GARLIC MUSTARD (*Alliaria petiolata* Bieb. [Cavara and Grande]) RATE OF SPREAD AND POTENTIAL IMPACT ON GROUNDLAYER SPECIES

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ABSTRACT:

Eleven permanent plots were established in seven forest communities in northern Illinois to monitor annual spread of the alien herb garlic mustard (*Alliaria petiolata*). Spread occurred at a relatively gradual pace throughout the region. Garlic mustard presence and mean frequency increased annually in all plots, and approximately doubled between 1989 and 1992, from 24% to 48% (presence) and from 31% to 55% (frequency). Mean cover increased annually for three years from 11.5% to 19.0%, but declined in 1992 to 10.5%, due to drought-induced mortality of rosettes (immature plants). Regionally, adult frequency in 1992 (18.7%) approximated adult frequency in 1989 (17.7%), implying little spread in one generation. However, adult survival was impacted by the drought, and the lack of increase over a single generation may be atypical. A separate population census showed a consistent annual increase in garlic mustard mean frequency and mean cover for all four years, and a total increase in both variables of >500% between 1989 and 1992.

Toothwort (*Dentaria laciniata* Muhl.) an ephemeral forest forb, experienced a highly significant decline in average cover after four years of association with garlic mustard. Toothwort cover averaged 79% when garlic mustard was absent all years, but averaged less than 31% after four years of co-occurrence.

At the community level, no clear effect of garlic mustard presence on herbaceous cover or on mean species richness could be detected. These changes may require a longer time period to become apparent. Community susceptibility to invasion appeared related to frequency and intensity of disturbance, with garlic mustard spreading more rapidly in communities with frequent disturbances than in rarely disturbed sites.

INTRODUCTION:

Invasive plant species pose a severe threat to the structure and integrity of native plant communities (Coblentz 1990, Mooney and Drake 1989, Usher 1988, Vitousek et al., 1987). Despite the acknowledged threat posed by invasive plants, there has been little study of either the rate of invasion or the impact of the invading plant species on native components of the invaded community. Invasion studies have been based primarily on herbarium specimens or other historic data sources (Lacey 1957, Mack 1981). Only a limited number of studies have been conducted to monitor the actual rate at which an alien plant species spreads through an invaded community over time. Myers and Berube (1983) monitored advance of diffuse knapweed (*Centaurea diffusa*), and determined that the front advanced 120m over a three year period. The area covered by iceplant (*Mesembryanthemum crystallinum*) within a 6m x 10m permanent quadrat approximately tripled in four years (Vivrette and Muller 1977).

The impact of an invading species on native species has been inferred through comparison of paired stands with and without the invading species (Forcella and Harvey 1983, Young and Evans 1970), and by comparison of the same stand or region at two different points in time, using quantitative data or a combination of historical photographs and writings, maps, herbarium specimens and GLO notes (Buffington and Herbel 1965, Lacey 1957, Mack 1985, Thompson et al., 1987). Both approaches provide useful information concerning compositional differences between invaded and intact communities. However, neither approach documents the process of change, nor ensures that the observed differences are due to the increased presence of the invading species; differences between paired sites may reflect initial inherent dissimilarities independent of alien invasion, while differences in one site between two widely spaced points in time may result from processes other than, or in addition to, presence of an alien species.

Garlic mustard (*Alliaria petiolata*), a naturalized European obligate biennial herb that aggressively invades forested communities in Illinois (Nuzzo 1992a), and throughout the upper Midwest (Nuzzo 1992b), is a relatively recent invader that appears to threaten community structure in deciduous forests (Schwegman 1989). The species was first recorded in Illinois in 1918, and in 1991 occurred in state parks, nature preserves and other natural areas in 44 counties (Nuzzo 1992a).

Field observations of garlic mustard in northern Illinois indicate that the plant frequently dominates the herbaceous layer of invaded deciduous forests within ten years of initial entry, and that the native herbaceous groundlayer appears to decline in species richness and cover. Rejmanek (1989) stated that an alien plant's total cover is greatest after 5-10 years, after which it remains stable or declines. This pattern of increase, domination, and subsequent gradual decline has been observed by the author in some (but not all) heavily infested forests, always in association with an apparent loss of much of the groundlayer community and a concomitant increase in amount of bare soil.

To quantify and verify these observations, a program was established to assess the rate at which garlic mustard spread through different forest communities, and to monitor groundlayer community structure relative to garlic mustard invasion. Specific research questions were: 1) How rapidly does garlic mustard spread through invaded deciduous forests? 2) Does continued presence of garlic mustard lead to a decline or overall change in species richness, species composition, or total cover of the groundlayer community? and 3) Do different natural communities differ in susceptibility to invasion, spread, or impact of garlic mustard?

Garlic mustard rate of spread within a community and potential impact upon the herbaceous groundlayer is related to the species life history. Aspects of garlic mustard's life history and biology have been investigated by Murley (1951), Trimbur (1973), Lhostka (1975), Cavers et al. (1979), Roberts and Boddrell (1983), Byers and Quinn (1987, 1988), Babonjo et al. (1990), and Kelley et al. (1991), and summarized in Cavers et al. (1979) and Nuzzo (1991).

Garlic mustard has a four year life cycle in northern Illinois: seeds germinate in early spring of year 1, immature plants overwinter as basal rosettes, flowering occurs the following spring, and seeds are produced and disseminated in summer of year 2. In northern Illinois plants produce an average of 350 seeds, and individual robust plants form up to 7,900 seeds (Nuzzo unpublished). Seeds remain dormant in the soil until germination in March through May of year 4 (Cavers et al,. 1979). Germination occurs in the spring of year 3 in southern locales (Baskin and Baskin 1992). The majority of germination occurs within two years after dormancy is broken, and seeds remain viable for up to 5 years (Lhotska 1975, Roberts and Boddrell 1983, Baskin and Baskin 1992).

METHODS

Study Sites

Eleven permanent plots were established in seven forested sites in northern Illinois in 1989 (Figure 1, Table 1): Selected sites met four criteria; 1) moderate to high garlic mustard density within a localized area, 2) Natural Area quality rank of A or B (*sensu* White and Madany 1978), 3) diverse herbaceous groundlayer, and 4) owner commitment to protect the study site for at least 3 years.

Study sites were located in dry-mesic and mesic upland forest, and in mesic and wet-mesic floodplain forest. The majority of the plots contained a single natural community. However, four plots crossed community borders: the three plots at Pilcher Park were located at right angles to Hickory Creek, traversing wet-mesic and mesic floodplain forest; and the plot at Indian Head was established on a north-facing ravine slope, resulting in a distinct topographic/microclimatic gradient from top to bottom.

Three sites were subjected to natural disturbance during the course of the project. Pecatonica was flooded for two weeks in July 1990, Bliss 2 was hit by a severe windstorm that blew down several large trees in July 1990, and Dan Wright underwent heavy browsing by white-tail deer each year. All sites experienced a severe drought in the fall of 1991 and again in the spring of 1992.

Data Collection

Each 25m x 50m plot contained six parallel 50m transects established at 5m intervals. One end of each plot was randomly established within a population of garlic mustard and the other end extended beyond the apparent front. Data were collected twice annually in May and August, from August 1989 to August 1992. Phenological indicators were recorded to ensure that data were collected at the same phenological date each spring. Garlic mustard presence and age class were recorded by square meter on either side of each transect in May (seedling and adult) and August (immature rosette), for a total of $600m^2$/plot. All other data were recorded within $1m^2$ permanent quadrats located at 5m intervals along each transect (36 quadrats/plot). Collected data consisted of garlic mustard adult density, and percent cover by seven cover classes (<1%, 1-7%, >7-25%, >25-50%, >50-75%, >75-93% and >93%) of garlic mustard adults, seedlings, and total cover in spring, and immature rosettes in summer. Presence and percent cover class were also recorded for all herbaceous and graminoid species, and all woody species <30cm tall rooted in the quadrat, and for exposed soil, leaves, and wood. A separate study site was established in an intermittent stream channel in MacArthur Woods Nature Preserve (dry-mesic upland forest) in Lake County, IL, where garlic mustard occurred at low density in August 1989. A permanent 125m transect was established in the center of the stream channel, and garlic mustard presence and percent cover by size class were annually recorded each July by m^2 relative to the transect. The entire garlic mustard population was mapped annually.

Data Analysis

Rate of spread was assessed using both qualitative (presence on maps) and quantitative (frequency and cover) data from each plot on a local level (individual plots) and a regional level (all plots combined). Spring data were used for seedlings, adults, and total garlic mustard, and fall data for rosettes.

