a minimum of 2 m. Low density plots contained four *A. petiolata* rosettes, medium density plots contained 10 rosettes and high density plots contained 20 rosettes. Rosette density among populations can vary greatly and the densities chosen for this experiment reflect the range found within this population. Differences in density within a population may reflect colonization events and subsequent spread or be a consequence of disturbance.

In order to characterize abiotic and biotic factors within plots, soil moisture, light availability, canopy cover and understory cover were measured every 2 wk from March to November (the approximate growing season for *Alliaria petiolata* in southeastern Ohio). Soil moisture was determined using the gravimetric method (Gardner, 1986) for two samples collected at the outside edge of each plot. A spherical densiometer was used to ascertain

the percent canopy cover at two points on opposite edges of each plot. Light availability was measured at 30 cm above ground level at the corners of each plot between 10:00 and 14:00 on sunny days using a Li-cor photometer (LI-189) equipped with a quantum sensor. The percent light reaching a plot was calculated as a percent of total available sunlight in a nearby open field. All herbaceous and woody vegetation within each plot was identified monthly and the percent cover of each species was determined.

Soil texture and chemistry were also analyzed. Soil samples were taken from three randomly selected plots each of low, medium and high rosette density and sent to the Research Extension Analytical Laboratory of Ohio State University (Wooster, Ohio) for soil chemistry analysis. The available phosphorus, potassium, calcium, magnesium and nitrate nitrogen; pH and cation exchange capacity were determined. Soil texture was analyzed using the hydrometer method (Sheldrick and Wang, 1993).

All *Alliaria petiolata* plants in each plot were marked using colored wire. Second year rosettes were monitored on a weekly basis in 1996 and survival, number of stems produced, plant height, fruit production and seed production were recorded. In addition, all emerging *A. petiolata* seedlings and first year rosettes were counted weekly from March–October 1996. In March 1997 and March 1998 plants were again marked and monitored as above throughout the *A. petiolata* growing season. Thus, plots were monitored from March 1996 until June 1998, at which time all *A. petiolata* first year rosettes and second year mature (flowering) plants were harvested; separated into roots, shoots (leaves and stems) and fruits with seeds; dried at 80 C and weighed. Percent total biomass allocated to roots, shoots and fruits was calculated, as was the root:shoot ratio.

Demographic data were grouped into four cohorts. Cohort 1 consisted of rosettes in 1996 that had germinated the previous year. These rosettes constituted the initial density treatments. Cohort 2 consisted of plants that germinated in 1996 and flowered and died in 1997. Cohort 3 consisted of plants that germinated in 1997, flowered in 1998 and were subsequently harvested and cohort 4 consisted of plants that germinated in 1998 and were harvested as rosettes in June of the same year. The density treatment that was initiated for cohort 1 affected seed production in 1996 and therefore directly affected the amount of fresh seed present for germination of cohort 3 in 1997. Due to the biennial nature of *Alliaria petiolata* and the tendency of populations to be cyclic (McCarthy, 1997), cohorts 2 and 4 were only indirectly influenced by the density treatment through presence of seeds from previous years in the seed bank.

Two soil cores were taken adjacent to each plot after seed germination (May) and after seed dissemination (October) of each year in order to estimate the number of seeds remaining in the seed bank. Soil cores were 5 cm deep and 28.26 cm². Samples were washed and sieved to remove organic debris. *Alliaria petiolata* seeds were then removed under a dissecting scope. Seeds were placed on moist filter paper in glass petri dishes in a germinator at 4 C to test for germinability. Most seeds were viable and the mean germination rate was 85.2%.

Statistical analysis.—Two-way GLM analysis of variance (ANOVA) was used to determine differences due to rosette density and year within each of the three environmental parameters measured weekly (percent overstory cover, percent sunlight and percent understory cover) and the one biotic parameter (understory cover excluding *Alliaria petiolata*). Significant differences among groups were then elucidated with Bonferroni tests. A one-way multivariate analysis of variance (MANOVA) was performed to detect any overall difference among soil chemistry and soil texture variables among plots of varying density. Variables for all statistical tests were log₁₀ transformed as necessary to meet the assumptions of nor-

mality and homogeneity of variances implicit in the parametric tests employed. All MANOVA and ANOVA analyses were performed in NCSS 6.0 (Hintze, 1997).

Differences in percent survival to flowering among density treatments for cohort 3 were analyzed using a one-way ANOVA for June 1998 data followed by a Fisher's LSD multiple comparison test. Significant differences among life history stages for cohorts 1 and 3 as a result of density treatment were explored using one-way ANOVAs with a Bonferroni correction (α/n) to account for the large number of ANOVAs performed, followed by Bonferroni post-hoc tests. Overall differences among density treatments in vegetative and reproductive parameters measured for harvested mature plants from cohort 3 were detected using a one-way MANOVA, followed by individual one-way protected GLM ANOVAs with a Bonferroni correction. Differences among treatment groups were elucidated using Bonferroni tests. Negative exponential functions were generated to describe rosette and mature plant biomass distributions within plots in relation to intraspecific density. To determine if there was any relationship between plant density and biomass, regardless of density treatment, linear regression analyses were performed on rosette dry weight biomass (cohort 4) and flowering plant dry weight biomass (cohort 3) for all *Alliaria petiolata* plants harvested in June 1998. Demographic data were analyzed using stage-based Lefkovich projection matrices (Lefkovich, 1965; Lee, 1992). Population growth rates and the relative importance of each of the measured stages were calculated using a mathematical model based on transition probabilities and variances among stages (Schemske *et al.*, 1994) constructed using RAMAS stage (Ferson, 1993). For many plant species, matrices based on morphological stages more accurately reflect life history than age-based models (Werner and Caswell, 1977; Byers and Meagher, 1997). Although we partitioned the life cycle of *A. petiolata* into distinct stages, since *A. petiolata* is an obligate biennial, a plant's age and stage classification are closely linked. The life cycle was partitioned into six discrete stages: ungerminated seeds, seedlings, spring rosettes, fall rosettes, second year rosettes (preflowering) and second year flowering plants. The biennial nature of *A. petiolata* necessitates that all stages of the life cycle, except ungerminated seeds, must progress to the next stage or die. Thus, stages cannot be skipped or repeated (except the seed stage).

The asymptotic population growth rate, λ , was also calculated. This parameter is the dominant eigenvalue of the projection matrix (Caswell, 1989) and provides a measure of the effect of the environment on a population by integrating demographic parameters with evolution (mean population fitness) and population growth and extinction (Werner and Caswell, 1977). A population with $\lambda = 1$ is in a steady state. If $\lambda > 1$, the population is increasing in size at a geometric rate, whereas $\lambda < 1$ implies that the population is declining to eventual extinction (Werner and Caswell, 1977; Caswell, 1989). Sensitivity analysis was performed using each matrix to measure the response of population growth to perturbations in the matrix (Ferson, 1993). In addition, elasticity analysis, which provides estimates of proportional sensitivity (de Kroon *et al.*, 1986), was performed. High sensitivity or elasticity values indicate that changes in the associated life history stage will lead to large changes in the asymptotic population growth rate (Caswell, 1989). Using the average transition probabilities from our matrices, we predicted the effect of demographic stochasticity on population size and growth rate in an environment with similar environmental stochasticity to that observed during our study over a 20 y period (RAMAS stage, 1000 iterations).

