

Differences in invasibility of two contrasting habitats and invasiveness of two mugwort *Artemisia vulgaris* populations

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Summary

1. Establishment success of non-native invasive species is often attributable either to habitat invasibility or inherent species traits. In this study we explored the interplay between these two factors in the establishment, expansion and plasticity in growth of the clonally reproducing invasive weed mugwort *Artemisia vulgaris* in two contrasting habitats, as well as the potential management practice of monthly mowing.

2. We investigated resource allocation patterns and spatial distribution of ramets originating from two naturalized populations over a 3-year period. Ramets from these morphologically distinct populations were transplanted into each of two contrasting habitats to determine the invasive potential of these populations and the relative resistance of each habitat to invasion.

3. Total ramet production, average ramet height and spatial distribution patterns differed significantly between the two populations, but the degree of variation in the response was habitat dependent. There were no interpopulation differences in total biomass production. Plastic responses in resource allocation patterns, spatial distribution of ramets and relative growth rates were observed, demonstrating differences in invasive potential between the two mugwort populations.

4. The two habitats differed in invasibility. This could have been the result of differences in community structure, competition for available resources, disturbance and/or invader traits. In addition, monthly defoliation (mowing) reduced mugwort ramet production by as much as 90% and as little as 10%.

5. *Synthesis and applications.* This study demonstrates that variation exists in habitat invasibility, and that intraspecific variation in growth patterns occurs in mugwort. The interaction between habitat traits and species characteristics was found to be important when determining invasion success. We also demonstrated that monthly mowing following the introduction of mugwort can substantially decrease the rate of spread of this clonal species, which may provide an effective management opportunity both for this species and for other clonal invaders.

Key-words: clonal reproduction, invasibility, invasive weeds, phenotypic plasticity, ramet distribution

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Introduction

Invasive species have been identified as the second greatest threat to biodiversity after habitat loss (Mack *et al.* 2000; Bartuska 2003), stimulating research into

invasion biology, and heightening awareness of the problem among land managers. Research has focused on the development of models to predict the potential distribution of invasive species and the susceptibility of specific habitats to invasion (Williamson 1989; Goslee, Peters & Beck 2001; Marco, Paez & Cannas 2002; Buckley, Briese & Rees 2003). In general, predictive models make use of known abiotic conditions favoured by the invasive species in their native ranges to generate

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probabilities of invasion in non-infested sites in their introduced range (Higgins, Richardson & Cowling 2001; Smith *et al.* 2001). However, models often lack information on the susceptibility of specific habitats to invasion, intraspecific variation in response to habitat heterogeneity, and potential establishment stress (e.g. defoliation) (Skalova *et al.* 1997; Rendon & Nunez-Farfan 2000).

Most studies of invasive plants have focused on sexually reproducing species, which has allowed workers the convenience of using seed rain and seedling recruitment as key variables in the invasion process (Thebaud *et al.* 1996; Meekins, Ballard & McCarthy 2001; Callaway *et al.* 2003). However, few studies have investigated the invasive potential of largely vegetatively reproducing plant species (Bailey 1994; Hollingsworth & Bailey 2000). Interestingly, plants that are primarily vegetative reproducers comprise approximately 40% of the alien flora (Pyesk 1997) and include some of the most persistent and aggressive invaders (e.g. *Fallopia japonica* (Houtt.) Ronse Decraene in the British Isles, and *Lythrum salicaria* L. in North America). At certain scales, introduced clonal species have been implicated as being a greater liability to native flora than seed-producing species (Pyesk 1997; Pyesk *et al.* 2003). Therefore, it is of critical importance to understand the impact of habitat characteristics, establishment stress and invader attributes on the success of clonal invaders.

Plasticity in the phenotype of a single genet has been cited as conferring an evolutionary advantage on weedy plant species because it accounts for their naturalization in spatially and temporally heterogeneous environments (Schlichting 1986; Via *et al.* 1995; Agrawal 2001). Invasive species often have the ability to adapt to changing environments and can tolerate highly disturbed habitats through morphological variation, altering resource allocation and, in clonal species, changing the spatial and/or temporal distribution of ramets (Rendon & Nunez-Farfan 2000; Sexton, McKay & Sala 2002; Elberse, van Damme & van Tienderen 2003). Thus, genotypes exhibiting phenotypic plasticity may be favoured during selection (Baker 1965; Noble 1989; Claridge & Franklin 2002). Despite the knowledge that invasive species can be highly plastic in their response to variable environments, species introduction studies have generally not fully considered the importance of the habitat or genetic history of the plant population under study (Bartuska 2003).