Plant species presence and cover data recorded in the same quadrat in spring and summer were overlaid, and the higher cover value assigned to each species in each quadrat was used for data analysis. Because the quadrats were located in the same position in May and August, selection of the higher of the two values accurately reflected maximum growth of each species within that quadrat. Percent cover of each species was based on cover class midpoints (for example, >25%-50% cover was recorded as 37.5% cover). These cover values were subsequently summed within life form groups to produce total herbaceous, graminoid and woody cover for each year. Graminoid cover was combined with herbaceous cover in sites where graminoid cover was low. Species richness/quadrat and /plot were derived from the overlaid data sheets. Garlic mustard was excluded from the quadrat species counts and included in the community counts.

Four species were selected for testing against garlic mustard presence and abundance based on life form and relative abundance in the plots. Selected species consisted of toothwort (*Dentaria laciniata*; ephemeral perennial), wild phlox (*Phlox divaricata*) and wild ginger (*Asarum canadensis*; both shallowly rooted rhizomatous evergreen perennial herb), and false solomon's seal (*Smilacina racemosa*; deeply rooted rhizomatous deciduous perennial herb).

Garlic mustard cumulative presence in each quadrat was based on number of years the species was recorded in a quadrat in spring; potential values ranged from 0 (never present) to 4 (present all four years). Number of years of high garlic mustard cover was determined by summing the number of times that combined cover of seedlings and adults equaled or exceeded 37.5% cover. Using this method, a quadrat could be assigned a value of 4 for continuous presence, but a value of 0 for high cover if recorded cover was consistently lower than 37.5%. Data were used to assess at the quadrat level changes in native vegetation relative to garlic mustard presence and abundance.

Differences between data sets were tested by one-way and two-way ANOVA, repeated measures ANOVA, independent t-tests, Kruskal-Wallis tests, and Chi-square. Repeated measures analyses of variance were used to test for change through time within quadrats and plots. Impact of garlic mustard cumulative presence on community structure and on individual species was tested by one-way ANOVA, and by the non-parametric Kruskal-Wallis test. Mean values were tested for homogeneity of variances by Cochrane's C test. Non-parametric tests were conducted when variances were heterogeneous ($p \leq 0.05$). Where appropriate, cover values were arc-sine transformed prior to statistical analysis; tests refer to transformed data, and results are reported as raw data. Results of one-way and two-way ANOVAs were used to interpret results of non-parametric tests. Data were analyzed using Statgraphic software on a 386 SX-20.

It is emphasized that the design of this project places restrictions on the interpretation of some statistical tests. First, all plots were randomly located within a selected area, but quadrats within the plots were systematically spaced. Second, data were collected in permanent quadrats to monitor actual change through time, and therefore are subject to autocorrelation. Third, plots within the same site were sufficiently different that their usefulness as replicates was limited.

RESULTS

Rate of Spread

Regional

During the four year period, garlic mustard presence doubled at the regional level, from an average of 24% presence in 1989 to an average of 48% in 1992 (Figure 2). During the same time period, mean frequency increased significantly from 30.83% to 55.29% (Figure 3); and average cover increased nonsignificantly for three years, from 11.46% in 1989 to 19.06% in 1991, before declining to 10.46% in 1992 (Figure 3). The decrease reflects the impact of a severe late summer drought in 1991, which reduced the rosette population in fall 1991 (after data collection) and consequently the adult population in spring 1992.

Local

Similar increases were recorded during the same time period within individual plots, although garlic mustard presence (Figure 2), frequency and cover varied substantially between plots, and fluctuated greatly between years within plots (Table 2). These variations reflect both the biennial nature of this plant, and the impact of different growing seasons. In general, all plots experienced an annual increase in garlic mustard presence and frequency. Within individual plots, presence increased by 1.4 to 10 fold during the four year period (Table 2); the average increase was 263%, or more than double the initial presence. During the same time period frequency rose 1 to 3 fold within plots, and the average within-plot increase was 186% in four years (Table 2). In contrast, average cover within individual plots increased annually between 1989 and 1991 with a few exceptions, but then declined in 1992 in 10 of the 11 plots (Table 2).

Age Class

The three age classes studied--seedling, rosette and adult--exhibited different scales of variation through time. Seedlings generally showed the least variability between years, while adult cover and density exhibited the greatest, both within individual sites and regionally.

Seedling and Rosette

On a regional basis, both seedling and rosette frequency increased annually (Figure 5). Seedling frequency increased from a mean of 39.45% in spring 1990 to 50.45% in spring 1992, and rosette frequency increased from 24.45% in fall 1989 to 54.64% in fall 1992. Seedling cover exhibited modest variation, averaging 10.81% in 1990, 13.58% in 1991 and 8.91% in 1992 (Figure 4). Rosette cover more than doubled in three years, from a mean of 5.69% in fall 1990 to 13.42% in fall 1992.

As would be expected, annual changes in cover and frequency were greater within individual plots than at the regional level (Table 3). Seedling and rosette frequency fluctuated widely through time within each plot, but in all cases were greater in 1992 than in 1990. In contrast, seedling percent cover was lower in 1992 than in 1990 in eight of the 11 plots. Average seedling cover consistently decreased each year in all three plots located in Pilcher Park, and alternately increased and decreased in the remaining plots. Rosette cover was greater in 1992 than in 1990 in ten of the plots.

Adult

Regionally, all measures of adult abundance--frequency, cover and density--increased between 1989 and 1991, but subsequently declined to near or below the 1989/1990 levels in 1992 (Tables 3 and 4). Average adult frequency increased between 1989 and 1991 from 17.73% to 28.72%, then dropped to 18.73% in 1992. Adult cover averaged 5.84% in 1990, 6.94% in 1991, and only 1.70% in 1992. Similarly, adult density increased from an average of $4.72/m^2$ in 1990, to $7.66/m^2$ in 1991, and then declined to $1.77/m^2$ in 1992, less than half the initial value. Average densities within sites ranged between 0 and $42.33/m^2$.

Adult frequency, cover and density in individual plots fluctuated greatly between years, more than any other age class, alternately increasing and decreasing, or consistently decreasing. Adult frequency varied by 200% to 400% between years within plots, while adult cover varied by up to 14 fold. Density exhibited the greatest variation between years; in one site (Bliss 3) density declined from an average of $30.82/m^2$ in 1991 to $0.22/m^2$ in 1992. Mean density was higher in 1992 than in 1990 in only one plot (Pecatonica), and was substantially lower in all other plots. In general, annual fluctuations in average adult cover mirrored, but greatly exceeded, fluctuations in average adult frequency within individual plots.

Generational Change

Garlic mustard is a biennial with a 20 month seed dormancy. Therefore, a generation requires four years (adult to adult) to complete. Frequency of one complete generation, 1989 to 1992, was followed during this study. Regionally, adult frequency averaged 17.73% in 1989. Seedlings in 1991, presumably produced by the 1989 adults, occurred at an average frequency of 46.45%. By August, frequency of rosettes declined to 35.91%, and in spring 1992 adults occurred at a frequency of 18.73%, approximately equal to the 1989 adult frequency (Figure 6). This low adult frequency is attributed to a severe late summer drought in 1991, which resulted in high overwinter mortality. The 48% decline in frequency from the rosette to adult stages in the 1989/92 generation may be atypical: The prior two generations experienced declines of 31% and 5% between the same growth stages. The 1990-1993 generation exhibited a trend similar to that of the 1989-1992 generation through the rosette stage; seed-producing adults and seedlings had similar and slightly higher frequencies than the prior generation (Figure 6). In contrast to the decline exhibited in the 1989-1992 generation, rosette frequency in the 1990-1993 generation increased slightly relative to seedling frequency. Adult frequency of this generation was not recorded in 1993 as the study was concluded in fall 1992; based on a three-year average overwinter decline of 28%, the potential 1993 adult frequency would be approximately 39%, more than double the initial 1990 adult frequency.

Census

Garlic mustard spread was censused annually in a single site (MacArthur Woods; Table 5). Total area occupied by garlic mustard increased annually from 124m^2 in 1989 to 136m^2 in 1990, 473m^2 in 1991 and 635m^2 in 1992, resulting in a >500% increase in four years. Total frequency and cover also increased annually, and each increased more than 500% over the four year period. In the single generation censused (1989-1992), adult frequency increased more than 38-fold, from 0.33% to 12.46%, and adult cover increased nearly 60-fold, from 0.05% to 2.96%. These increases are substantially greater than those recorded in the 11 plots, and may reflect the impact of different habitat type (an intermittent stream bed vs upland or lowland forest), or inherent differences between a census and a sample. Overwinter changes between rosette and adult stages were recorded for three years. Each year, frequency of adults relative to rosettes consistently declined (by 26%, 99%, and 36%), while mean cover consistently increased (by 339%, 118%, and 106%).

