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Experimental demography of the old-field perennial *Solidago altissima*: the dynamics of the shoot population

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Summary

1 Control strategies are needed for the clonal species *Solidago altissima*, which is an aggressive invader in Europe that propagates vegetatively by persistent rhizomes that produce annual shoots.

2 The shoot dynamics of a population of *S. altissima* that had invaded an old-field site in 1984 were studied from 1987 to 1992. Shoots from 120 genets of the same cohort were followed in relation to their parent genets. We assessed the effect of yearly mowing, yearly cutting of rhizomes and repeated removal of close neighbour plants on growth, survival, probability of reproduction and flux of these shoots.

3 In unmown plots, both shoot survival until the end of the growing season and the proportion of shoots producing seeds decreased (59% to 36% and 67% to 32%, respectively, from 1988 to 1992). The proportion of rhizomes producing shoots, however, rose (from *c*. 50% to more than 90%) so that annual shoot density increased almost fivefold by the end of the study, when it had almost reached equilibrium.

4 In contrast, shoot density in mown plots remained roughly constant from 1988 to 1992, after an increase from 1987 to 1988. Shoots were much smaller and a smaller proportion of them reproduced than in unmown plots.

5 Rhizome cutting (reduced clonal integration) produced a small but consistent decrease in height and in the percentage of sexually reproducing shoots.

6 The removal of close neighbour plants increased shoot density, and a higher percentage of these shoots survived and reproduced.

7 Experimental demographic studies thus show that (i) continued regular mowing reduces the production of both seeds and shoots, and so would prevent further spread of an invading *S. altissima* population; (ii) clonal integration may contribute to the species' success as an invader because disconnected rhizomes produce smaller shoots with a lower chance of sexual reproduction; and (iii) competition decreases shoot density, mainly as a consequence of reduced shoot survival, and can therefore control *S. altissima* growth.

Keywords: biological invasions, clonal plants, competition, experimental demography, rhizome cutting, shoot dynamics, *Solidago altissima*

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Introduction

Biological invasions may threaten the composition and stability of plant communities (Drake *et al*. 1989; Primack 1993), and the establishment and spread of invasive species outside their home ranges should therefore be prevented. However, effective control requires knowledge of the demographic processes involved during colonization and establishment (Crawley 1987; Simberloff 1989). Tall goldenrod *Solidago altissima* L. was introduced to Europe from North America and is now considered a noxious weed (Zwölfer 1976; Weber & Schmid 1993). We therefore compared the effects of various experimental manipulations on demographic parameters to determine why, and under what conditions, some populations are invasive, and to aid development of effective control measures to stop the further spread of this species.

Demographic studies give insight into the birth and

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death rates of plant species at particular life-history stages, and have been used widely in the past to model the dynamics of natural populations (for example Sarukhán & Harper 1973; Harper 1977; Jackson *et al*. 1985; Sackville Hamilton *et al*. 1987; Solbrig *et al*. 1988; Van Groenendael & de Kroon 1990; Silvertown *et al*. 1993; Dai & Wiegert 1996). Such studies do not, however, explain the mechanisms controlling population dynamics (Watkinson 1986). Prediction of the response of a population, for example of an invasive plant species to environmental change or control measures, requires deliberate manipulation of potential control factors and measurement of the effects on demographic transitions within the life cycle (Caswell 1989; Schmid 1990; Bullock *et al*. 1994a; Cousens 1995).

Initial colonization of a site by *S. altissima* involves establishment of genets from seeds, but subsequent population development usually occurs only by the production of ramets via clonal growth (Hartnett & Bazzaz 1985; Eriksson 1993). We followed the complete life cycle of these ramets in 120 marked genets over a period of up to 5 years and recorded all relevant demographic transitions. A ramet life cycle starts when a shoot develops from a rhizome and ends when the shoot, which may carry seeds and new rhizomes, senesces. Experimental treatments were applied in the field at the plot and genet level to assess the influence of (i) yearly mowing, (ii) cutting of rhizome systems, and (iii) reduced neighbour competition.