We examined population-level variability in growth and clonal expansion in the largely vegetatively reproducing invasive species mugwort *Artemisia vulgaris* (L.). Mugwort is native to Eurasia and was reportedly introduced to North America in *c.* 1535 by Jesuit clergy colonizing the St John region of eastern Canada (Fernald 1900). This species is now common in disturbed sites (e.g. roadsides), waste areas, vineyards and, most recently, natural areas and agro-ecosystems. Mugwort can be found from the high Himalayas of central Asia to the warm temperate regions of South America, exhibiting

wide variation in morphology (Holm *et al.* 1997; Barney & DiTommaso 2003). Mugwort has recently been classified as one of the top 10 most troublesome weeds in the USA nursery industry, where it infests field-grown horticultural crops and is transported to new habitats in balled-and-burlapped nursery stock (Holm *et al.* 1997; Barney & DiTommaso 2003). Despite some seed production, regeneration in this species occurs primarily via an extensive rhizome system (Holm *et al.* 1997), allowing this species to tolerate most chemical and cultural management strategies (Bing 1983; Henderson & Weller 1985). As a result of its rapidly expanding geographical range and more recent invasion of natural areas, mugwort is gaining attention in North America as a noxious invasive species.

Using plants from two morphologically and possibly allelochemically distinct mugwort populations, the objectives of this study were to answer the following questions: (i) Do two contrasting habitats, a turfgrass lawn and fallow field, differ in their resistance to mugwort invasion? (ii) Do two morphologically and chemically distinct mugwort populations exhibit different growth and/or resource allocation patterns in the two habitats? (iii) Is the response of the two populations different in the two habitats when subjected to an establishment stress, mowing, and if so, can this strategy be employed as a practical management option?

Materials and methods

PLANT MATERIAL AND FIELD DESIGN

Rhizome fragments used in this study were selected from mugwort plants of two naturalized field populations that differ in morphology and leaf surface chemistry (Barney, Hay & Weston 2005). The mugwort populations were found in two locations 8 km apart in Ithaca, New York, USA, and are referred to as ITH-1 and ITH-2. These two collection sites were managed turfgrass areas, in which mugwort comprised more than 75% of the ground cover. Vegetation in these areas was mowed weekly to a height of 5 cm during the growing season and had received no irrigation or fertilization for at least 5 years prior to collection of plants for this study. The two populations are probably genetically distinct because of their geographical isolation, visible morphological differences and their typically clonal mode of reproduction (Holm *et al.* 1997). Plants from the ITH-1 population have densely pubescent (woolly) stems and light green leaves with relatively few deeply lobed margins (Barney 2003). Plants from the ITH-2 population exhibit nearly glabrous stems and dark green leaves with numerous deeply lobed margins. Previous work has shown that the concentration of volatile compounds and subsequent volatile toxicity are greater in the ITH-1 population than the ITH-2 population (Barney, Hay & Weston 2005).

The growth responses of ITH-1 and ITH-2 plants were assessed in a fallow (abandoned) field and a turfgrass

lawn, two contrasting habitat types frequently colonized by mugwort (Rogerson & Bingham 1971; Holm *et al.* 1997; Barney & DiTommaso 2003). The two habitats were 50 m apart and were located at the Cornell University Turfgrass Research Farm in Ithaca, New York, USA (42°27'36"N, 76°27'40"W). The habitats were located on an Arkport fine sandy loam (psamentic Hapludlafs, coarse loamy mixed mesic), with an organic matter content of 4.8% and a pH of 5.9. Plant available soil concentrations of nitrogen (N), phosphorus (P) and potassium (K) averaged 8.4, 4.9 and 53 mg kg⁻¹, respectively, in the two habitats at the beginning of the study in 2001, and levels were not significantly different ($P > 0.05$) between the study habitats (data not shown).

In April 2001, the fallow field site was prepared by killing all standing vegetation with a glyphosate application, followed by roto-tilling to a depth of 20 cm prior to transplanting mugwort tillers. The cultivated area had been sown to perennial grasses (e.g. *Festuca* spp. and *Poa* spp.) 2 years previously and was mowed every 2 weeks prior to the start of this study. Following this initial tilling operation, the area was left unmanaged for the duration of the 3-year experiment. The turfgrass habitat was an established 3-year pure stand of perennial ryegrass *Lolium perenne* (L.) that had been mown bimonthly to 6 cm prior to the experiment.

Each habitat type measured 30 × 30 m in size (900 m²) and treatment plots within each habitat measured 5 × 5 m (25 m²) with 2 m alleys on all sides. Within each habitat, plots were arranged in a randomized complete block design with eight blocks. Within each block, combinations of population source (i.e. ITH-1 and ITH-2) and mowing regime (i.e. not mowed and mowed monthly to 6 cm) comprised a treatment, and these were randomly allocated to one of four plots per block. Mugwort plant material was harvested from the two collection sites in Ithaca on 6 June 2001. Eighty mugwort ramets of a single genet were collected from a 20 × 5 m area at each location using a sod cutter set at a depth of 10 cm. Ramets were immediately separated, washed of soil and shoots (5 cm) and rhizomes (2.5 cm) cut to uniform length. On the same day, five ramets were transplanted at a depth of 3 cm at the centre of each 5 × 5 m plot in the tilled field and in the turfgrass area. Target plants received 1.5 L of water at this time, with no supplemental irrigation thereafter.