RESULTS

Average temperatures and precipitation for the duration of the study fell within the range typical for this region. The greatest precipitation occurred in 1996 (123.2 cm), followed by 1998 (109.9 cm) and 1997 (102.4 cm). Soil moisture reflected this pattern, with significantly

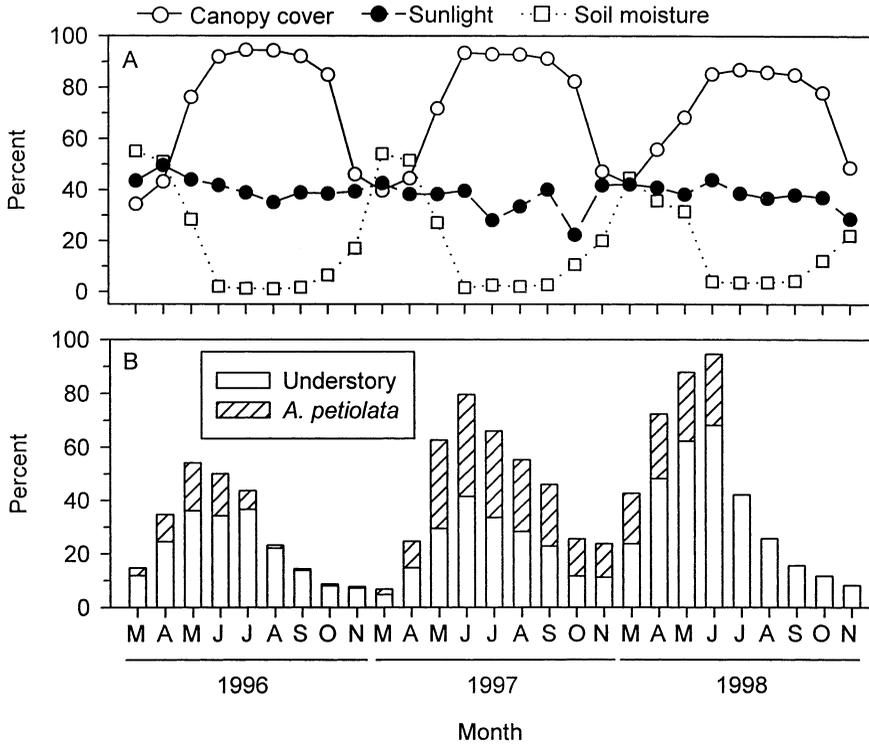


FIG. 1.—(A) Percent canopy cover, percent full sunlight, and percent soil moisture values for all *A. petiolata* demography plots in Athens, Ohio for the months of March through November 1996–1998. (B) Percent understory cover for all plots from March through November 1996–1998. Bars represent total cover subdivided into *Alliaria petiolata* cover and cover of all other understory plants

greater soil moisture during the *Alliaria petiolata* growing season ($F = 20.06$, $P < 0.001$) in 1996 ($41.1\% \pm 1.4$) compared with 1998 ($38.2\% \pm 1.5$) and 1997 ($36.1\% \pm 2.3$; Fig. 1A). Soil moisture ranged from 22.5% to 49.7% with soil moisture levels remaining fairly constant over the months measured, although in 1997 there were some fluctuations in soil moisture over the summer and autumn months. There was no significant effect of *A. petiolata* density on soil moisture ($F = 2.06$, $P = 0.134$) and no significant interaction of year and density ($F = 0.57$, $P = 0.682$).

Canopy cover ranged from 38.8% in March (before leaf out) to 90.3% in June (after canopy leaf out was complete; Fig. 1A). There were no significant differences in percent canopy cover among plots due to year ($F = 1.06$, $P = 0.350$), density ($F = 2.44$, $P = 0.094$) or the interaction of year and density ($F = 0.86$, $P = 0.494$). As canopy cover increased over the growing season, light availability decreased from 51.3% in March to 2.5% in June (Fig. 1A). There were no significant differences in understory light availability among plots due to year ($F = 2.53$, $P = 0.086$), density ($F = 0.88$, $P = 0.418$) or their interaction ($F = 0.27$, $P = 0.898$).

In general, understory species cover excluding *Alliaria petiolata* increased from March (7.1%) to June (39.1%) and then decreased again toward the end of the summer in August (25.3%; Fig. 1B). Percent understory cover was not significantly different among years (F

TABLE 1.—Soil chemistry and texture variables measured for *Alliaria petiolata* plots. A one-way multivariate analysis of variance (MANOVA) indicated no significant (Wilks' Lambda = 0.085, $P = 0.874$) effect of plot density on soil parameters. Soil texture variables included percent sand, clay and silt. Soil chemistry variables included pH; available phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg); nitrate nitrogen (NO_3N) and cation exchange capacity (CEC) in milliequivalents (meq)

Variable	Sand (%)	Clay (%)	Silt (%)	pH	P ($\mu\text{g}\cdot\text{g}^{-1}$)	K ($\mu\text{g}\cdot\text{g}^{-1}$)	Ca ($\mu\text{g}\cdot\text{g}^{-1}$)	Mg ($\mu\text{g}\cdot\text{g}^{-1}$)	NO_3N ($\mu\text{g}\cdot\text{g}^{-1}$)	CEC (meq)
Minimum	25	7	60	4.7	6	83	750	113	3	10
Mean	26	9	66	5.4	8	114	1300	174	3	16
Maximum	30	13	67	5.7	18	178	1970	283	4	20

= 0.22, $P = 0.806$), densities ($F = 0.38$, $P = 0.688$) or their interaction ($F = 0.16$, $P = 0.957$). Species richness per plot ranged from 10 (March) to 23 (June) across the growing season and was similar across plots. Species with the greatest cover included: *Claytonia virginica*, *Impatiens capensis* and *Viola sororia* in spring and *Fraxinus americana*, *Pilea pumila* and *Polygonum virginianum* in summer.

There were no significant differences in soil texture or chemistry variables among plots of differing density treatments (Table 1). Soil in the study area was a silt loam. The pH was moderately acidic and soil in the study area was of moderate fertility.

Thus, the biotic and abiotic profiles of all experimental plots were indistinguishable. Density has been effectively isolated as the only treatment effect with no obvious covariates. Population density of seedlings and flowering plants was much greater in plots in alternate years (Fig. 2), reflecting the cyclic structure often documented for *Alliaria petiolata* populations. In 1996 an average of 10.7 ± 0.5 flowering plants per plot was present across all plots. The following year, only 1.0 ± 0.2 flowering plants were present per plot. The number of flowering plants increased in 1998 to 38.8 ± 6.8 per plot. Seedling numbers fluctuated from 59.0 ± 19.0 per plot in 1996 up to 86.8 ± 9.0 in 1997 and down to 5.1 ± 1.3 in 1998.