<u>Abiotic Conditions</u>

No significant relationship was detected between garlic mustard presence/absence in spring and percent cover of soil, wood or leaf litter in any year at eight of the plots. In the three plots at Pilcher Park, quadrats with garlic mustard present had significantly lower leaf litter and higher soil cover than quadrats without garlic mustard, in one or more years. However, all three plots are adjacent to Hickory Creek, which annually floods the portions with garlic mustard: Floodwaters remove leaf litter and expose soil, and the relationship between these variables and garlic mustard is more a reflection of flood impact than of garlic mustard site requirements.

Seedling cover in spring was unrelated to percent cover of soil or leaf litter in either the current spring or the prior fall. In a single plot (Bliss 3) seedling cover increased non-significantly as bare soil decreased and leaf litter increased.

Community Structure over Time

Species Richness

Total species richness within each plot did not vary significantly between 1990 and 1992, with the exception of Bliss 2 (Table 6). This plot was hit by a severe windstorm in July 1990, which uprooted many of the canopy trees; the significant increase in species richness is attributed to natural disturbance rather than garlic mustard presence.

Within-plot mean species richness did not vary significantly between 1990 and 1992 at any of the sites, with the exception of Indian Head (Table 7). This plot experienced a significant increase in species richness, from a mean of 7.58 species/m^2 in 1990 to 10.25/m^2 in 1992. No explanation is proposed for this increase. Interestingly, this plot also experienced a non-significant decline in total number of species present during the same time period.

Percent Cover

Mean herbaceous and mean woody cover within each plot varied between years, and no between-plot trends were apparent (Table 8). In nine plots mean herbaceous cover was similar in two of the three years, and higher in one year. The year that higher cover occurred varied among plots, both within and between sites. Repeated measures ANOVA indicated significant differences between years in five plots, four of which had a large increase or decrease in cover one of the three years. The differences may be weather related; spring 1991 had higher than usual precipitation, while summer 1991 and sprig 1992 had lower than normal precipitation. The significant difference in herbaceous cover at Dan Wright reflects the impact of deer herbivory. These differences were attributed to natural variation through time rather than to influence of garlic mustard presence (see below); additional research is needed to determine if these differences actually represent a trend and not normal variation.

Mean woody cover (all woody vegetation <30cm height, including woody vines) also varied between years within plots. As with mean herbaceous cover, no particular trends were apparent over time, although the presence of tree seedlings was much lower in 1992 than in prior years.

Garlic Mustard Impact on Community

Comparisons between 1992 herbaceous cover and cumulative presence and cover of garlic mustard yielded mixed results (Table 9). No significant differences were detected in six plots. At Bliss 2 herbaceous cover consistently declined with increased presence of garlic mustard. This likely reflects the impact on toothwort (see below), which accounted for >80% of total herbaceous cover. At Indian significant variations in herbaceous cover were unrelated to increased presence or cover of garlic mustard. In all three Pilcher plots herbaceous cover increased significantly with increased presence and increased cover of garlic mustard: however, this apparent relationship is attributed to differences in community and not to impact of garlic mustard. The floodplain portion of each plot had higher vegetation cover and was the site of initial colonization by garlic mustard, whereas the upland portions had very low herbaceous cover and limited invasion by garlic mustard. Several additional years of data are needed to detect actual differences that may be attributed to garlic mustard influence on community structure.

Comparisons between 1992 species richness and cumulative presence and cover of garlic mustard likewise yielded inconclusive results (Table 10). Significant changes in species richness were detected only at Bliss 1 and all three Pilcher plots. At Bliss 1 species richness was significantly greater in quadrats that contained garlic mustard one or more years than in quadrats that never contained garlic mustard. However, no significant differences were detected between species richness and cumulative cover of garlic mustard. It is assumed that any effect of garlic mustard presence on other vegetation would increase with greater abundance of garlic mustard: the significant effect of presence, but not of abundance, on species richness the interpretation of this result. At the three Pilcher plots significant increases in species richness were attributed to the variable influence of two distinct communities and not to the cumulative presence or cover of garlic mustard. No apparent trends in species richness were detected in the other nine plots: species richness appeared to increase with garlic mustard presence in some plots, and to decline in other plots.

Garlic Mustard Impact on Individual Species

Of the species tested, toothwort was the only forb that exhibited a strong and highly significant difference in cover with increased association with garlic mustard presence (X^2=34.0035) and cover (X^2=31.5612), p<0.0001; Table 11, Figure 7). In the three Bliss plots, toothwort mean cover exceeded 78% in quadrats that had no garlic mustard during the four year period, in contrast to <31% mean cover in quadrats with four years exposure to garlic mustard. Mean cover decreased from 66% (garlic mustard cover <37.5% all years) to less than 33% (four years with garlic mustard cover ≥37.5%). Two-way ANOVA indicated that the reduction in toothwort cover occurred independent of the effect of plot.

A noticeable decrease in toothwort height and flowering activity was apparent in quadrats with high garlic mustard cover. Although these variables were not measured, toothwort plants appeared stunted and failed to flower in quadrats that had abundant garlic mustard. In contrast, toothwort were taller and more robust, and had numerous flowers, in quadrats that lacked garlic mustard.

DISCUSSION

Garlic mustard spread at a moderate rate during the three and one half year study period. Some individual plots experienced very rapid increases while in other plots spread was more gradual. The pattern of spread within sites was one of a ragged advancing front, supplemented by establishment of satellite plants distant from the front, and by invasion of plants from fronts outside the plot. This general pattern was detected at the regional level (Nuzzo 1992a, 1992b). Because the front was discontinuous, lineal spread (meters/year) was not quantifiable.

Across the region on an annual basis, garlic mustard's presence and frequency consistently increased, from an average of 24% presence (30.8% frequency) in 1989 to 48% presence (55.3% frequency) in 1992. During the same time period garlic mustard abundance, as measured by percent cover, showed a modest and nonsignificant increase for the first three years, followed by a sharp decline in the fourth year. Similar results were obtained in the population census, with cover and frequency consistently increasing each year. These results imply an invasion strategy whereby garlic mustard initially spreads relatively rapidly through a region at low abundance, and subsequently increases population size within invaded communities.

As would be expected, cover and frequency varied more within communities than across the region, alternately increasing and decreasing. These annual fluctuations in frequency and cover are of lesser importance than overall change through time. At all sites, garlic mustard occurred more frequently in 1992 than in 1989, and at two sites covered a greater proportion of the study area at the end of the four year period.

The greatest increases in presence occurred in sites subjected to large-scale natural disturbances. Pecatonica, flooded in mid summer 1990, experienced a 241% increase in presence between 1989 and 1992. The flood distributed the seedbank throughout the site, and the following spring (1991) seedlings carpeted the forest floor, occurring with 100% frequency and 46% mean cover. Garlic mustard presence at Bliss 2, hit by a severe windstorm in summer 1990, increased 1000% during the same time period. This response substantiates the premise that spread of invasive species is facilitated by site disturbance (Forcella and Harvey 1983, Lepart and Debussche 1991, Henderson and Wells 1986). Anthropogenic disturbance presumably has a similar effect on spread rate of this invasive plant, which is frequently observed spreading along trails and roads within forested areas (Nuzzo 1992a). Anthropogenic disturbance has been implicated in the invasion of many alien species into natural areas (MacDonald et al. 1989).

Frequency and cover of each age class fluctuated from year to year within each plot, either alternately increasing and decreasing, or continuously decreasing through time or, in the case of seedling frequency, increasing at three plots through time. No age class exhibited a continuous increase in cover through time at any site. Across the region, seedling frequency increased annually, and rosette and adult frequency increased for three of the four years.

Annual fluctuations in population size are typical of biennial species. Modifying factors in the case of garlic mustard are the twenty month seed dormancy, and the moderate seedbank survival time (2 to 5 years). These factors combine to alter the typical "all or nothing" strategy of many biennial species (Kelly 1985), and to maintain garlic mustard's presence in a community on an annual basis. This is exemplified by the presence of seedlings at all sites every year, at frequencies ranging from 8% to 100%. Once a large number of plants survive to reproduction, a seedbank is established that will maintain garlic mustard presence despite one or more years of low seed production. Following a year of high seed production a site may have few or no flowering adults present, depending on initial abundance and mortality rates. Seedlings germinate two years after seed production, and are frequently obscured by taller vegetation, even at high densities. If a large proportion of these seedlings survive to adulthood (as occurred in 1991), the "sudden appearance" of an extensive population of flowering plants creates an impression of a population explosion. In reality, invasion and spread occur more gradually, with years of rapid increase modified by years of gradual spread or even decline.