RAMET EXPANSION ON A SPATIOTEMPORAL SCALE

In order to document vegetative spread, plant growth was monitored every 2 weeks during three consecutive growing seasons. Observations began in June 2001, May 2002 and May 2003 and ended with the first frost in autumn (i.e. early October). At each sample date, data collected included average height of ramets, total number of ramets, number of newly emerged ramets, and distance (cm) of each ramet from the initial planting location. Average height of ramets was estimated by

determining the height of five randomly selected ramets in each plot. From preliminary observations, naturalized mugwort populations expand symmetrically from the initial planting point (J. N. Barney, personal observation). Therefore, data on ramet distance from the planting location (2001) were taken at 10 cm radial increments for all ramets in each plot.

RESOURCE ALLOCATION PATTERNS

In order to detect shifts in allocation among various plant parts, a common expression of plasticity (Claridge & Franklin 2002), a destructive harvest was performed collecting all above-ground plant material from all plots in both habitats after the third growing season (2003). Plant material was dried at 60 °C for 5 days and separated after drying into leaves (including petioles), stems and inflorescences (including peduncles), and weighed. Because of the substantial labour and time required for below-ground sampling, only three blocks in each habitat were harvested to estimate below-ground biomass accumulation. Below-ground sampling consisted of centring a 50 × 50 cm square quadrat on the initial planting location in each plot, which was then excavated. To estimate radial expansion from the centre, we excavated consecutive adjacent 25 × 25 cm blocks along one transect direction (west from the adjacent initial 50 × 50 cm quadrat) in each plot until no rhizome fragments were found. All sampling blocks were harvested to a depth of 20 cm, which was determined to be the depth containing > 98% of the below-ground plant biomass (data not shown). Below-ground biomass, consisting of rhizomes and roots collected from each subsampling quadrat, was dried separately at 60 °C for 5 days, and weighed. Total below-ground dry biomass data are presented on a per unit area basis. For example, the first 25 × 25 cm block along the transect sampled 10% of the ring between 25 and 50 cm from the centre of the plot, while the second block sampled 6% of the ring between 50 and 75 cm from the centre of the plot, etc. Rhizome length was estimated by measuring the length of a 10 g subsample from each 5 × 5 m plot and extrapolating based on the length per unit biomass.

STATISTICAL ANALYSES

Cumulative ramet number and height at the end of the final year

Because the two habitats were not randomly selected and were not replicated, they were treated as separate experiments. Using the MIXED procedure in SAS (v.8; SAS Institute Inc., Cary, NC), a three-way ANOVA was used to analyse the total number of ramets per plot and shoot height, with population source and mowing regime used as fixed effects and block as a random effect. In years 2 and 3 of the study, a few plots in each habitat were abandoned as a result of transplant mortality, and thus were not included in the analysis.

Total ramet number as a function of time

To test the effect of time on ramet number, and to determine any interactions between populations, mowing regime and/or days after initial planting, a mixed-model regression analysis was used (SAS v.8). Average ramet number per plot was \log_{10} -transformed to comply with variance assumptions. Transformed values were then modelled against mugwort population source and mowing regime (fixed effects) and days after initial planting (random effect). Means for each population and mowing regime were compared using Tukey tests ($P < 0.05$).

Biomass

A two-way ANOVA was used to test the effects of population and mowing on total biomass, leaf, stem and root biomass, and rhizome length. Means were separated using Tukey tests ($P < 0.05$).

Results

RAMET EXPANSION ON A SPATIOTEMPORAL SCALE

Overall, mugwort population establishment and response to mowing were habitat dependent. Although formal statistical comparisons could not be made across habitat types, mugwort growing in the fallow field produced nearly 10 times more ramets than mugwort growing in turf, especially in mowed plots (Fig. 1). After the final growing season (2003), the main effects of mugwort population source and mowing regime were significant predictors of the number of ramets produced in the fallow field, while in the turfgrass habitat a population

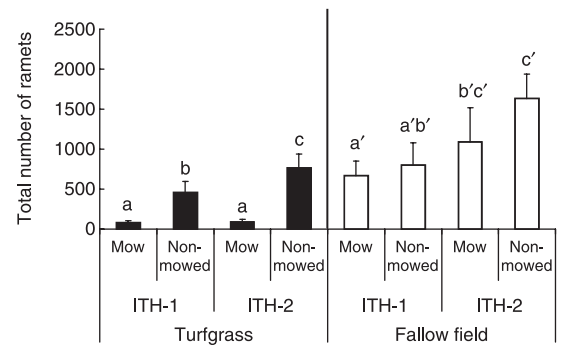


Fig. 1. Final ramet number (\pm SE) at the end of the third growing season (2003) for all population-mowing combinations in two contrasting habitats. Means were compared using Tukey tests, and bars with different letters within habitats are significantly different ($P < 0.05$).

by mowing regime interaction was observed (Table 1). Blocking was not significant in either the fallow field ($\chi^2 = 0$, d.f. = 7, $P = 1$) or the turfgrass lawn ($\chi^2 = 0.8$, d.f. = 7, $P = 0.9$).