The survivorship curve for cohort 2 most resembled a type III curve (Fig. 3; Deevey, 1947), implying greater selection at a specific stage in the life cycle (Harper and White, 1974). Only $1.4\% \pm 0.8$ of seedlings germinating in 1996 survived to flower in 1997. However, for cohort 3, rosette mortality was more evenly distributed from June 1997 to April 1998 and the survivorship curve more closely resembled a type II curve (Fig. 3; Deevey, 1947). Over $42.3\% \pm 5.4$ of seedlings germinating in 1997 survived to flower in 1998. There was a significant ($F = 4.95$, $P = 0.016$) effect of density on survival to flowering in cohort 3. Mortality was greater in high density plots ($31.3\% \pm 3.4$) than in either medium ($50.3\% \pm 5.6$) or low ($45.2\% \pm 7.3$) density plots. There was no significant difference in survival between medium and low density plots.

There was a significant ($P < 0.00625$, Bonferroni correction) effect of density on the number of *Alliaria petiolata* plants present in most stages of the life cycle for cohorts 1 and 3 (Fig. 4). There were significantly ($F = 487.09$, $P < 0.001$) more flowering plants present in high density plots in 1996 and significantly ($F = 16.22$, $P < 0.001$) greater seed production. The density effect from 1996 was also apparent in 1997 and 1998. There were significantly more seedlings ($F = 21.33$, $P < 0.001$), summer rosettes ($F = 20.69$, $P < 0.001$) and fall rosettes ($F = 8.33$, $P = 0.002$) in 1997 and more second year rosettes ($F = 6.42$, $P = 0.005$) in 1998. However, there were no significant differences among densities in number of flowering plants ($F = 4.77$, $P = 0.017$) or seed production ($F = 0.79$, $P = 0.466$) in 1998.

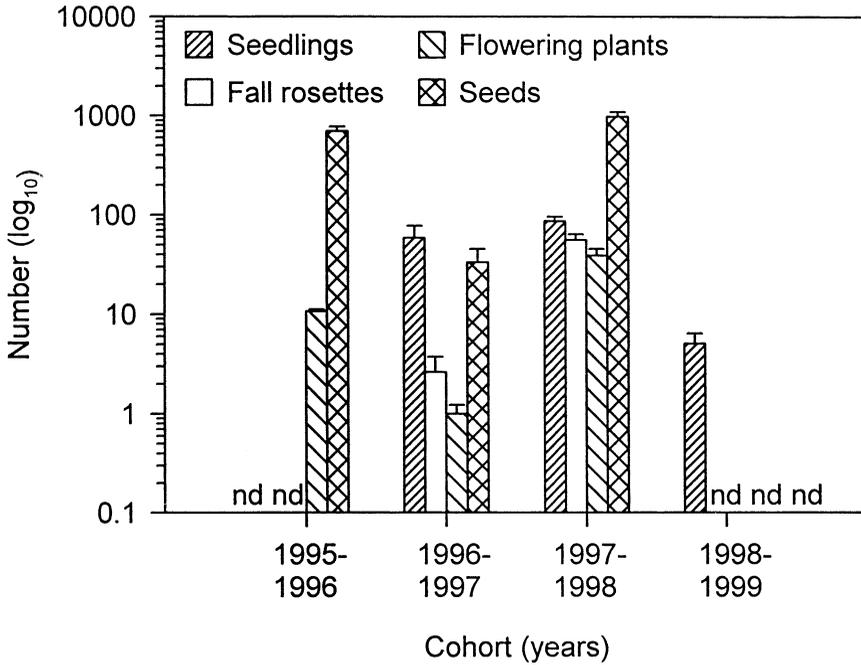


FIG. 2.—Mean number (+SE) of *Alliaria petiolata* plants of different stages present and number of seeds produced per plot for the four cohorts examined (1995–1996, 1996–1997, 1997–1998 and 1998–1999). Demographic data collection began March 1996 and ended June 1998, so data for 1995 and 1999 are not available (nd = no data)

The MANOVA indicated that there were significant differences overall among vegetative and reproductive characteristics measured for flowering *Alliaria petiolata* plants in June 1998. Flowering plants in low density plots were significantly taller ($F = 18.77$, $P < 0.001$); had significantly greater root ($F = 18.03$, $P < 0.001$), shoot ($F = 26.15$, $P < 0.001$), fruit ($F = 12.90$, $P < 0.001$) and total ($F = 22.44$, $P < 0.001$) biomass and produced more fruits ($F = 19.36$, $P < 0.001$) than plants in either the medium or high density plots (Table 2). There were no significant differences between medium and high density plots. A subsequent one-way MANOVA to test for an overall difference between low density plots and the combination of medium and high density plots indicated a significant difference (Wilks' Lambda = 0.918, $P < 0.001$) between them.

Biomass distribution for both rosettes and flowering plants in June 1998 followed a negative exponential curve (Fig. 5). Biomass distributions were described by the following negative exponential functions: rosettes, $y = e^{-0.16*(x-31.84)}$ ($R^2 = 0.97$), mature plants, $y = e^{-0.006*(x-1177.70)}$ ($R^2 = 0.99$). Rosette dry weight biomass varied from 0.2 to 53.2 mg, but over 95% of all rosettes weighed under 15 mg. Flowering plant dry weight biomass also showed substantial variation (4.9–5834.0 mg), but most of the plants (86%) weighed under 450 mg. Rosette density in 1998 was low, particularly when compared with 1997, and there was no significant relationship between number of rosettes per plot and rosette biomass (Fig. 6). Flowering plant density, in contrast, was quite high in 1998 and there was a significant negative relationship between number of flowering plants per plot and flowering plant biomass.