Mowing is a low-cost potential control measure, but little is known about its effects on the demographic processes within populations. The cutting of rhizome connections has been used successfully in controlled environments to demonstrate the importance of clonal integration for ramet performance in *S. altissima* (Hartnett & Bazzaz 1983, 1985; Schmid & Bazzaz 1987, 1991; Schmid *et al*. 1988a; Abrahamson *et al*. 1991), but little is known about the effects of reduced clonal integration in the field. Because, irrespective of clonal integration, the demographic behaviour of ramets belonging to the same genet may be correlated (Cook 1983; Pitelka & Ashmun 1985), we explicitly considered genet identity as an additional explanatory variable. The removal of neighbours was expected to intensify clonal growth (Schmid & Bazzaz 1992), even though it is also conceivable that clonal growth is restricted more by internal architectural constraints (the compact growth form of genets; Sackville Hamilton *et al*. 1987) than by neighbour competition. The removal of neighbours might indicate indirectly whether the planting of other species could be used to control the further spread of *S. altissima*.

We predicted that in *S. altissima* (i) repeated yearly mowing would control the growth of ramet populations, (ii) cutting of rhizome connections would have a negative effect on ramet dynamics, and (iii) above-ground competition from neighbours would reduce the spatial expansion of established genets.

Materials and methods

THE STUDY SPECIES

Solidago altissima was introduced to central Europe in the 18th century and became naturalised in the 19th century (Voser-Huber 1983; Weber & Schmid 1993). The species is now one of the most invasive species in this region, where it can endure a wide range of environmental conditions (Thompson 1975; Werner *et al*. 1980; Voser-Huber 1983; Weber 1994). *Solidago altissima* may retard succession and this, together with its ability to displace other plant species with their associated fauna, led to it being considered as a potential target for biological control, particularly in nature reserves (Zwölfer 1976; Werner *et al*. 1980).

The aerial shoots are unbranched and, at the study site, are up to 2 m tall. Most of them flower in August or September, producing up to 20 000 seeds (achenes) per shoot. Under field conditions a seedling usually consists of a single small shoot that, like larger shoots of established genets, starts vegetative propagation in summer through the initiation of one to several rhizomes. The rhizomes elongate in autumn and then stay dormant during winter before they grow out into new shoots in the following spring (April–May). After seed maturation (October–November) the shoots senesce but the seeds are dispersed by wind until March and are then able to germinate from May onwards. The rhizomes are used for transport and storage of assimilates and nutrients (Bradbury & Hofstra 1977), vary in length between 1 cm and 20 cm, and may persist for several years. Shoot systems may consist of more than 20 connected shoots. When the oldest rhizomes decay the genets fragment into several shoot colonies. Further information on the biology of *S. altissima* can be found in Werner *et al*. (1980) and Voser-Huber (1983).

FIELD SITE

The study site is located in the Reinacher Heide Nature Reserve, *c*. 15 km south of Basel, Switzerland (47°30′N, 7°36′E, altitude 280 m a.s.l.). It was an arable field until 1982, when the last maize crop was not harvested. All genets in the population probably belong to the cohort of plants that germinated in 1984, as the morphological analysis of a sample of 42 genets excavated in 1987 yielded a uniform age of 3 years. By August 1987, when the project began, an old-field vegetation, dominated by *Erigeron annuus* L., *Melilotus alba* Desr., *Pastinaca sativa* L. and *S. altissima*, had established. The climate of the region is characterized by relatively hot and wet summers and cold and relatively dry winters (Fig. 1). May and June 1989 were exceptionally dry, while winters 1988/89 and 1989/90 were much warmer than usual.