In both habitats, the number of ramets established per plot over the three growing seasons was significantly influenced by population, mowing regime and date after planting (Table 1b and Fig. 2b). However, the nature of the interactions with time (date after planting) differed between the two habitats. In the turfgrass lawn, the two-way interaction between the number of days after planting and population and the number of days after planting and mowing regime significantly influenced the number of ramets established (Table 1b and Fig. 2a). Blocking had a significant effect in both the fallow field ($\chi^2 = 51.7$, d.f. = 7, $P < 0.0001$) and the turfgrass lawn ($\chi^2 = 76.4$, d.f. = 7, $P < 0.0001$) habitats when analysing the number of ramets established vs. time.

Table 1. Summary of ANOVA for (a) total ramet number at the end of the third growing season (2003), (b) ramet number (\log_{10} -transformed) regressed against time after introduction, and (c) average ramet height at the end of each season in the turfgrass lawn and fallow field habitat

Source	Turfgrass lawn			Fallow field		
	d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>
(a)						
Population (P)	1	23.24	0.0002	1	18.82	0.0015
Mow (M)	1	259.41	< 0.0001	1	5.39	0.0427
P × M	1	19.01	0.0004	1	1.94	0.1937
(b)						
P	1	95.63	< 0.0001	1	67.68	< 0.0001
M	1	1585.81	< 0.0001	1	16.41	< 0.0001
P × M	1	3.97	0.0468	1	0.20	0.6564
Date (D)	23	541.73	< 0.0001	23	620.68	< 0.0001
D × P	23	2.28	0.0006	23	1.04	0.4094
D × M	23	64.75	< 0.0001	23	5.71	< 0.0001
D × P × M	23	0.64	0.8996	23	0.88	0.6223
(c)						
Year 1	1	8.02	0.0133	1	0.06	0.8132
Year 2	1	1.59	0.2362	1	2.00	0.1790
Year 3	1	4.85	0.0923	1	8.54	0.0119

NS, non-significant ($P > 0.05$).

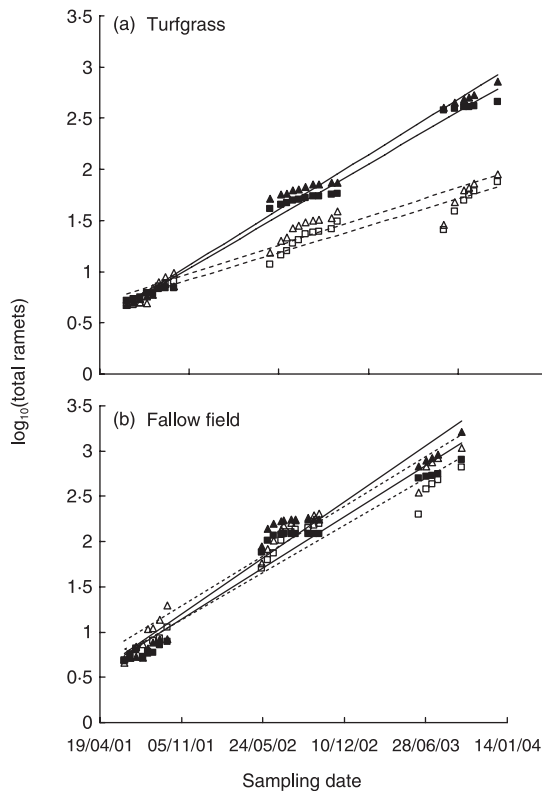


Fig. 2. Relationship between the total number of ramets per plot (\log_{10} -transformed) at various sampling dates during the three growing seasons for (black squares) ITH-1 non-mowed plants, (white squares) ITH-1 mowed plants, (black triangles) ITH-2 non-mowed plants and (white triangles) ITH-2 mowed plants in the (a) turfgrass lawn and (b) fallow field habitat. Refer to Table 1 for significance values.

The ITH-2 population averaged more ramets per plot than the ITH-1 population in both the fallow field (1360 vs. 733) and the turfgrass lawn (425 vs. 266). Moreover, ITH-2 plants produced more ramets per unit time after initial planting in both habitats compared with target plants from the ITH-1 population (Fig. 2).

For both populations, the mowing regime had a differential effect on spatial expansion of ramets depending on the habitat type (Figs 3 and 4). Within the fallow field, the non-mowed plots contained an average of 1214 ramets, while mowed plots contained 879 ramets. Similarly, in the turfgrass lawn, non-mowed plots averaged 585 ramets vs. 82 ramets in mowed plots. Mowing also drastically reduced the number of ramets establishing per unit time in the fallow field, while exhibiting less influence on the establishment rate in the turfgrass lawn (Fig. 2).