Frequency may be a more accurate measurement than cover of the invasive potential presented by this species, as presence, rather than abundance, is believed to be the critical factor in the potential spread of this alien. Cover reflects both abundance and vigor of plants, which is affected by local growing conditions. Drought frequently contributes to the small stature of plants, particularly of rosettes. However, all rosettes that survive the winter produce flowers the following spring (Cavers et al.1979). Since garlic mustard is self-compatible (Cavers et al.1979) a single plant is theoretically sufficient to repopulate a site, and once a seedbank is established the species will presumably remain present at a site.

A generation requires four years to complete, based on a 20 month seed dormancy, and the four years of this study monitored progression of plants from parts of three generations. A single generation was followed in entirety, from 1989 adult to 1992 adult. This generation experienced substantial mortality at the rosette stage due to a severe drought in fall 1991, resulting in an overall decline in adult cover and frequency at most sites. In the population census site, located in a dry streambed of a seasonal stream, the drought may have favored survival and spread of plants, as under conditions of normal or greater than normal precipitation, plants in this streambed would be removed by flooding.

The overwinter rosette-to-adult stage may be the most sensitive stage in spread of this plant. Under typical conditions, cover increases between the rosette and adult stages, as plants expand in early spring and produce flower stalks. This occurred in only three plots in 1989/1990, five plots in 1990/1991, and in none of the plots in 1991/1992. However, in the population census at MacArthur Woods, mean cover increased annually between the rosette and adult stages, despite a consistent decrease in frequency.

In the early stages of invasion a site may be dominated by either seedlings or adults (Nuzzo 1991). Once the seedbank is adequately established, seedlings and adults will co-occur, and increase the rate at which this mustard spreads through a forest. The effect of seedbank can be monitored at Pecatonica, where a 1990 midsummer flood eliminated the rosette (1991 adult) population. Seedlings that germinate in 1993 (after this study was terminated) will be entirely from the seedbank.

There is some question regarding garlic mustard's seed dormancy period. In southern climates the plant has been demonstrated to have an 8 month dormancy (Baskin and Baskin 1992), compared to the 20 month dormancy demonstrated in northern climates (Cavers et al., 1979). The Baskins theorized that dormancy is broken following exposure to temperatures fluctuating near 0 degrees Celsius, and that continuously low temperatures inhibit germination. It is unclear whether this dormancy is genetically or environmentally controlled, or both. If environmentally controlled, a mild winter in northern Illinois could result in germination of seeds produced both one and two years earlier, which in turn would lead to an increase rate of spread. Additional study is needed to ascertain what factors control seed dormancy of this species.

The impact of garlic mustard on community structure was difficult to detect after three years of monitoring. There was no clear trend in herbaceous cover or species richness that could be directly attributed to garlic mustard's presence. Changes at this scale may require a longer time period to become apparent. Monitoring all sites in 1994 and again in 1997 may be sufficient to detect changes at the community level, and will permit following two generations (1991-1994, and 1994-1997).

Rejmanek (1989) theorized that the amount of vegetative cover, and/or total species richness, may be an accurate indicator of a community's resistance to alien invasions. Such an interaction was not apparent in this study, nor was the inverse i.e.; the amount of bare soil was not related to invasion of garlic mustard. Rejmanek (1989) also theorized that invading species may have different rates of invasion in different communities, depending on succession, moisture gradient, and natural disturbance regime. For example, the same community at different ages or successional stages will support more aliens in early stages than in late stages. Again, qualitative comparisons in garlic mustard increase between community types (oak dominated vs maple dominated) and along a moisture gradient (dry-mesic to mesic to wet) failed to yield any apparent trends.

The only factor that appeared related to the observed increase in garlic mustard presence over the four year period was disturbance. Each plot was ranked relative to other plots by an arbitrarily assigned disturbance level: major disturbances (summer flood and windthrow) were ranked highest, annual disturbances (flooding and deer herbivory) were placed in the middle, and sites without apparent natural or anthropogenic disturbance were ranked last (Table 12). Plots with severe or frequent disturbances had larger increases in garlic mustard frequency than plots with comparatively low disturbance levels. Although this is an arbitrary ranking, it does imply that invasion of garlic mustard, and possibly other alien species, is enhanced by various disturbance regimes. Different disturbance regimes have been strongly implicated in the spread of invasive species (Hobbs 1989, Mack 1981, Mack 1988).

While the impact of garlic mustard at a community level was unclear, the impact on a single species was dramatic and clearcut. Toothwort is an ephemeral mustard that completes its lifecycle in April and May, the same time period when garlic mustard seedlings germinate, and rosettes experience a rapid growth expansion and flower stalk elongation. The significant decline in toothwort cover may result from direct competition for resources, and/or from alleopathic chemicals produced by garlic mustard, an effect demonstrated in the laboratory (Kelley et al., 1991). The stunted growth and failure to flower of toothwort plants growing adjacent to garlic mustard lends support to an alleopathic interaction.

The reduction in toothwort cover implies that garlic mustard may directly impact other crucifer species, and/or may reduce presence and cover of other ephemeral species. Tests of this potential interaction on three other ephemeral species failed to show such an interaction: Cover of spring beauty (*Claytonia virginiana*) and of two trillium species (*Trillium flexipes* and *T. recurvatum*) did not vary significantly relative to garlic mustard presence or cover. Again, the three year period of this study was too short to detect vegetational changes that occur over a longer time period. Additional monitoring is needed to verify if there is an impact on other individual species or on the community as a whole that can be attributed to garlic mustard.

CONCLUSIONS

Garlic mustard spread at a moderate rate across the region, doubling in frequency in four years, and increasing 138% to 1000% within communities. Advance occurred in the form of an irregular front with multiple satellite populations occurring beyond the front.

No direct relationship between garlic mustard presence and species richness or total cover of the groundlayer community was detected. At the species level, however, a strong effect was detected: Toothwort, an ephemeral perennial crucifer, decreased significantly in mean cover after four years association with garlic mustard, from an average of 78% to 30% cover. The natural communities in this study did not appear to differ in susceptibility to invasion, spread, or impact of garlic mustard. Disturbance regime appeared most closely, although conjecturally, related to spread rate, with garlic mustard spreading faster through sites experiencing large scale disturbances and slower in sites with no apparent disturbance regime.

To prevent disturbance-related invasion and spread of garlic mustard, it is suggested that new trail construction be limited in areas of high natural quality. Results of this study imply that spread is related to frequency and intensity of disturbance, and circumstantial evidence indicates that visitors disperse garlic mustard seed within and between sites (Nuzzo 1992a). Disturbed soils and altered microenvironments provide habitat for alien species (MacDonald and Frame 1988), and increased visitation (linked to presence and number of trails) has been directly related to increased invasion by alien species (Macdonald et al. in Usher 1988).

Control efforts may be most effective if directed towards reduction of the rosette population in late fall or very early spring, to take advantage of natural late summer and over-winter mortality. Control methods are described in Nuzzo (1991, 1992c).

Additional monitoring in 1994 and 1997 is recommended to detect changes at the community level, and to permit following two generations of garlic mustard (1991-1994, 1994-1997).

Acknowledgements

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FIGURE 1: Study site locations in northern Illinois.

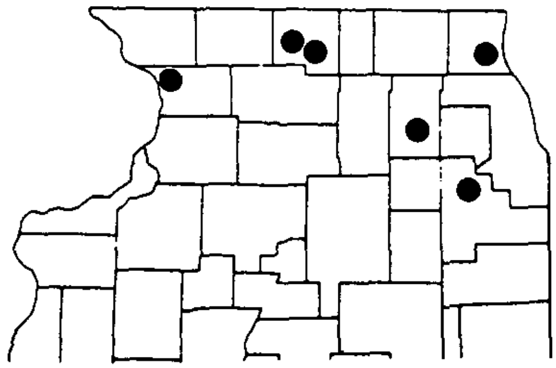
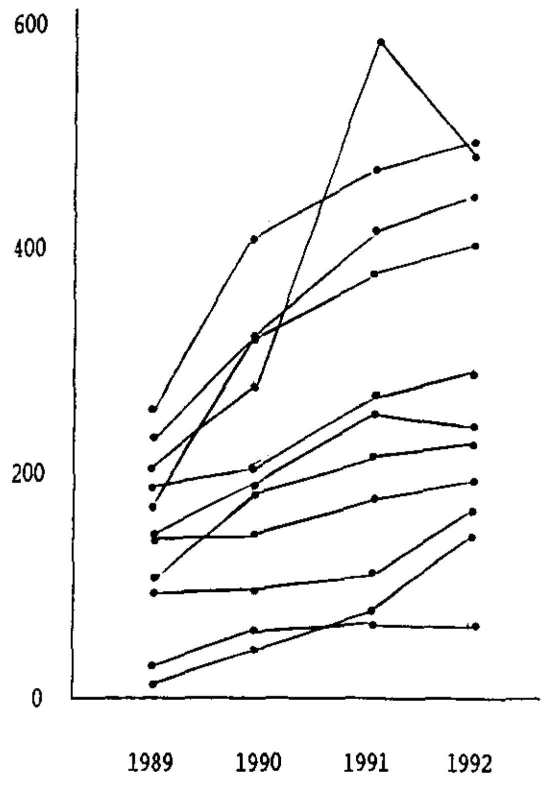


FIGURE 2: Garlic mustard presence from 1989 to 1992 in 11 plots (600 m^2/plot) separately (left) and combined (right).