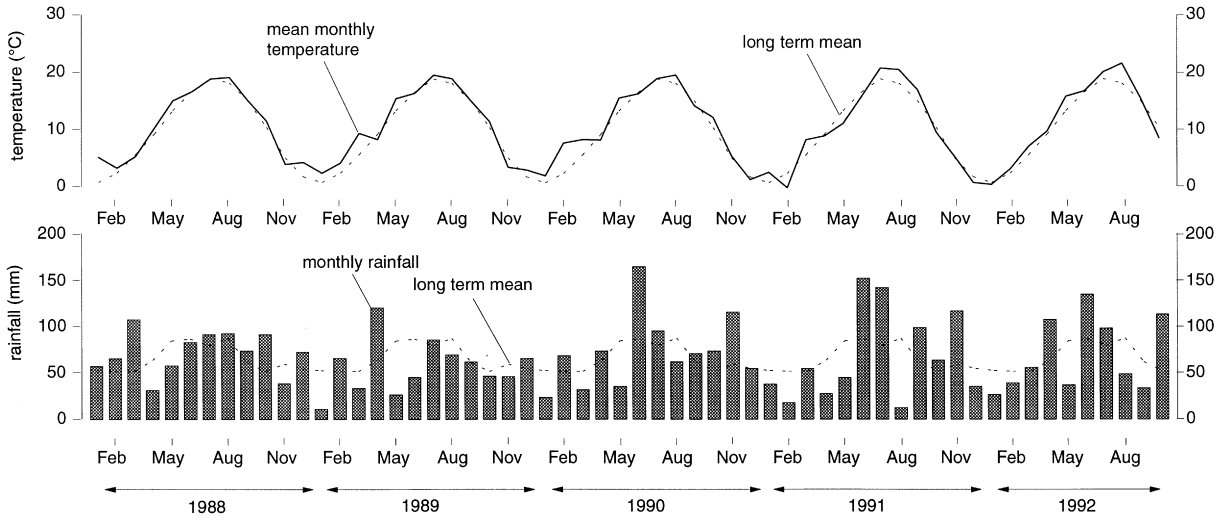


Fig. 1 Monthly temperature (top) and rainfall (bottom) for the period August 1987–92. The data were recorded at the Basel–Binningen meteorological station, *c.* 8 km north of the field site (47°35′N, 7°35′E, 317 m a.s.l.).

EXPERIMENTAL DESIGN

The study was carried out from August 1987 to August 1992. In August 1987 the study area was divided into three adjacent blocks, each consisting of two 16 × 8 m plots. One plot within each block was mown to a height of 5 cm once a year (at the end of August 1987 and 1988, in mid-September 1989, 1990 and 1992, and in mid-October 1991) and the mowings removed ('mown plots'). The other plot within each block was left unmown. Initially each plot contained several hundred genets of *S. altissima*, most of them consisting of two to seven shoots ⩾ 50 cm tall. Within each plot we randomly marked 20 genets that were clearly identifiable by morphological shoot characteristics, such as leaf shape and colour, or the position and direction from which stem bases arose (the direction of a rhizome from a presumed genet centre can be inferred from the upwards bend at the stem base). Genets were separated from each other by at least 50 cm.

In each plot, the 20 marked genets were randomly assigned, four to each of five different treatments.

1 Cutting of rhizomes

In March–April of every year from 1988 to 1992 the rhizome systems were carefully exposed (litter and soil removed) as far as necessary to locate interconnections between the shoot bases that were left from the previous year. These rhizome connections were severed and the removed soil put back. Next year's rhizomes were therefore all derived from isolated parent shoots.

2 Repeated leaf removal on one shoot per genet

Every third fully expanded (> 4 cm long) main-stem leaf on the selected shoot was cut at the base where it joined the stem. The procedure was applied on 30 May, 28 June and 16 August in 1988, and on 20 May, 20 June and 28 July in 1989.

3 Combination of rhizome cutting and leaf removal

This was done at the same dates as in treatments 1 and 2.

4 Repeated removal of neighbours

A plastic ring of 65 cm diameter was centred over the genet. All above-ground plant parts of neighbours, both of the same and other species, within the ring boundary were cut to a height of 2 cm. The procedure was applied monthly from May to August from 1988 to 1990 and once in May 1991.

5 Control

None of the above treatments was applied on control genets. In March 1988, one genet from each of the five treatments was selected from each plot at random: the rhizome systems of these 30 genets were mapped each March–April from 1988 to 1992. The rhizome systems were exposed *in situ* by removing the soil, the number of newly produced rhizomes (⩾ 0.5 cm in length) and rhizome buds (< 0.5 cm in length) was counted, and the soil was then immediately put back. In March 1990 the 90 genets for which the rhizome system was not repeatedly mapped were dug out and used for analyses other than reported here. Therefore all field data taken later than March 1990 were restricted to the 30 rhizome-mapped genets. The influence of exposure and mapping on the characters measured on all genets was not significant ($P > 0.1$, split-plot ANOVA).