The spatiotemporal distribution of ramets from each population-by-mowing regime combination showed marked inter- and intrahabitat variation (interhabitat differences were not compared statistically, as noted above). After 3 years, mugwort ramets in the fallow field had reached distances of nearly 2 m from initial planting locations (Fig. 4), while ramets in the turfgrass habitat had attained a maximum distance of only 1.4 m from the initial planting location (Fig. 3). Across populations,

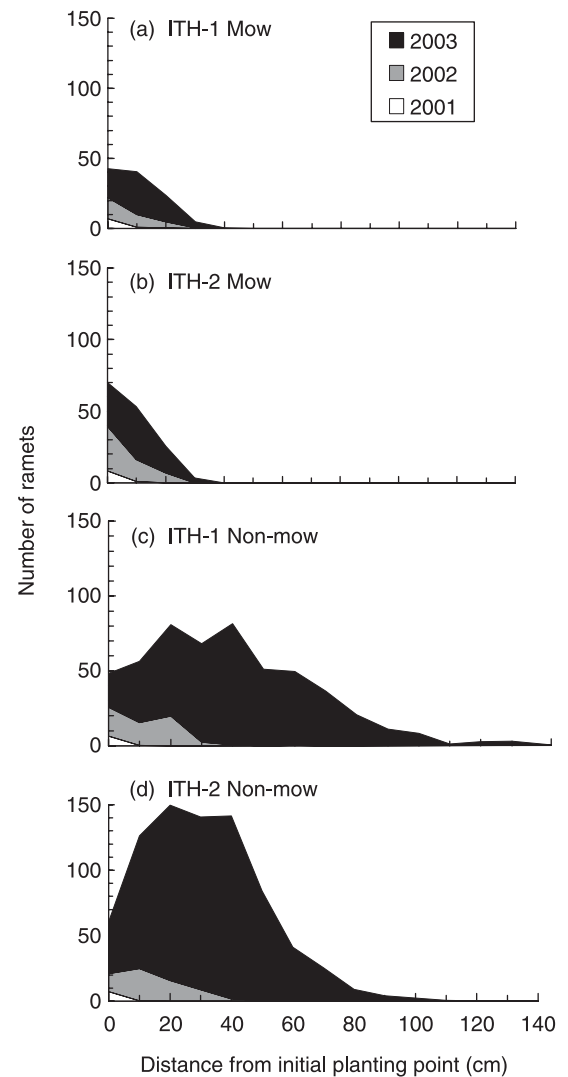


Fig. 3. Number of ramets produced at 10 cm intervals from the initial planting point in the turfgrass lawn for the mowed treatment of the (a) ITH-1 and (b) ITH-2 populations, and non-mowed treatment of the (c) ITH-1 and (d) ITH-2 populations for the 2001–03 growing seasons.

the area occupied by mugwort in the mowed plots was 10-fold greater in the fallow field compared with the turfgrass lawn, while the area occupied by mugwort in the non-mowed plots was 1.4-fold greater in the fallow field than the turfgrass habitat by the end of 2003.

Across habitats, ITH-2 produced more ramets at greater distances from the planting location, but the relative percentage of ramets within each distance interval was similar among populations (data not shown). However, mowing had a substantial influence on the spatial distribution of ramets. In the non-mowed turfgrass plots > 60% of ramets emerged at distances between 31 and 90 cm from the planting location, while in the mowed plots > 94% of ramets emerged within 30 cm of the planting location. Similarly, non-mowed plots in the fallow field contained > 57% of total ramets at distances greater than 60 cm from the planting location, while mowed plots contained > 85% of total ramets at distances between 0 and 60 cm from the planting location.

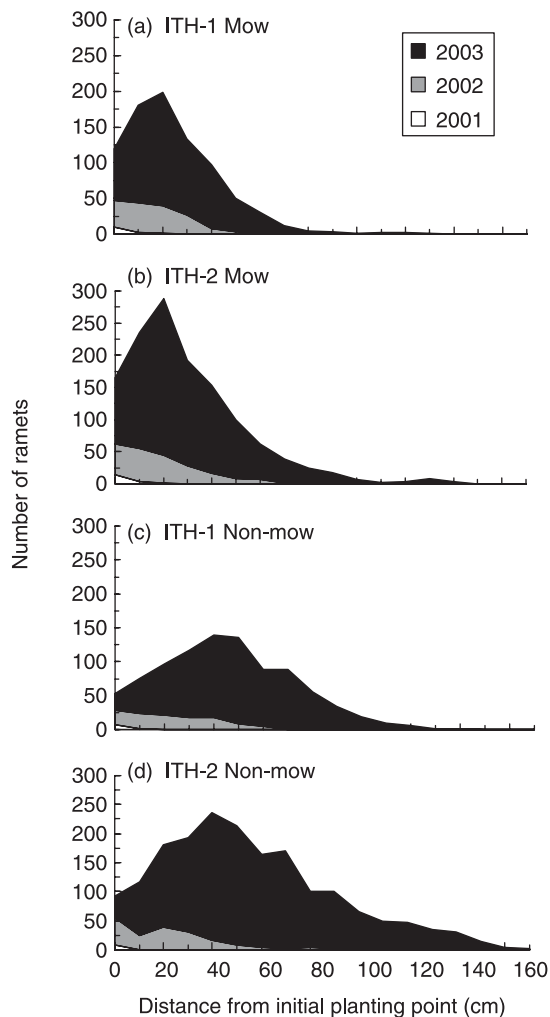


Fig. 4. Number of ramets produced at 10-cm intervals from the initial planting point in the fallow field for the mowed treatment of the (a) ITH-1 and (b) ITH-2 populations, and non-mowed treatment of the (c) ITH-1 and (d) ITH-2 populations for the 2001–03 growing seasons.