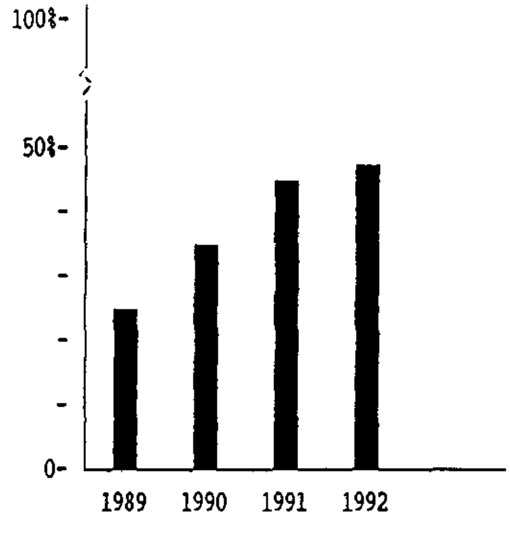


FIGURE 3: Garlic mustard mean frequency (left) and mean percent cover (right) from 1989 to 1992. (n=11 plots, 36m²/plot).

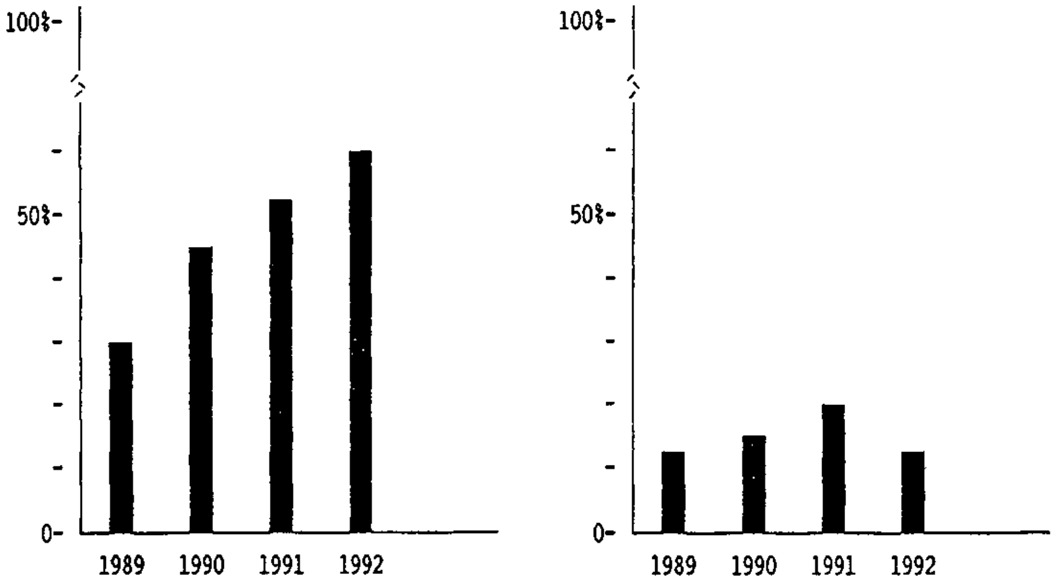
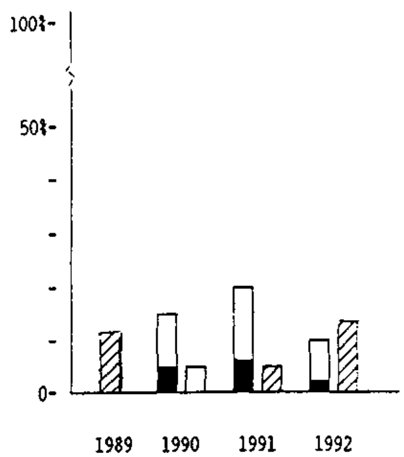


FIGURE 4: Garlic mustard mean percent cover by size class from 1989 to 1992. Seedling and adult cover recorded in May, immature rosette cover recorded in August. (n=11 plots, 36m²/plot).

FIGURE 5: Garlic mustard mean frequency by size class from 1989 to 1992. Seedling and adult frequency recorded in May, immature rosette frequency recorded in August. (n= 11 plots, 36m²/plot).



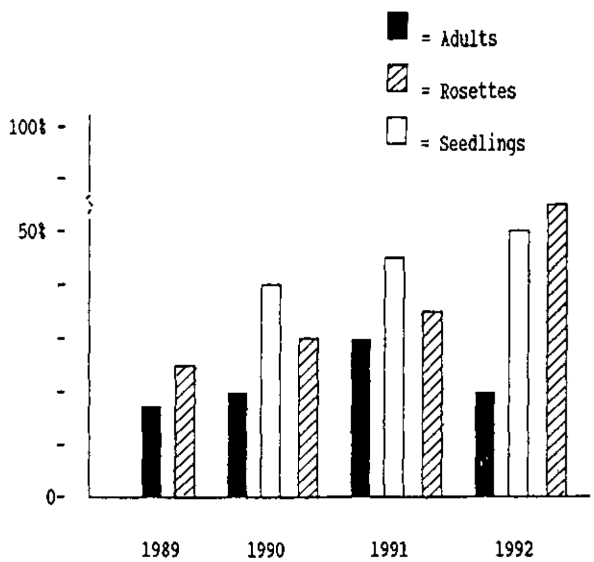
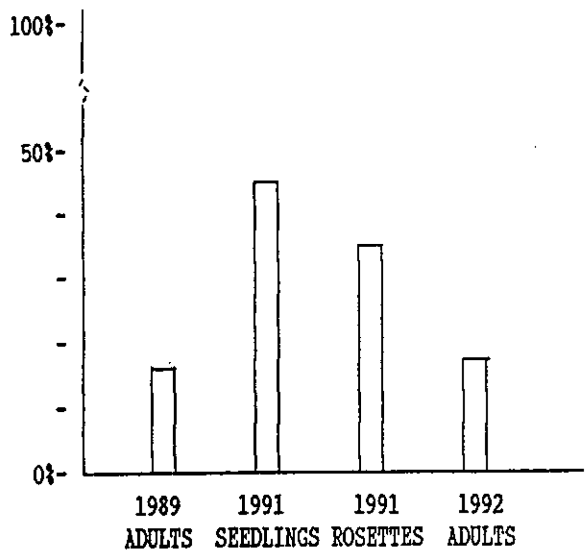


FIGURE 6: Garlic mustard mean frequency by size class of two generations. Figure on left depicts the 1989-1992 generation; adults in 1989, seedlings in May 1991, immature rosettes in August 1991, and adults in 1992. Seeds have a 20 month dormancy period. Figure on right depicts the 1990-1993 generation through the rosette stage. (n=11 plots, $36m^2$/plot).



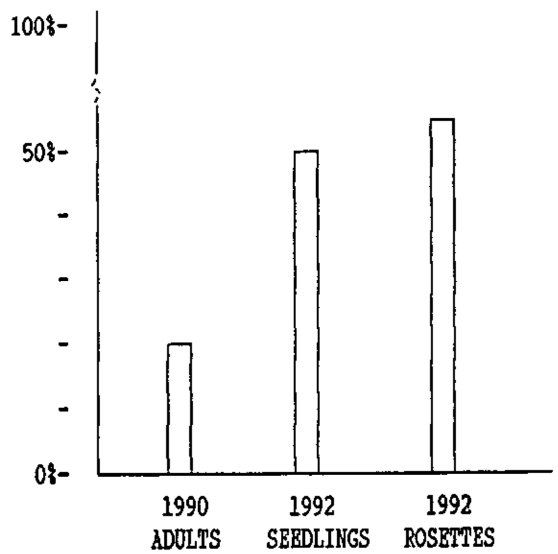


FIGURE 7: Mean cover of toothwort (<u>Dentaria laciniata</u>) in 1992, ranked by number of years of co-occurrence with garlic mustard from 1989 to 1992 (n=108 m^2 quadrats).