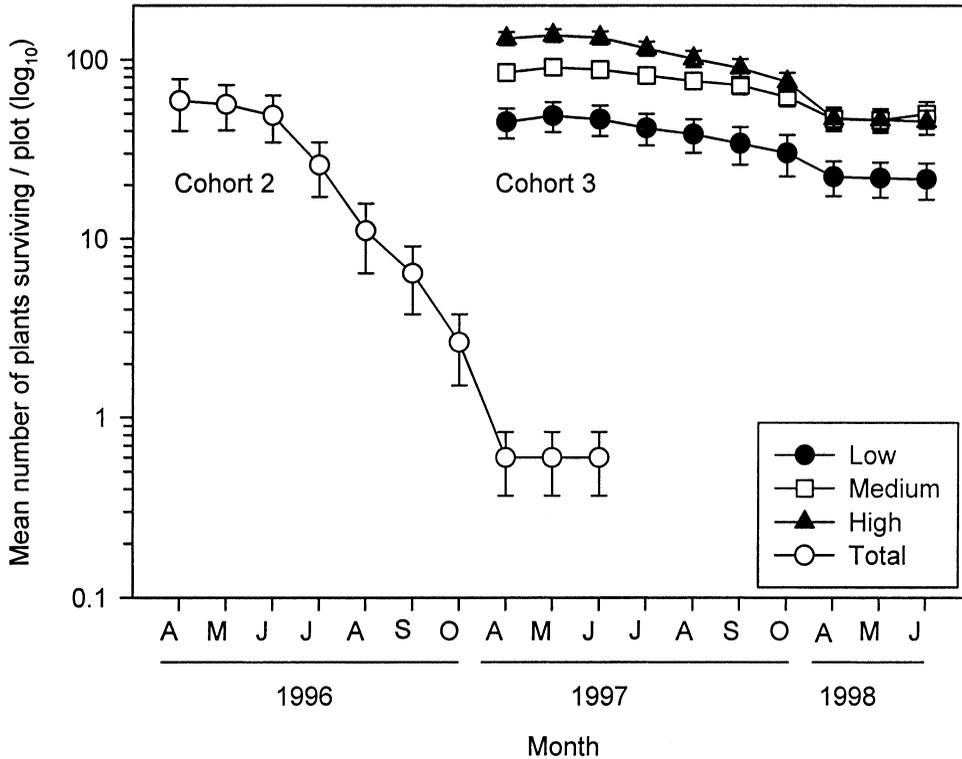


FIG. 3.—Percent survival (\pm SE) of *Alliaria petiolata* plants from April 1996 to June 1998. Data presented are from April–October 1996–1997 and April–June 1998. The line on the left side of the graph (“total”) represents survival across all plots for cohort 2 (1996–1997), whereas the lines on the right side of the graph represent survival across low, medium and high density plots for cohort 3 (1997–1998)

Projection matrices for density manipulation plots indicated high seed production but low seed to seedling transition values (Table 3). Transition proportions for stages among densities were similar. All density treatments for cohort 3 had asymptotic population growth rates above 1.0, indicating that the number of plants within the experimental plots is growing. Low density plots are growing at the fastest rate ($\lambda = 1.45$), while high density plots are growing at the slowest rate ($\lambda = 1.26$). The projection matrix for cohort 2, in contrast, indicated that this component of the population is declining ($\lambda = 0.68$).

Since most stages in the life cycle of *Alliaria petiolata* progress directly from one stage to the next without regressing to previous stages or remaining in a stage for an extended period of time, most sensitivity and elasticity values among stages were similar, with the exception of the seed to seed transition (Fig. 7). Sensitivity values for the seed to seedling transition were highest, indicating that this is an important element in the matrix. Values were comparable across density treatments. Elasticity values for transitions within low density plots were 0.160 for all transitions except the seed to seed transition, which was 0.042. Elasticities for medium density plots were 0.159 (seed to seed = 0.046) and for high density plots were 0.158 (seed to seed = 0.053). Models estimating population growth for low,

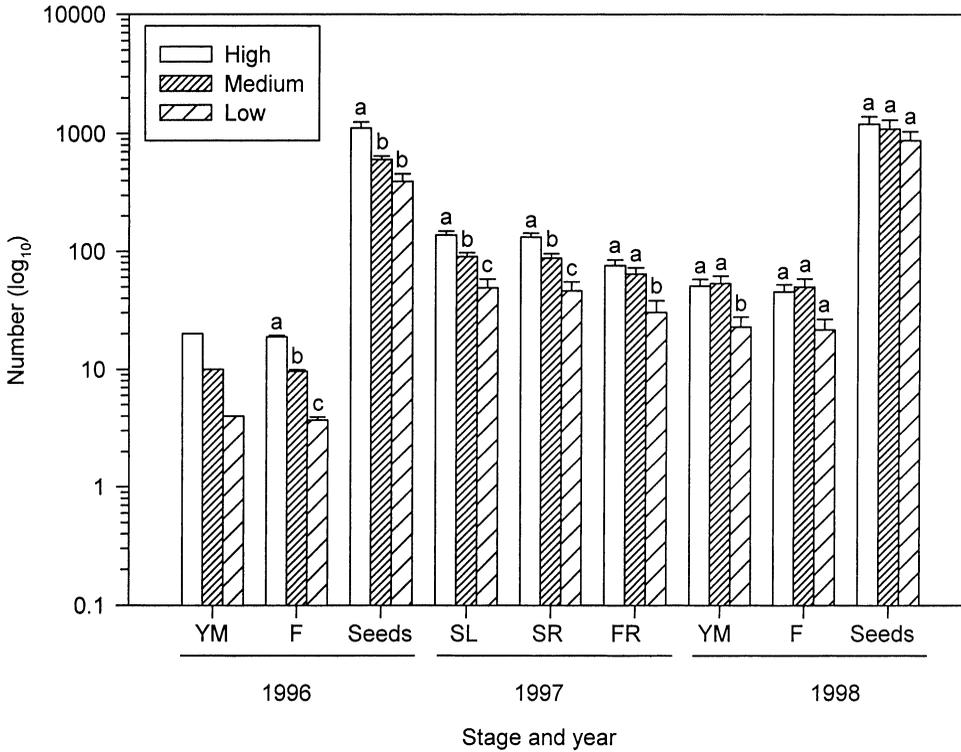


FIG. 4.—Number of *Alliaria petiolata* plants (+SE) present in low, medium and high density plots for cohorts 1 and 3 (1996–1998). Stages represented are seeds, seedlings (SL), summer rosettes (SR), fall rosettes (FR), second year young mature plants (YM) and second year flowering plants (F). Different letters above the bars indicate significant differences among density treatments within a stage class

medium and high density populations indicate steady growth over time with little risk of extinction under present environmental conditions (Fig. 8).

DISCUSSION

Demographic parameters may be affected by spatial factors including differences in local substrate (Huenneke and Sharitz, 1990) and variation in plant cover (Klemow and Raynal, 1983; Hartnet and Bazzaz, 1985), and by temporal factors including fluctuations in rainfall throughout the year (Klemow and Raynal, 1983; Wagner and Spira, 1994). In the present experiment survival, growth and fecundity of *Alliaria petiolata* were significantly affected by spatial variation in intraspecific plant density. Survival of plants in high density plots was lower than in either medium or low density plots, whereas plant biomass and seed production in 1998 were greater for plants in low density plots.