Because the removal of main-stem leaves had no

measurable effect on any variable, the five original treatments were combined in all analyses into three 'genet treatments', namely yearly cutting of rhizomes (1 plus 3), repeated removal of neighbour plants, and control (2 plus 5).

MEASUREMENTS

In August 1987 and at the beginning of May of every year from 1988 to 1990, all shoots of each of the 120 genets were marked (in 1987 only shoots $\geqslant 50$ cm tall), as were shoots emerging later on in the same year. Subsequently similar procedures were applied to the remaining 30 genets. Height and phenological status (rhizome, rosette, bolted, with flower heads, with open flowers, flowers wilting, pappus visible, standing dead) of all marked shoots were recorded in August 1987, seven times between May and August 1988, seven times between May and September 1989 and 1990, three times between May and October 1991, and four times between May and August 1992. Phenological status was also measured in October from 1988 to 1990. Because more than 99% of all shoots that flowered also fruited, the term 'reproductive' includes flowering as well as fruiting shoots unless otherwise specified.

In mown plots data on shoot growth were obtained up to the mowing dates. In order to see whether genets were able to produce replacement shoots, we recorded those emerging after the 1988 and 1989 mowings. In 1988, height and phenological status of such shoots were measured four times from September to November and phenological status on 11 January and 6 March 1989. In autumn 1989, the number of late emerging shoots and the maximum shoot height per genet were measured on 31 October.

The density of genets within the study area was estimated in 1989 from counts in four randomly placed 2×2 m quadrats in each plot.

STATISTICAL ANALYSIS

Analysis of variance (ANOVA) and logistic regression (McCullagh & Nelder 1989) were used to analyse the data. The full experimental design was a split-plot involving randomized complete blocks and two or three treatment factors (Table 1). The covariate 'genet size' was defined as total height of the shoots that a genet had produced by the end of the previous growing season. All model fitting and significance tests were done using Genstat 5 (release 3; Payne *et al.* 1993). If necessary, data were square-root or log-transformed to achieve normality and homoscedasticity of residuals.

Results

MEAN SHOOT HEIGHT PER GENET AT THE END OF THE GROWING SEASON FROM 1987 TO 1992

In August 1987, before the first application of any treatment, the mean shoot height per genet was 108.1 ± 1.9 cm (pooled over all genets) and was not significantly different between the groups assigned to the different treatment combinations.

From 1988 onwards mean shoot height (measured before mowing) was strongly reduced in mown plots compared with unmown plots (Tables 2 and 3a). Mean shoot height was highest in genets with neighbours removed and lowest in genets with cut rhizomes (Tables 2 and 3a). Its value decreased from 1988 to 1992 (linear trend in Table 2) but year-to-year fluctuations were high (significant quadratic term in Table 2) and showed a different pattern in unmown and mown plots (Table 3a). Mean shoot height at the end of the growing season varied significantly between genets.

DEVELOPMENT OF SHOOTS EMERGED AFTER MOWING

Over 90% of new shoots that emerged after mowing in 1988 remained in the rosette stage and none of them flowered. The height data for these shoots were analysed separately for each of the four census dates and showed that the mean value was not affected either by the removal of neighbour plants or by rhizome cutting. Mean shoot height (when pooled over genet treatments) was 5.1 cm in November, although it varied significantly between genets for all census dates. In 1989 genets produced few new shoots after mowing. The height of the tallest shoot per genet was on average 2.8 cm and was not significantly influenced by any treatment.

SHOOT SURVIVAL WITHIN GENETS

All reproductive shoots died soon after seed maturation. In unmown plots, shoots that remained vegetative survived longer, but by December all were dead. Shoots that appeared after mowing in 1988 were mostly dead by January 1989, but a few survived until March 1989.

Mowing had no influence on the survival of shoots until the end of the growing season (Table 2). However, more shoots survived in genets with neighbours removed than in other treatments (Tables 2 and 3b). Shoot survival decreased over time (linear trend in Table 2), especially in genets with cut rhizomes and in control genets, although year-to-year fluctuations were high (significant quadratic term in Tables 2 and 3b) and shoot survival also varied significantly between genets.