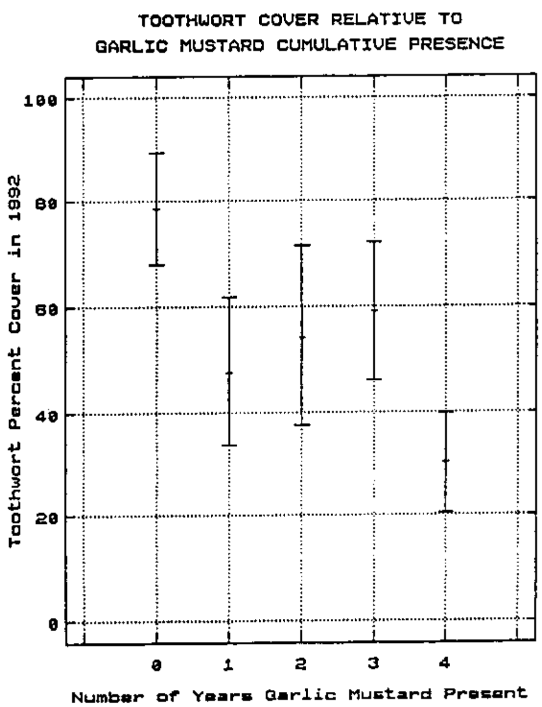


TABLE 1: Study sites.

Site name	County	Natural Divisions	Number of plots	Natural Community
Atwood Park	Winnebago	Winnebago Section of the Northeast Morainal Division	1	dry-mesic upland forest
Bliss Woods Forest Preserve	Kane	Morainal Section of the Northeast Morainal Division	3	dry-mesic, mesic upland forest
Daniel Wright Forest Preserve	Lake	Morainal Section of the Northeast Morainal Division	1	mesic upland forest
Indian Head	Carroll	Wisconsin Driftless Division	1	dry-mesic upland forest
Pecatonica Bottoms Nature Preserve	Winnebago	Freeport Section of the Rock River Hill Division	1	wet-mesic upland forest
Pilcher Park	Will	Morainal Section of the Northeast Morainal Division	3	mesic floodplain forest and wet-mesic floodplain
Sentinal	Carroll	Wisconsin Driftless Division	1	dry-mesic upland forest

TABLE 2: Garlic mustard percent presence, mean frequency, and mean percent cover from 1989 to 1992 in 11 plots. ($n=600m^2$/plot for presence, and $36m^2$/plot for frequency and cover). Last column indicates percent change (1992 value divided by 1989 value) over the four year period. Lower right box indicates average regional change (left number) and average within-plot change (right number).

SITE	PRESENCE 1989	1990	1991	1992	change 1992/1989
Atwood	32%	34%	46%	49%	153%
Dan Wright	17	16	19	28	165
Bliss 1	40	54	70	75	188
Bliss 2	2.5	7	13	25	1000
Bliss 3	43	68	78	83	193
Indian Head	24	24	30	33	138
Pecatonica	34	47	99	82	241
Pilcher 1	28	52	63	67	239
Pilcher 2	19	30	35	38	200
Pilcher 3	5	10	13	11	220
Sentinal	24	31	43	41	169
$\bar{X}$ =	24%	34%	46%	48%	264% \ 200%

SITE	COVER 1989	1990	1991	1992	change 1992/1989
Atwood	9.71%	14.79%	22.11%	4.17%	-57%
Dan Wright	23.82	8.49	2.94	2.79	-88%
Bliss 1	20.46	34.21	44.89	36.51	+78%
Bliss 2	0.58	2.10	2.88	4.33	+647%
Bliss 3	38.64	35.92	35.39	26.71	-31%
Indian Head	3.67	4.87	9.39	3.13	-15%
Pecatonica	4.24	22.57	46.57	18.31	+332%
Pilcher 1	6.30	13.88	14.04	4.58	-17%
Pilcher 2	7.53	15.83	9.57	5.82	-23%
Pilcher 3	2.57	3.39	1.69	0.14	-95%
Sentinal	8.57	10.33	19.89	8.57	n/c
$\bar{X}$ =	11.46%	15.13%	19.03%	10.46%	+66% \ -9%

SITE	FREQUENCY 1989	1990	1991	1992	change 1992/1989
Atwood	33.3%	33.3%	52.8%	47.2%	142%
Dan Wright	22.2	27.8	33.3	27.7	125%
Bliss 1	44.4	66.7	6.7	88.9	200%
Bliss 2	11.0	22.2	19.4	33.3	303%
Bliss 3	44.4	77.8	80.6	86.1	194%
Indian Head	30.6	27.8	30.6	36.1	118%
Pecatonica	55.5	61.1	100.0	86.1	155%
Pilcher 1	30.6	72.2	72.2	83.3	272%
Pilcher 2	25.0	36.1	38.9	38.9	156%
Pilcher 3	16.7	22.2	27.8	27.8	166%
Sentinal	25.0	33.3	50.0	52.8	211%
$\bar{X}$ =	30.79%	43.68%	46.57%	55.29%	186% \ 180%

TABLE 3: Garlic mustard mean frequency and mean percent cover by size class from 1989 to 1992 in 11 plots. (n=36m^2/plot). Seedlings and adults recorded in May, rosettes recorded in August.

Frequency

SITE	Seedlings 1990	Seedlings 1991	Seedlings 1992	Adults 1989	Adults 1990	Adults 1991	Adults 1992	Rosettes 1989	Rosettes 1990	Rosettes 1991	Rosettes 1992
Atwood	0.31	0.53	0.47	0.19	0.28	0.22	0.14	0.33	0.28	0.47	0.47
Dan Wright	0.25	0.33	0.33	0.14	0.22	0.08	0.06	0.19	0.08	0.27	0.31
Bliss 1	0.64	0.61	0.88	0.33	0.31	0.61	0.11	0.19	0.61	0.31	0.72
Bliss 2	0.19	0.08	0.36	0	0.08	0.14	0	0.11	0.14	0.06	0.47
Bliss 3	0.78	0.58	0.86	0.42	0.19	0.72	0.11	0.25	0.78	0.33	0.92
Indian Head	0.28	0.33	0.36	0.22	0.11	0.19	0.17	0.22	0.17	0.31	0.31
Pecatonica	0.39	1.00	0.64	0.06	0.53	0	0.81	0.56	0	1.00	0.61
Pilcher 1	0.72	0.53	0.81	0.22	0.22	0.58	0.08	0.31	0.64	0.42	0.83
Pilcher 2	0.31	0.36	0.39	0.17	0.14	0.31	0.19	0.14	0.28	0.28	0.39
Pilcher 3	0.19	0.19	0.28	0.06	0.08	0.14	0	0.14	0.19	0.11	0.31
Sentinal	0.28	0.47	0.53	0.14	0.28	0.17	0.39	0.25	0.17	0.39	0.47
$\overline{X}$ =	39.45	46.45	50.45	17.73	19.18	28.72	18.73	24.45	30.36	35.91	54.64

Cover

SITE	Seedlings 1990	Seedlings 1991	Seedlings 1992	Adults 1990	Adults 1991	Adults 1992	Rosettes 1990	Rosettes 1991	Rosettes 1992
Atwood	9.36%	21.69%	4.17%	6.17%	2.21%	0.17%	0.76%	4.28%	7.08%
Dan Wright	3.14	2.94	2.79	6.31	0.14	0.13	0.90	2.08	9.55
Bliss 1	30.28	20.82	36.51	6.11	29.46	0.68	20.56	2.24	41.39
Bliss 2	1.56	0.14	4.33	1.00	2.73	0	1.29	0.46	9.13
Bliss 3	35.92	13.39	26.71	1.99	28.89	0.06	25.12	0.36	36.81
Indian Head	4.78	7.32	2.53	0.15	2.01	0.18	1.22	2.76	2.86
Pecatonica	5.10	46.57	3.25	21.08	0	15.72	0	21.83	7.58
Pilcher 1	11.99	11.19	4.15	1.46	2.89	0.65	3.25	1.46	10.19
Pilcher 2	14.18	6.04	5.72	1.72	2.63	0.19	8.15	1.63	16.10
Pilcher 3	1.65	1.31	0.14	1.97	0.17	0	1.06	0.06	0.61
Sentinal	0.96	17.92	7.68	10.11	5.17	0.96	0.28	3.83	6.32
$\overline{X}$ =	10.81%	13.58%	8.91%	5.81%	6.94%	1.70%	5.69%	3.73%	13.42%

TABLE 4: Garlic mustard (<u>Alliaria petiolata</u>) adult mean density/m^2 recorded in May from 1990 to 1992 in 11 plots ($n=36\ m^2$/plot).