All *Alliaria petiolata* individuals surveyed followed an obligate biennial life cycle. The biennial nature of *A. petiolata* offers several benefits. Under conditions in which all stages of the life cycle are equally affected by environmental risks, there is no clear advantage to being biennial, but a biennial habit is beneficial when compared with an annual habit in environments with hazardous conditions for seedling establishment (Harper, 1967). *Alliaria petiolata* seeds may be dispersed to a wide range of habitats and being a biennial may be

TABLE 2.—Means (and SE) for vegetative and reproductive parameters measured for mature *Alliaria petiolata* plants grown under different original densities and harvested in June 1998. A one-way MANOVA indicated significant differences among density treatments (Wilks' Lambda = 0.902, $P < 0.001$). Different letters next to means indicate significant differences among densities for each variable ($\alpha = 0.005$). Percent total biomass allocated to shoot production was not included in the MANOVA due to autocorrelation with other variables

Variable	Density		
	Low	Medium	High
Number stems/plant	1.03 (0.02) ^a	1.01 (0.01) ^a	1.00 (0.00) ^a
Plant height (cm)	33.0 (1.3) ^a	25.7 (0.7) ^b	25.5 (0.8) ^b
Root biomass (mg)	75.6 (6.9) ^a	44.3 (2.7) ^b	45.5 (2.6) ^b
Shoot biomass (mg)	215.4 (22.0) ^a	102.8 (6.8) ^b	114.0 (7.6) ^b
Root:shoot ratio	1.1 (0.5) ^a	0.6 (0.03) ^a	0.6 (0.04) ^a
Fruit biomass (mg)	85.5 (8.5) ^a	49.0 (3.0) ^b	57.4 (4.1) ^b
Total biomass (mg)	376.5 (36.1) ^a	196.1 (12.1) ^b	216.9 (13.7) ^b
Root allocation (%)	25.9 (1.0) ^a	27.8 (0.5) ^a	27.6 (0.6) ^a
Shoot allocation (%)	54.3 (0.7)	50.9 (0.4)	50.1 (0.4)
Fruit allocation (%)	19.8 (0.6) ^a	21.3 (0.4) ^a	21.9 (0.5) ^a
Number fruits	4.0 (0.3) ^a	2.6 (0.1) ^b	2.7 (0.1) ^b

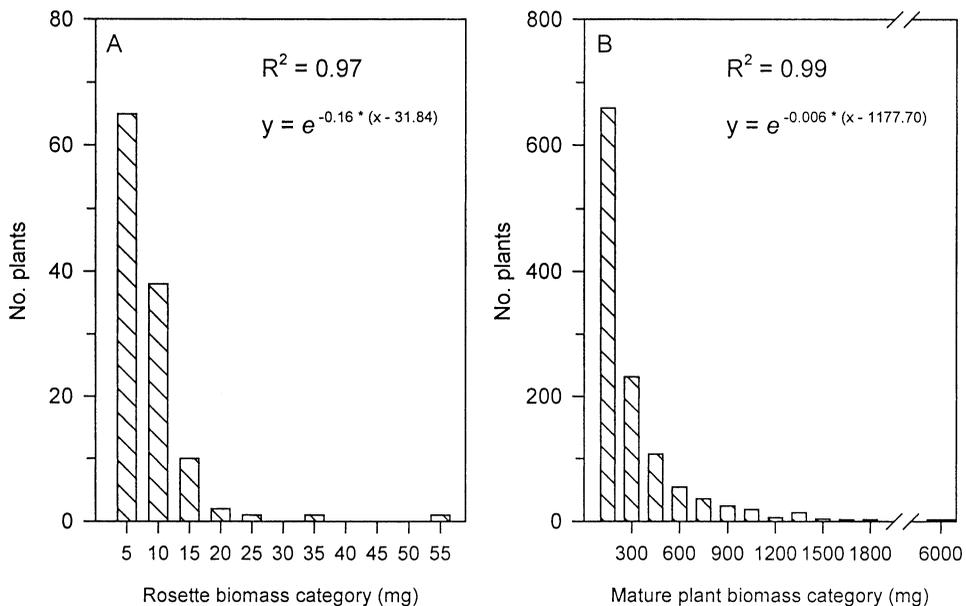


FIG. 5.—Number of plants present in each weight class across all plots at harvest in June 1998. Classes range from 0–5 to 50–55 mg for rosettes and from 0–150 to 5850–6000 mg for mature plants. (A) Number of rosette plants. (B) Number of mature, flowering plants

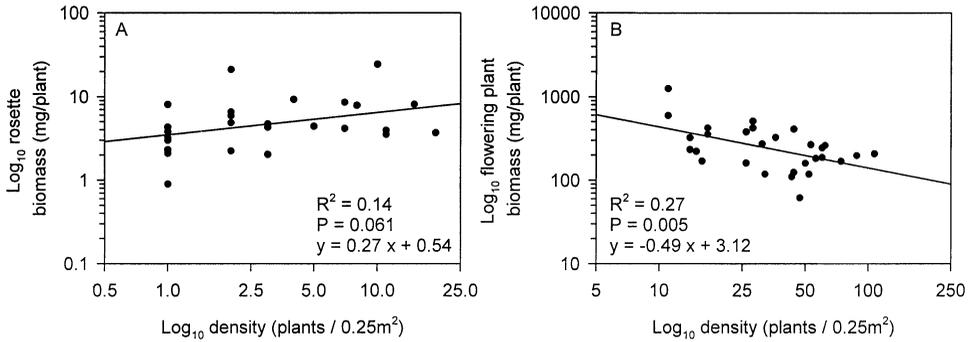


FIG. 6.—(A) Relationship between log₁₀ mean *Alliaria petiolata* rosette biomass and log₁₀ number of rosettes per plot for 30 plots. (B) Relationship between log₁₀ mean *A. petiolata* mature flowering plant biomass and log₁₀ number of flowering plants per plot for 30 plots

advantageous for this invasive plant when colonizing these new and potentially risky sites. An interesting consequence of its biennial habit is the cyclic nature of many *A. petiolata* populations, with vegetative plants dominant in one year and flowering plants dominant the next (Nuzzo, 1991; McCarthy, 1997). The population of *A. petiolata* in our study site actually functioned as two subpopulations that are one phase out of synchrony with each other (*i.e.*, one subpopulation is flowering at the same time the other is in the first year rosette stage). At this site, one subpopulation was greater in number than the other with vegetative plants clearly dominant one year (*e.g.*, 1997) and flowering plants dominant the next (*e.g.*, 1996, 1998). There were, however, both flowering and vegetative plants present each year. These two subpopulations may have arisen from two or more separate colonization events of the site occurring in different years. Having two subpopulations that are out of synchrony with each other may offer the advantage of increasing overall genetic diversity of the metapopulation, particularly since seed can remain dormant for several years and so seed from the same plant may germinate in different years (Roberts and Boddrell, 1983; Baskin and Baskin, 1992; Anderson *et al.*, 1996).