Non-mowed ITH-1 plants were significantly taller than ITH-2 plants in year 3 in both the turfgrass lawn (1.4 m vs. 0.89 m) and the fallow field (1.75 m vs. 1.45 m) (Table 1c). In all other years not previously mentioned, average height was not significantly different between the two mugwort populations ($P > 0.05$).

RESOURCE ALLOCATION PATTERNS

Despite an inability to perform statistical comparisons between habitats, total biomass (i.e. above- and below-ground) within each population-mowing combination was always greater in the fallow field than in the turfgrass lawn. However, while plants established in the fallow field were generally larger, no apparent differences in allocation to overall biomass were found (Fig. 5). In both habitats, there were no differences between populations in total biomass accumulation (Fig. 5a and Table 2). In the turfgrass lawn, ITH-1 individuals had more inflorescence structures (400 g) than plants from the ITH-2 population (148 g), but allocation patterns

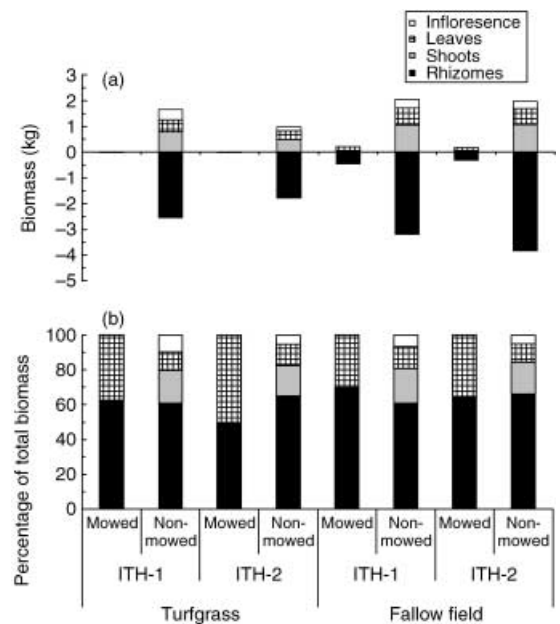


Fig. 5. Biomass allocation to above-ground and below-ground structures for each mugwort population (ITH-1 and ITH-2) and mowing regime (mowed and non-mowed) combination for the turfgrass lawn and fallow field habitats expressed as (a) dry weight and (b) relative percentage of overall biomass.

were not statistically different (Fig. 5a and Table 2). No other differences existed between populations.

Mowing regime had a significant impact on total biomass in both the turfgrass lawn and fallow field habitats. In both populations, allocation to photosynthetic tissue (leaves) decreased sharply when subjected to monthly mowing. Mowed plants in both habitats averaged 3% biomass allocation to leaf tissue (dry weight), while non-mowed plants allocated on average 19% to leaf tissue. In absolute numbers, a near 40-fold decrease in leaf biomass was observed in mowed plants (10 g) compared with non-mowed plants (390 g) in the turfgrass lawn (Fig. 5a). Interestingly, rhizome weight was reduced 165-fold in mowed vs. non-mowed plots in the turfgrass lawn, but mowing only resulted in 10-fold reductions in the fallow field plots (Fig. 5a).

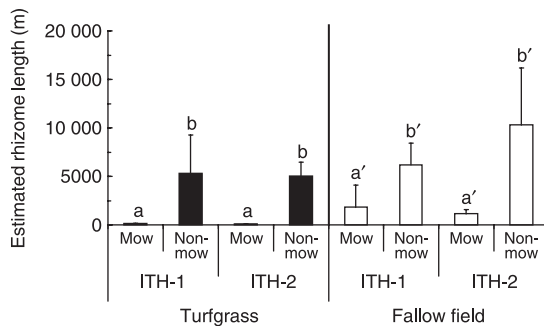
In both habitats, the percentage biomass allocated to leaves differed between mowing regimes, with mowed and non-mowed plants investing on average 46% and 12% of their total biomass to leaf tissue, respectively (Fig. 5b). After 3 years, rhizomes/roots accounted for 50–70% of the total biomass of plants in both habitats (Fig. 5b and Table 2). Plants from both populations allocated resources differently to below-ground rhizome/root material depending on mowing regime. As expected, mowed plants produced less below-ground biomass than non-mowed plants in both the fallow field and the turfgrass lawn, yet still allocated 50% of biomass to rhizome formation.