SITE	1990	1991	1992
Atwood	6.75	1.58	0.25
Dan Wright	5.08	0.5	0.08
Bliss 1	5.86	42.33	0.58
Bliss 2	0.14	0.66	0
Bliss 3	1.30	30.83	0.22
Indian Head	0.22	1.39	0.36
Pecatonica	12.17	0	16.11
Pilcher 1	1.94	1.42	0.33
Pilcher 2	1.00	4.10	0.33
Pilcher 3	0.31	0.28	0
Sentinal	17.41	1.22	1.25
$\overline{X}$ =	4.72	7.66	1.77

TABLE 5: Population census at MacArthur Woods Nature Preserve, Lake County IL. Adult and rosette data collected in July. Census area 2400 m^2.

	1989	1990	1991	1992
ROSETTES:				
Frequency	4.87%	3.63%	19.42%	21.04%
Cover	0.71%	0.33%	2.78%	2.22%
ADULTS:				
Frequency	0.33%	3.58%	0.01%	12.46%
Cover	0.05%	2.41%	0.39%	2.96%
TOTAL:				
Frequency	5.17%	5.67%	19.41%	26.46%
Cover	0.76%	2.69%	3.15%	4.33%

TABLE 6: Species richness in 11 plots from 1990 to 1992. Garlic mustard included in species count. Change in species richness over time tested by Chi square (*=significant at the 0.05 level, n.s.= non-significant).

SITE	1990	1991	1992	Chi^2	sl
Atwood	50	48	44	0.399	n.s.
Bliss 1	38	40	33	0.703	n.s.
Bliss 2	21	29	38	4.956	*
Bliss 3	41	39	40	0.050	n.s.
Dan Wright	29	25	28	0.318	n.s.
Indian Head	74	61	63	1.480	n.s.
Pecatonica	40	43	43	0.143	n.s.
Pilcher 1	39	28	37	1.979	n.s.
Pilcher 2	41	39	40	0.050	n.s.
Pilcher 3	42	39	45	0.429	n.s.
Sentinal	52	51	55	0.165	n.s.

TABLE 7: Mean number of species/m^2 in 11 plots from 1990 to 1992. Garlic mustard excluded from species count ($n=36m^2$/plot). Change in mean species number tested by repeated measures ANOVA. (** = significant at the 0.01 level, n.s. = non-significant).

SITE	1990	1991	1992	F	sl
Atwood	8.44	7.17	8.00	1.951	n.s.
Dan Wright	4.08	3.31	3.89	1.427	n.s.
Bliss 1	6.19	6.50	6.06	0.241	n.s.
Bliss 2	3.17	3.31	3.42	0.137	n.s.
Bliss 3	5.69	6.06	5.36	0.738	n.s.
Indian Head	7.53	9.53	10.25	4.903	**
Pecatonica	11.86	8.50	11.50	0.899	n.s.
Pilcher 1	4.56	3.58	4.67	1.521	n.s.
Pilcher 2	4.81	4.17	5.39	1.353	n.s.
Pilcher 3	6.89	5.69	6.36	2.700	n.s.
Sentinal	8.06	8.50	8.72	0.644	n.s.

TABLE 8: Mean herbaceous cover and mean woody (<30cm tall) cover /m^2 in all plots ($n=36m^2$/plot) Differences in mean cover between year tested by repeated measures ANOVA. significance levels: * = <0.05, ** = <0.001, *** = <0.001, ns = non-significant.

	Herbaceous Cover					Woody Cover				
SITE	1990	1991	1992	F	s.l.	1990	1991	1992	F	s.l.
Atwood	78.33%	75.58%	47.67%	7.1614	**	15.71%	16.58%	25.67%	4.451	*
Bliss 1	130.0	149.39	133.86	1.002	ns	7.34	4.92	4.51	0.584	ns
Bliss 2	69.96	71.43	70.93	0.013	ns	1.93	0.97	2.26	1.116	ns
Bliss 3	96.43	122.94	92.40	6.342	**	2.93	2.31	3.19	0.285	ns
Dan Wright	16.61	12.46	5.58	5.689	**	5.81	4.51	4.83	0.162	ns
Indian Head	29.92	40.54	25.56	11.238	***	21.19	29.04	35.06	2.322	ns
Pecatonica	132.39	128.35	87.08	7.841	***	4.34	4.49	4.44	0.003	ns
Pilcher 1	42.55	31.57	32.29	0.637	ns	7.21	1.82	6.75	4.376	*
Pilcher 2	44.85	37.01	34.51	0.450	ns	20.77	9.93	22.50	2.302	ns
Pilcher 3	34.75	59.60	62.31	0.863	ns	7.43	2.00	5.18	14.180	***
Sentinal	60.36	91.67	53.07	12.231	***	27.24	31.06	37.76	3.577	ns

TABLE 9: Mean herbaceous cover in 1992, ranked by number of years of co-occurrence with garlic mustard (NYGM) and by number of years of co-occurrence when garlic mustard cover ≥37.5% (NYHIGM). Subscript indicates number of quadrats in each group. Differences between groups tested by ANOVA. Significance levels: * = <0.05, ** = <0.01, *** = < 0.001, n.s. = non-significant.

	F-test	sl	Years of Co-occurrence with Garlic Mustard: 0	1	2	3	4
Atwood							
NYGM	0.740	n.s.	$51.44_{(16)}$	$51.17_{(3)}$	$68.50_{(4)}$	$32.75_{(2)}$	$42.91_{(11)}$
NYHIGM	0.367	n.s.	$52.64_{(25)}$	$36.00_{(3)}$	$42.17_{(3)}$	$42.50_{(5)}$	$0.00_{(0)}$
Bliss 1							
NYGM	2.064	n.s.	$96.38_{(4)}$	$176.33_{(6)}$	$153.13_{(4)}$	$152.92_{(6)}$	$115.34_{(16)}$
NYHIGM	1.587	n.s.	$149.97_{(16)}$	$205.00_{(1)}$	$95.00_{(4)}$	$147.38_{(4)}$	$113.18_{(11)}$
Bliss 2							
NYGM	3.146	*	$86.65_{(20)}$	$68.63_{(8)}$	$35.67_{(3)}$	$40.50_{(3)}$	$31.50_{(2)}$
NYHIGM	0.846	n.s.	$74.03_{(31)}$	$55.00_{(4)}$	$38.50_{(1)}$	$0.00_{(0)}$	$0.00_{(0)}$
Bliss 3							
NYGM	0.564	n.s.	$114.63_{(4)}$	$72.75_{(2)}$	$85.25_{(4)}$	$92.10_{(10)}$	$91.28_{(16)}$
NYHIGM	0.013	n.s.	$92.95_{(20)}$	$86.00_{(1)}$	$90.83_{(3)}$	$92.42_{(1)}$	$0.00_{(0)}$
Dan Wright							
NYGM	0.635	n.s.	$5.00_{(15)}$	$7.63_{(8)}$	$2.75_{(6)}$	$4.75_{(4)}$	$9.83_{(3)}$
NYHIGM	1.484	n.s.	$4.97_{(29)}$	$4.88_{(4)}$	$12.50_{(3)}$	$0.00_{(0)}$	$0.00_{(0)}$
Indian							
NYGM	2.799	*	$18.50_{(21)}$	$48.50_{(5)}$	$4.50_{(1)}$	$17.75_{(2)}$	$35.57_{(7)}$
NYHIGM	1.672	n.s.	$23.30_{(30)}$	$27.25_{(2)}$	$52.17_{(3)}$	$10.00_{(1)}$	$0.00_{(0)}$
Pecatonica							
NYGM	0.266	n.s.	$0.00_{(0)}$	$106.33_{(3)}$	$82.39_{(9)}$	$88.36_{(7)}$	$84.00_{(17)}$
NYHIGM	0.086	n.s.	$90.57_{(14)}$	$82.94_{(8)}$	$82.70_{(10)}$	$87.13_{(4)}$	$0.00_{(0)}$
Pilcher 1							
NYGM	6.884	***	$1.75_{(6)}$	$31.25_{(2)}$	$14.50_{(3)}$	$16.70_{(15)}$	$79.55_{(10)}$
NYHIGM	6.743	**	$15.24_{(23)}$	$45.92_{(6)}$	$93.90_{(5)}$	$33.50_{(2)}$	$0.00_{(0)}$
Pilcher 2							
NYGM	7.007	***	$14.10_{(20)}$	$42.00_{(2)}$	$77.50_{(2)}$	$37.38_{(4)}$	$71.50_{(8)}$
NYHIGM	3.880	*	$21.50_{(26)}$	$67.83_{(3)}$	$62.67_{(3)}$	$68.83_{(3)}$	$85.50_{(1)}$
Pilcher 3							
NYGM	1.446	n.s.	$58.72_{(23)}$	$46.63_{(4)}$	$69.33_{(3)}$	$46.75_{(2)}$	$101.13_{(4)}$
NYHIGM	5.960	**	$56.98_{(33)}$	$159.00_{(1)}$	$101.75_{(2)}$	$0.00_{(0)}$	$0.00_{(0)}$
Sentinal							
NYGM	1.149	n.s.	$51.83_{(15)}$	$27.83_{(3)}$	$67.00_{(9)}$	$37.00_{(1)}$	$51.19_{(8)}$
NYHIGM	0.340	n.s.	$54.61_{(27)}$	$60.83_{(3)}$	$43.00_{(2)}$	$41.88_{(4)}$	$0.00_{(0)}$