Alliaria petiolata seeds were dormant when shed in the summer and required several months cold stratification before initiation of germination, as observed by other researchers (Cavers *et al.*, 1979; Baskin and Baskin, 1992). Seeds germinated predominantly in March and April of all three study years, and seedlings were well established before the completion of canopy closure in June. Mortality was high across seedling and young rosette growth stages, although overall survival of cohort 2 (1996–1997) was much lower than survival of cohort 3 (1997–1998). Different life cycle stages often show differential responses to variation in environmental factors (Harper and White, 1974). High seedling mortality in the earliest stages of plant growth is well documented (*e.g.*, Silvertown and Dickie, 1981). Mortality can be due to such factors as drought, burial by soil (Silvertown and Dickie, 1981) or litter, predation, competition with pre-existing vegetation or other members of the same cohort and disease (Fenner, 1985). Competition, in particular, can be a serious threat to seedling survival (Fenner, 1985). In addition, for seedlings growing in dense populations or in forest understory environments, an ability to persist under conditions of low light availability is important (Fenner, 1985). Seedlings that germinate early and become established first have an advantage over later germinating seedlings (Ross and Harper, 1972; Weaver and Cavers, 1979; Zimmerman and Weis, 1984).

Alliaria petiolata seedlings germinated early in the spring when canopy cover and un-

TABLE 3.—Projection matrices and finite rates of increase (λ) for plots of *Alliaria petiolata* growing at varying initial densities. Proportions (and variances) are presented for stage transitions of seeds (S), seedlings (SL), rosettes in summer (RS), rosettes in fall (RF), second year rosettes (2R), and flowering plants (FP)

	S	SL	RS	RF	2R	FP
A. Low density ($\lambda = 1.45$)						
S	0.301 (0.015)	0	0	0	0	102.142 (2145.145)
SL	0.158 (0.013)	0	0	0	0	0
RS	0	0.935 (0.010)	0	0	0	0
RF	0	0	0.672 (0.058)	0	0	0
2R	0	0	0	0.787 (0.044)	0	0
FP	0	0	0	0	0.925 (0.028)	0
B. Medium density ($\lambda; = 1.38$)						
S	0.311 (0.009)	0	0	0	0	62.997 (218.390)
SL	0.153 (0.002)	0	0	0	0	0
RS	0	0.972 (0.001)	0	0	0	0
RF	0	0	0.724 (0.028)	0	0	0
2R	0	0	0	0.802 (0.025)	0	0
FP	0	0	0	0	0.960 (0.009)	0
C. High density ($\lambda = 1.26$)						
S	0.316 (0.007)	0	0	0	0	58.766 (470.396)
SL	0.147 (0.006)	0	0	0	0	0
RS	0	0.958 (0.002)	0	0	0	0
RF	0	0	0.569 (0.027)	0	0	0
2R	0	0	0	0.663 (0.017)	0	0
FP	0	0	0	0	0.940 (0.005)	0

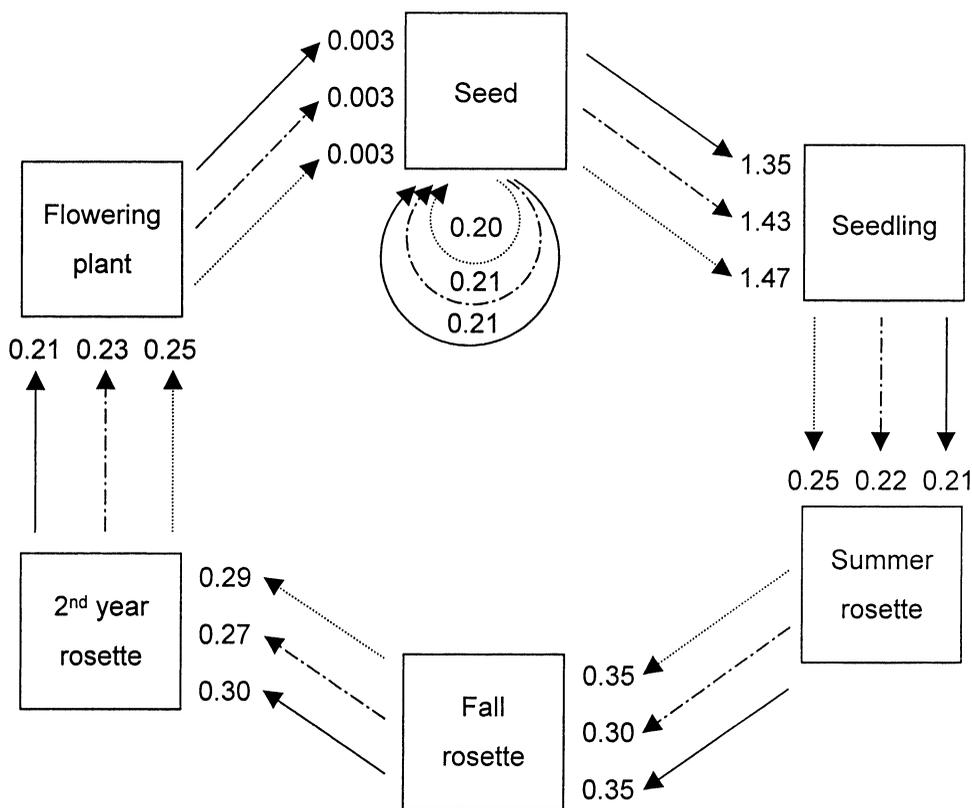
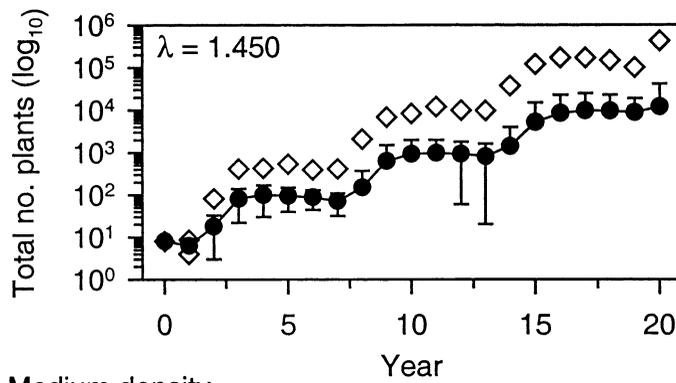


FIG. 7.—Generalized life cycle diagram of *Alliaria petiolata*, an obligate biennial. Arrows indicate transitions from one stage to another stage. Sensitivity values are shown and are based on data from Table 3. Dotted lines indicate low density plots, dashed lines indicated medium density plots and solid lines indicate high density plots

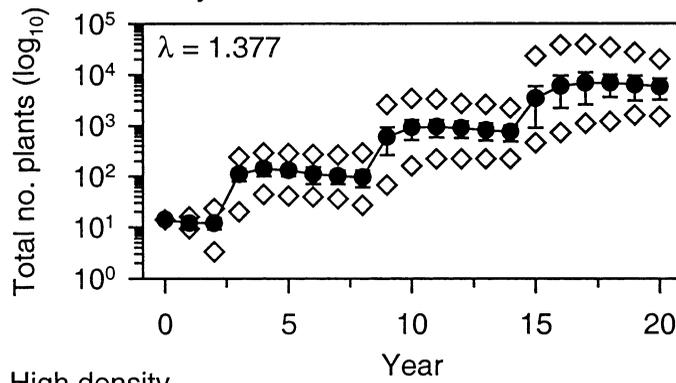
derstorey plant cover were low and light availability was high. This early germination clearly gives them an advantage over other understory species in establishment and usurpation of habitat space and environmental resources. In addition, plants remained green all winter and even though there was no appreciable increase in rosette size, the green rosettes can take advantage of the rising temperatures and high light availabilities of March and April to bolt and produce flowers and fruits as other understory plants are still germinating.