No differences in rhizome length were found between the two populations in either habitat (Fig. 6). However, there was large variation in the estimated rhizome length between mowing treatments in both the turfgrass lawn

Table 2. Summary of a mixed model analysis of absolute values and proportions of several mugwort growth parameters in the turfgrass lawn and fallow field habitats. The population by mowing regime interaction was not significant ($P > 0.05$) for all analyses

Dependent variable	Source of variation	Turfgrass lawn			Fallow field		
		d.f.	<i>F</i>	<i>P</i>	d.f.	<i>F</i>	<i>P</i>
Total biomass	Population	1	0.54	0.487	1	0.01	0.9116
	Mowing regime	1	12.37	0.0098	1	21.85	0.0023
Inflorescence (I)	Population	1	9.08	0.0236	1	0.22	0.6741
	Mowing regime	1	—*	—	1	—	—
Leaves (L)	Population	1	2.04	0.1674	1	0.14	0.7126
	Mowing regime	1	87.34	< 0.0001	1	20.96	0.0006
Stems (S)	Population	1	2.84	0.1432	1	0	0.9721
	Mowing regime	1	—	—	1	—	—
Rhizomes (R)	Population	1	0.41	0.5424	1	0.13	0.7294
	Mowing regime	1	12.71	0.0092	1	21.14	0.0025
Proportion (I)	Population	1	0.23	0.6497	1	1.72	0.2813
	Mowing regime	1	—	—	1	—	—
Proportion (L)	Population	1	0.45	0.5086	1	0.13	0.7278
	Mowing regime	1	169.17	< 0.0001	1	61.96	< 0.0001
Proportion (S)	Population	1	0.09	0.7706	1	0.19	0.6895
	Mowing regime	1	—	—	1	—	—
Proportion (R)	Population	1	0	0.9814	1	0.86	0.3852
	Mowing regime	1	1.58	0.249	1	0.87	0.3811

*—, non-testable parameter.

NS, non-significant ($P > 0.05$).**Fig. 6.** Estimated rhizome length (\pm SE) for each mugwort population (ITH-1 and ITH-2) and mowing regime (mowed and non-mowed) combination in both the turfgrass lawn and the fallow field habitats. Values for bars with the same letter are not significantly different ($P > 0.05$) within habitat.

($F_{1,6} = 20.58$, $P < 0.0001$) and fallow field ($F_{1,6} = 13.82$, $P = 0.009$). The average estimated rhizome length for non-mowed mugwort plants in the turfgrass lawn and fallow field was 4152 m and 8243 m per plot, respectively (Fig. 6). The mean estimated rhizome length per plot for mowed plants in the turfgrass lawn and fallow field was 90 and 1458 m, respectively (Fig. 6).

Discussion

Differences between mugwort establishment and expansion in mowed and fallow field habitats were substantial. The fallow field, which was denuded of all standing vegetation at the time of mugwort introduction, was clearly more invasible than the established turfgrass lawn. Regardless of the mugwort population or mowing

treatment, 10-fold more ramets (i.e. 200 ramets m^{-2} producing an astounding 11 km of rhizomes) established in the fallow field than the turfgrass lawn. Moreover, identical mugwort genets planted in the fallow field established ramets up to twice the distance from the planting location than in the turfgrass lawn and occupied an area nearly 10 times as large. There were also marked differences in the pattern of mugwort clonal expansion between the two habitats. For example, in the turfgrass habitat ramet establishment followed a more stochastic pattern, with mugwort ramets interspersed within patches of turfgrass (i.e. a 'guerrilla' strategy of clonal expansion). In the fallow field, however, a clearly defined ramet front was observed, with little competing vegetation found within or behind the advancing front (i.e. a 'phalanx' strategy of clonal expansion) (Pysek 1997).

In addition to disturbance, the characteristics of the habitat, such as plant community diversity, can also influence the success of plant invasions (Levine 2000; Kennedy *et al.* 2002). Although the fallow field had greater alpha diversity than the turfgrass lawn, both prior to and following tillage, it was also most susceptible to invasion by mugwort. Clearly in this instance, the disruption of the resident plant community in the fallow field following tillage had a greater effect in determining habitat invasibility than pre- or post-tillage plant community diversity.

Along with habitat invasibility, invasive success is also a function of the traits of the introduced species. Numerous reviews and empirical studies have attempted to qualify which plant traits are most important for invasion of novel habitats and the displacement of native vegetation (Blossey & Notzold 1995; Rejmanek &

Richardson 1996; Callaway & Aschehoug 2000; Bliker, Olson & Engel 2002; Claridge & Franklin 2002; Van der Putten 2002). Mugwort possesses several traits that have been suggested to increase the invasive success of plants, including a high relative growth rate, the ability to spread vegetatively and the expression of phenotypic plasticity. However, mugwort populations exhibit wide variation in morphology across a range of ecosystems, suggesting that intraspecific variation in establishment success may be the result of the specific genet/morphotype in question (Kurokawa *et al.* 2003; Pysek *et al.* 2003).

We examined two local mugwort populations that exhibited differences in foliar and rhizome morphology, leaf surface chemistry and overall growth form. There were large differences in the establishment characteristics and vegetative expansion between the two populations tested. The shorter ITH-2 population established a greater number of ramets per unit area and per unit time across both habitats in all 3 years. Moreover, the ITH-2 population produced substantially more ramets at greater distances from the planting location compared with the ITH-1 population, and was thus able to 'forage' and colonize a greater proportion of the habitat. Surprisingly, there were no differences in total biomass production between the two populations within each of the habitats, although different spatial growth patterns were observed. Variation in growth strategies between the two populations could be because of differences in the degree of phenotypic plasticity exhibited by each population (Agrawal 2001), suggesting disparity in invasiveness between the two populations.