TABLE 10: Mean number of species/m^2 in 1992, ranked by number of years of co-occurrence with garlic mustard (NYGM) and by number of years of co-occurrence when garlic mustard cover ≥37.5% (NYHIGM). Subscript indicates number of quadrats in each group. Differences between groups tested by ANOVA. Significance levels: * = <0.05, ** = <0.01, *** = < 0.001, n.s. = non-significant.

	F-test	sig	Years of Co-occurrence with Garlic Mustard: 0	1	2	3	4
Atwood							
NYGM	1.385	n.s.	$7.69_{(16)}$	$7.67_{(3)}$	$7.50_{(4)}$	$6.00_{(2)}$	$9.18_{(11)}$
NYHIGM	1.768	n.s.	$7.52_{(25)}$	$8.67_{(3)}$	$8.67_{(3)}$	$9.80_{(5)}$	$0.00_{(0)}$
Bliss 1							
NYGM	4.023	**	$2.75_{(4)}$	$5.33_{(6)}$	$7.75_{(4)}$	$8.33_{(6)}$	$5.88_{(16)}$
NYHIGM	1.116	n.s.	$5.38_{(16)}$	$8.00_{(1)}$	$5.50_{(4)}$	$8.25_{(4)}$	$6.27_{(11)}$
Bliss 2							
NYGM	2.563	n.s.	$2.80_{(20)}$	$4.50_{(8)}$	$6.30_{(3)}$	$3.00_{(3)}$	$1.50_{(2)}$
NYHIGM	2.658	n.s.	$3.06_{(31)}$	$5.75_{(4)}$	$5.00_{(1)}$	$0.00_{(0)}$	$0.00_{(0)}$
Bliss 3							
NYGM	0.677	n.s.	$4.50_{(4)}$	$5.00_{(2)}$	$4.75_{(4)}$	$4.80_{(10)}$	$6.13_{(16)}$
NYHIGM	3.339	*	$4.65_{(20)}$	$5.00_{(1)}$	$3.70_{(3)}$	$7.00_{(12)}$	$0.00_{(0)}$
Dan Wright							
NYGM	0.178	n.s.	$3.80_{(15)}$	$4.00_{(8)}$	$3.33_{(6)}$	$4.50_{(4)}$	$4.33_{(3)}$
NYHIGM	1.099	n.s.	$3.66_{(29)}$	$4.25_{(4)}$	$5.67_{(3)}$	$0.00_{(0)}$	$0.00_{(0)}$
Indian							
NYGM	2.320	n.s.	$9.95_{(21)}$	$14.20_{(5)}$	$2.00_{(1)}$	$10.00_{(2)}$	$9.57_{(7)}$
NYHIGM	0.245	n.s.	$10.43_{(30)}$	$11.00_{(2)}$	$8.67_{(3)}$	$8.00_{(1)}$	$0.00_{(0)}$
Pecatonica							
NYGM	2.017	n.s.	$0.00_{(0)}$	$10.00_{(3)}$	$11.89_{(9)}$	$10.29_{(7)}$	$12.29_{(17)}$
NYHIGM	1.269	n.s.	$10.71_{(14)}$	$12.25_{(8)}$	$12.00_{(10)}$	$12.50_{(4)}$	$0.00_{(0)}$
Pilcher 1							
NYGM	16.304	***	$2.50_{(6)}$	$1.50_{(2)}$	$3.00_{(3)}$	$3.74_{(15)}$	$8.40_{(10)}$
NYHIGM	10.476	***	$3.22_{(23)}$	$5.83_{(6)}$	$8.80_{(5)}$	$7.00_{(2)}$	$0.00_{(0)}$
Pilcher 2							
NYGM	5.982	**	$3.60_{(20)}$	$5.00_{(2)}$	$8.00_{(2)}$	$6.50_{(4)}$	$9.25_{(8)}$
NYHIGM	6.759	***	$4.12_{(26)}$	$7.67_{(3)}$	$8.00_{(3)}$	$12.00_{(3)}$	$8.00_{(1)}$
Pilcher 3							
NYGM	2.762	*	$6.00_{(23)}$	$6.75_{(4)}$	$4.62_{(3)}$	$7.00_{(2)}$	$9.25_{(4)}$
NYHIGM	3.248	n.s.	$6.12_{(33)}$	$10.00_{(1)}$	$9.00_{(2)}$	$0.00_{(0)}$	$0.00_{(0)}$
Sentinal							
NYGM	1.033	n.s.	$9.33_{(15)}$	$7.67_{(3)}$	$9.22_{(9)}$	$6.00_{(1)}$	$7.88_{(8)}$
NYHIGM	1.100	n.s.	$9.00_{(27)}$	$9.67_{(3)}$	$7.00_{(2)}$	$7.25_{(4)}$	$0.00_{(0)}$

TABLE 11: Mean toothwort (Dentaria laciniata) cover/m^2 in 1992, ranked by number of years of co-occurrence with garlic mustard (NYGM) and by number of years of co-occurrence when garlic mustard cover ≥37.5% (NYHIGM). Subscript indicates number of quadrats in each group (36 m^2 quadrats/plot). Differences between groups tested by ANOVA. Significance levels: * = <0.05, ** = <0.01, *** = < 0.001, n.s. = non-significant.

		Bliss 1	Bliss 2	Bliss 3	All 3 plots
# years garlic mustard present	0	$73.25_{(4)}$	$79.43_{(20)}$	$79.50_{(4)}$	$78.56_{(28)}$
	1	$50.08_{(6)}$	$45.31_{(8)}$	$50.25_{(2)}$	$47.72_{(16)}$
	2	$93.38_{(4)}$	$0_{(3)}$	$56.25_{(4)}$	$54.41_{(11)}$
	3	$63.42_{(6)}$	$38.67_{(3)}$	$62.70_{(10)}$	$59.13_{(19)}$
	4	$31.69_{(16)}$	$31.25_{(2)}$	$28.34_{(16)}$	$30.09_{(34)}$
	X =	51.52	59.15	47.89	

		Bliss 1	Bliss 2	Bliss 3	All 3 plots
# years garlic mustard cover ≥37.5%	0	$70.38_{(16)}$	$65.76_{(31)}$	$64.78_{(20)}$	$66.57_{(67)}$
	1	$84.00_{(1)}$	$13.38_{(4)}$	$37.50_{(1)}$	$29.17_{(6)}$
	2	$32.13_{(4)}$	$37.50_{(1)}$	$54.17_{(3)}$	$41.07_{(8)}$
	3	$40.63_{(4)}$	---	$19.04_{(12)}$	$24.44_{(16)}$
	4	$40.63_{(4)}$	---	---	$32.14_{(11)}$
	X =	51.52	59.15	47.89	

TABLE 12: Qualitative relationship between disturbance level, frequency and type, and rate of garlic mustard increase.

SITE	Disturbance Level	Disturbance Frequency	Disturbance Type	Percent increase in Garlic mustard presence 1990-1992
Bliss 2	High	Once	Wind storm	1000%
Pecatonica	High	Once	Flood	241
Pilcher 1	Med	Annual	Flood	239
Pilcher 2	Med	Annual	Flood	200
Pilcher 3	Med	Annual	Flood	220
Dan Wright	Med	Annual	Deer	165
Bliss 1	Low	----	----	188
Bliss 3	Low	----	----	193
Sentinal	Low	----	----	169
Atwood	Low	----	----	153
Indian	Low	----	----	138