The observed difference in mortality for cohorts 2 and 3 with high survivorship in 1997 for cohort 3 was somewhat surprising since high mortality in the seedling and early rosette stages is commonly documented for *Alliaria petiolata* populations (Baskin and Baskin, 1992; Anderson *et al.*, 1996; Byers and Quinn, 1998). *Alliaria petiolata* is susceptible to drought stress (Mackenzie, 1995) and high mortality in plants is often correlated with dry summers (Cavers *et al.*, 1979; Byers and Quinn, 1998). However, our study area was in a moist forested habitat and it is likely that soil moisture levels remained high enough, even over the summer months, to prevent some of the drought-induced mortality observed in other habitats. Byers and Quinn (1998) noted higher survival to flowering in floodplain populations of *A. petiolata* compared with populations located in drier habitats. The higher mortality for cohort

A. Low density



B. Medium density



C. High density

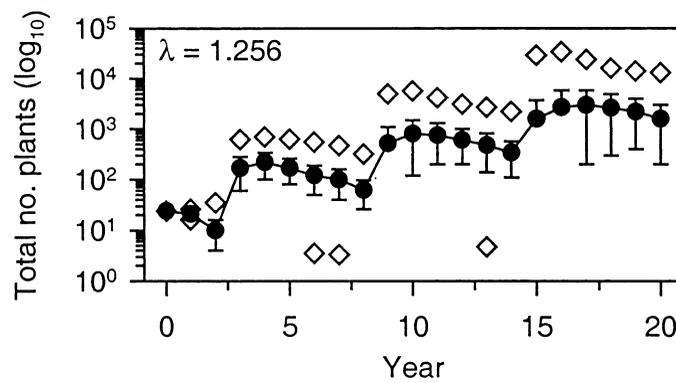


FIG. 8.—Simulated population growth over a 20 y period within *Alliaria petiolata* plots of (A) low, (B) medium and (C) high densities. Lines indicate mean population size (± 1 standard deviation). Closed circles are mean population size. Open diamonds indicate extreme values possible as a result of stochastic events

2 seedlings and rosettes may have been due to intraspecific competition with second year plants rather than abiotic factors. Baskin and Baskin (1992) documented 100% mortality of *A. petiolata* seedlings growing in plots with second year plants. When they removed second year plants, survival to flowering increased to 3%. Average survivorship of *A. petiolata* second year plants was high for all cohorts and density treatments (Anderson *et al.*, 1996; Byers and Quinn, 1998).

There were also significant differences in survival among plots for cohort 3 with the greatest survival in low density plots. These differences may reflect the significant differences among plots with respect to the number of seedlings and rosettes present in 1997. Low density plots had significantly fewer plants present in 1997, but due to lower mortality, by 1998 there were no longer any differences among plots in number of flowering plants present or in total seed production. In fewer than 3 y, the number of mature plants present increased in all plots, and differences in plant numbers previously documented among plots due to density, disappeared.

Seed production was high for cohorts 1 and 3. High seed yield is characteristic of many biennials and monocarpic perennials whose life cycles end with a "big bang of seed production" (Harper and White, 1974). Seed production in *Alliaria petiolata* ranged from 168–7756 seeds/m² in 1996 and from 1056–8034 seeds/m² in 1998. In contrast, in 1997 only 0–1400 seeds/m² were produced. These values are high, in general, but are low compared to estimates of seed production from other *A. petiolata* populations (19,060–38,025 seeds/m² in Ohio, Trimbur, 1973; 19,800–107,580 seeds/m² in Canada, Cavers *et al.*, 1979; 9533 seeds/m² in Northern Illinois, Nuzzo, 1991; 15,000 seeds/m² in Central Illinois Anderson *et al.*, 1996). Plant density, however, was lower on average for cohort 2 (1–4 plants/m², 1997) than for these populations (42 plants/m², Nuzzo, 1991; 60 plants/m², Anderson *et al.*, 1996), but higher for cohort 3 (86–199 plants/m², 1998). Lower seed production in 1997 was probably due to a smaller number of flowering plants, whereas lower seed production in 1998 may have been due to both low light availability at this forested site and high *A. petiolata* density within plots, both of which are related to reduced seed production (Meekins and McCarthy, 2000).

We found that *Alliaria petiolata* did produce a seed bank at this site. Seed viability was quite high in the laboratory (95.0% \pm 1.2), but in the field few seedlings were present compared with the number of seeds produced. Seed germination in the field is often low, but can range from 5% (Cavers *et al.*, 1979) to 87.5% (Baskin and Baskin, 1992). Although we found high viability for seeds in the seed bank, it is possible that much of the seed that remains in the seed bank will never germinate. Other invasive species have been reported to have high germination under controlled settings but low germination in the field (Bazzaz, 1986). It is possible that for many plant invaders, successful colonization of a site will be dependent on multiple introductions of a large number of propagules (Bazzaz, 1986).

Alliaria petiolata has been reported to form a small and short-lived seed bank (Baskin and Baskin, 1992), although in some habitats a seed bank seems to be absent, possibly due to habitat disturbances such as flooding (Byers and Quinn, 1998). Nuzzo (1991) and Anderson *et al.*, (1996) found that most seed germination occurred within 2 y of seed maturation. However, germination for up to 5 y after dispersal is possible, although percentages are low (0.1–1.5%, Roberts and Boddrell, 1983). If seed production is not a high risk stage of the life cycle, it would be advantageous for most of the seed produced to germinate each year. In contrast, seed bank formation would be an advantage in an environment in which synchronous seed germination poses a serious hazard for population survival (Harper and White, 1974). Clearly, seed bank formation would, therefore, pose a great benefit to an invasive species (Templeton and Levin, 1979).