Plasticity in plants can be expressed through changes in physiology (i.e. net assimilation rate, leaf area ratio), morphology and resource allocation (Hirose 1987; Stearns 1989; Callaway, Pennings & Richards 2003). The ability of a genotype to alter its phenotype in response to heterogeneous environments allows that individual to survive a greater number of ecosystem filters (i.e. stressful conditions) than non-plastic individuals (Agrawal 2001). There were clear size differences between the two mugwort populations, particularly when subjected to mowing. In the mowed treatments both populations reallocated resources towards the production of photosynthetic tissue (leaves), while reducing resources invested in support (stem) and sexual reproductive tissues. In addition, mowed plants generally had a greater, but non-significant, increase in the proportion of resources invested in below-ground structures, especially in the ITH-1 population. This shift in allocation of resources demonstrates the potential for plasticity to alter plant growth and morphology under stressful conditions. Previous studies have demonstrated that changes in morphology and resource allocation patterns are key features of plastic individuals and probably confer a competitive advantage, particularly in novel habitats (Rendon & Nunez-Farfan 2000; Zizumbo-Villarreal & Colunga-GarciaMarin 2001; Claridge & Franklin 2002).

As expected, monthly removal of above-ground plant tissue in mowed plots reduced overall biomass produc-

tion and the distance new ramets established from the planting location. Barthram *et al.* (2002) also found reduced vegetative expansion in defoliated grassland species (e.g. *Agrostis*, *Festuca* and *Poa*) in Scotland. Similar reductions in productivity and relative growth rate were demonstrated in sagebrush populations *Artemisia tridentata* (Nutt.) that were defoliated experimentally (Messina *et al.* 2002). Slower growing sagebrush populations were better able to withstand partial defoliation because of increased anti-herbivore defences, but were out-competed by faster growing competitors in non-browsed treatments (Messina *et al.* 2002). In previous work, we have determined that plants from the ITH-1 population contained more than 20 times greater levels of anti-herbivore and potentially allelopathic foliar compounds, primarily monoterpenes, than plants from the ITH-2 population (Barney, Hay & Weston 2005). It is possible that the metabolic cost of producing these compounds may have diverted resources from other structures and metabolic processes, especially in resource-limited environments (Coley, Bryant & Chapin 1985; Bazzaz *et al.* 1987), and may explain the reduced growth and expansion of ITH-1 plants relative to ITH-2 plants in this study.

Clearly, the vigorous growth and production of rhizomes, which allows mugwort to tolerate cultivation and herbicide application, affords land managers few options when faced with a mugwort infestation. In this study, we evaluated the efficacy of monthly mowing, which resulted in near-complete defoliation of mugwort plants, as a potential management strategy for this troublesome species. Mowing drastically reduced mugwort growth rate, biomass and area colonized, in both populations and habitats. Mowing had a much greater effect in the turfgrass habitat, reducing the number of established ramets by 10-fold and the total area infested 22-fold, compared with non-mowed plots. In the fallow field, monthly mowing reduced the number of mugwort ramets by 10–40% and the area colonized by 30% compared with non-mowed plots. Thus, mowing could be an effective means of suppressing mugwort growth and clonal expansion. However, monthly mowing over the three growing seasons in this study did not result in the eradication of either mugwort population. Furthermore, despite a significant reduction in photosynthetic capacity in mowed plants, mugwort continued to establish and spread, suggesting that more frequent mowing may be required to reduce carbohydrate stores further, thus decreasing growth and expansion of this species.

Recent studies conducted on North American mugwort populations have demonstrated the potential for several herbicides to reduce growth of this species (Foy 2001; Bradley & Hagood 2002). Therefore, monthly (or more frequent) mowing used in combination with herbicide application may result in the eradication of these mugwort populations. However, the success of this strategy depends on the size of the mugwort stand and the genotype under study, as demonstrated in this research. The likelihood of success will be much greater

if these management efforts are expended along invasion fronts or on isolated satellite populations or 'nascent foci', rather than on large, well-established mugwort stands (Moody & Mack 1988).

In conclusion, the fallow field and turfgrass lawn differed in their resistance to mugwort invasion, while the two mugwort populations differed in their growth pattern but not in their allocation of resources to above- and below-ground structures. Monthly mowing in either habitat drastically slowed the rate of spread of the two populations but did not eliminate the invader. This study highlights the need to view invasion success (or failure) in light of the possible interactive effects between habitat characteristics, invader traits and disturbance. With the ever-increasing number of invasions by largely vegetatively reproducing plant species, which are often tolerant to cultivation and chemical control, this study demonstrates that monthly mowing alone may not be sufficient to suppress growth and expansion of mugwort effectively. Future research should focus on assessing the efficacy of an integrated management approach for this and other clonal species that makes use of several tactics, including more frequent mowing and chemical applications. Finally, findings from this study underscore the view that the greatest chance of success for invasive species management programmes is dependent on the targeting of newly introduced, often slow-to-establish, populations/species, which are potentially easier to manage yet are most often overlooked (Stephens & Sutherland 1999).

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