In addition to dissemination to the new area and seed bank formation, tolerance of the primary periodic risks that typify an environment is important for species persistence in an area; therefore, species develop adaptations to accommodate those risks and they are not anticipated to be a significant determinant of population size (Harper and White, 1974). However, plants cannot adapt to intraspecific crowding and for this reason competition with neighbors for the same limiting resources is major source of plant mortality in populations (Harper and White, 1974). As the overall number of *Alliaria petiolata* rosettes per plot increased, plant biomass also increased. This positive relationship indicates that density dependent mortality was not an important determinant of survival for cohort 4 rosettes in these plots. In contrast, as the overall number of flowering *A. petiolata* plants per plot increased in 1998, plant biomass decreased, indicating that plants in cohort 3 may have been experiencing the detrimental effects of crowding. Although there was a negative relationship between flowering plant density and biomass, the slope of the regression line was still well below the self-thinning line slope of -1.5 proposed by Yoda *et al.* (1963), so it is possible that flowering plant density within plots could continue to increase before the full effects of self-thinning are apparent. Most rosette and flowering individuals present in the plots in June 1998 were of similar size, but there were also several very large individuals. Larger plants typically produce more fruits and seeds and could therefore make a greater contribution to the genetic constitution of the population over time.

The intrinsic rate of growth and reproductive rate of an invasive species, as well as the type of habitat invaded, will determine its rate of spread (Cronk and Fuller, 1995). Lambda values based on cohort 3 indicate that numbers of *Alliaria petiolata* in plots of different densities are increasing. A high population growth rate in a plant species may arise from clonal spread or seed production (Harper and White, 1974). Often plants that rely on high seed production are good colonizers that have a fugitive habit and are r -selected. In addition, the growth rate of a population of invasive plants may be tied with its ability to disperse (Auld and Coote, 1980). An advantage of a species being capable of dispersing its propagules and spreading away from parent plants is that it may suffer fewer of the detrimental effects of intraspecific density, disease and predation that can affect nonspreading species. Since *A. petiolata* is not capable of clonal spread, population increase is due solely to copious seed production (Cavers *et al.*, 1979). *Alliaria petiolata* is a good colonizer and can enter both disturbed and relatively intact habitats (Cavers *et al.*, 1979; Nuzzo, 1991). Although it is probable that most seeds are dispersed by gravity and land near the parent plant, seeds are also dispersed by water downstream of extant populations (Susko and Lovett-Doust, 1998) and by animals throughout a habitat (Lhotská, 1975). Spread is therefore either as an advancing population front or by establishment of disparate satellite populations (Nuzzo, 1993).

High growth rates are not uncommon in invasive species and species existing in non-equilibrium situations (Sarukhan and Gadgil, 1974; Werner and Caswell, 1977). Werner and Caswell (1977) reported λ values ranging from 0.63 to 2.60 for experimental populations of the semelparous, fugitive herb *Dipsacus sylvestris*, and Sarukhan and Gadgil (1974) reported similar high values ($\lambda = 0.095\text{--}4.665$) for three species of *Ranunculus*. *Cirsium vulgare*, a semelparous perennial common as a nonindigenous weed of pastures had λ values ranging from 0.81–2.53 (Bullock *et al.*, 1994). If the *Alliaria petiolata* population we studied continues to grow at a high rate, eventually the effects of intrapopulation density or some environmental change will limit further population expansion (Werner and Caswell, 1977).

The habitat of a population can impact which life history components have the greatest influence on population growth rates. The population growth rates of many forest understory plants depend on growth and survival more than seed production (Silvertown *et al.*,

1993; Silvertown *et al.*, 1996; Damman and Cain, 1998). For most semelparous herbs, however, λ is more profoundly influenced by the growth and fecundity transitions than by the stasis transitions (Silvertown *et al.*, 1993; Bullock *et al.*, 1994). *Alliaria petiolata* sensitivities indicated that the most important transition was from seed to seedling.

It is important to consider stochasticity when evaluating and predicting forest understory herb performance (Damman and Cain, 1998). Compared with low variability populations that live in predictable habitats, highly variable populations that live in stochastic environments tend to have greater extinction risks (Pimm *et al.*, 1988; Menges, 1991). However, it is possible that slow growth rates, high survival (Ehrlén, 1995), linear size-fecundity relationships, nonseed limited recruitment of new individuals and asymmetric plant competition can result in stable growth rates in stochastic environments (Crawley, 1990). The models of *Alliaria petiolata* growth in this habitat over the next 20 y indicated that numbers of plants in all density plots will increase over time with a greater possibility of rapid population increase than of extinction. Population growth will likely slow due to self-thinning, but this may occur after *A. petiolata* has had an opportunity to form a dense, virtually monospecific stand to the detriment of the resident understory community. A small population may quickly become extinct when confronted with demographic or environmental stochasticity (Boyce, 1977; Tuljapurkar, 1982; Benton and Grant, 1996). With an invasive species, however, even a small population may have the capacity to grow rapidly and behave like a big population. From a management perspective this means we cannot assume a small population means a small problem. In particular, invasive species that are autogamous or facultatively xenogamous can still pose serious threats.

However, caution must be used when forecasting population dynamics over time and sites since there can be considerable demographic variation among populations of herbaceous species (Angevine, 1983; Matlack, 1987; Menges and Dolan, 1998). Even late successional forests, which are assumed to be fairly stable environments, show evidence of spatial and temporal variation, both of which can affect plant performance (Barkham, 1980; Matlack, 1987; Horvitz and Schemske, 1995). Differences among sites, plots and years can significantly affect plant growth, survival and reproduction (Barkham, 1980; Svensson and Callaghan, 1988; Nobel, 1992; Oostermeijer *et al.*, 1996; Damman and Cain, 1998), therefore data collected for one population over a short time span may not reflect the general demographic trends of the species as a whole (Horvitz and Schemske, 1995; Silvertown *et al.*, 1996; Byers and Meagher, 1997). In addition, estimations of population growth rates that do not account for stochastic environmental and demographic variation may be inflated and incorrectly indicate sustained population persistence (Boyce, 1977; Tuljapurkar, 1982; Benton and Grant, 1996). For these reasons, long-term studies spanning a decade or more provide valuable information regarding demographic trends within populations and aid evaluation of different projection procedures (Kephart and Paladino, 1997).

Demographic variability for plant species among sites means that habitat heterogeneity needs to be taken into account when planning management strategies (Kephart and Paladino, 1997). The results of this experiment indicate what might happen within a newly established *Alliaria petiolata* population in a mesic hardwood forest. Growth rates within plots of varying density were all high and the number of plants in low density plots quickly expanded to equal the numbers present in high density plots. Thus, a small colonizing population can quickly become a threat to the understory community. Since *A. petiolata* is drought-sensitive, in a drier habitat, successful establishment may require the introduction of a larger number of seeds and both survival and population growth rates may be lower. The phenotypically plastic nature of *A. petiolata* and its ability to tolerate a wide range of environmental conditions (Dhillon and Anderson, 1999; Meekins and McCarthy, 2000)

means that many different types of habitats are vulnerable, and its behavior and spread in these habitats is likely to vary. The potential for rapid population growth in *A. petiolata* means that to be successful, management strategies need to be implemented early in the invasion process.

Future studies comparing *Alliaria petiolata* demography in native areas with invaded habitats, and surveying demographic variation over different types of invaded habitats, would further our knowledge about the spread of this and other nonindigenous species. Invasive species can present special problems for biodiversity conservation and therefore deserve further research.

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