SEXUAL REPRODUCTION

To analyse the percentage of reproducing shoots per genet, we considered those shoots that had bolted and which were still alive at the end of the growing season. In 1987, 42% of all shoots reached the reproductive stage and this percentage was not significantly differ-

Table 1 Skeleton analysis of variance/deviance for measured ramet characters. The split-plot design consisted of blocks, plots and subplots (=genets). The main-plot factor was mowing and varied between plots within blocks. The subplot factor contained the three treatments applied to the genets. These genet treatments consisted of rhizome cutting, neighbour removal and control (see the Materials and methods). The block effect was used to eliminate variation caused by spatial differences within the sample site. In cases where the block effect was small (i.e. F-value of $\leqslant 2$; Green & Tukey 1960), it was pooled with the plot effect. To test the effects related to the term year (i.e. effect of the factor year plus all interactions with year), the approach of orthogonal contrasts to repeated-measures analysis was used (Elashoff 1986). In this approach polynomial contrasts are formed and tested against their own error terms. This avoids the problem of serial correlation and therefore the need to adjust the degrees of freedom (Rosenthal & Rosnow 1985, p. 65). Here, only linear and quadratic contrasts were tested as the interpretation of higher order polynomials is biologically less relevant. Because 120 genets were observed from 1988 to 1989 but only 30 genets from 1990 to 1992 (see the Materials and methods) the d.f. for the last line in the table is reduced. Effects were always adjusted for effects that preceded them. Significance tests are based on F-tests (ANOVA) or quasi-F-tests (analysis of deviance). Three-way interactions are omitted. For the effect of mowing, 10% significance levels were also computed as this test was based on only 2 d.f. in the denominator when the block effect was also fit

Source of variation	d.f. (d.f. change)	Mean square (deviance change)	Variance ratio (approx. F)
Genet size	1	MS_{gs}	MS_{gs}/MS_{g}
Block	2	MS_{b}	MS_{b}/MS_{p}
Mowing	1	MS_{m}	MS_{m}/MS_{p}
Plot	2	MS_{p}	
Genet size × mowing	1	MS_{gsm}	MS_{gsm}/MS_{g}
Genet treatments	2	MS_{gt}	MS_{gt}/MS_{g}
Mowing × genet treatments	2	MS_{mgt}	MS_{mgt}/MS_{g}
Genet	120–1–11	MS_{g}	MS_{g}/MS_{gy}
Year			
Year (linear)	1	MS_{yl}	MS_{yl}/MS_{gyl}
Year (quadratic)	1	MS_{yq}	MS_{yq}/MS_{gyq}
Mowing × year			
Mowing × year (linear)	1	MS_{myl}	MS_{myl}/MS_{pyl}
Mowing × year (quadratic)	1	MS_{myq}	MS_{myq}/MS_{pyq}
Plot × year (including block × year)			
Plot × year (linear)	4	MS_{pyl}	
Plot × year (quadratic)	4	MS_{pyq}	
Genet treatment × year			
Genet treatment × year (linear)	2	MS_{gtyl}	MS_{gtyl}/MS_{gyl}
Genet treatment × year (quadratic)	2	MS_{gtyq}	MS_{gtyq}/MS_{gyq}
Genet × year (=residual term)		MS_{gy}	
Genet × year (linear)	120–1–7	MS_{gyl}	
Genet × year (quadratic)	30–1–7	MS_{gyq}	

ent between the groups assigned to the different treatment combinations.

Mowing strongly decreased the percentage of reproducing shoots per genet (Tables 2 and 3c). The percentage of reproducing shoots was highest in genets with removed neighbours and lowest in genets with cut rhizomes. Genets suffering from resource deprivation (whether caused by removal of aboveground parts, competition or reduction of clonal integration) therefore appeared to have lowered reproductive activity. There was a decrease in the percentage of reproducing shoots from 1988 to 1992, although year-to-year fluctuations were high (Table 2), and the percentage of reproductive shoots per genet varied significantly between genets.

THE INFLUENCE OF GENET SIZE ON WITHIN-GENET SHOOT PERFORMANCE

Larger genets had greater mean shoot height at the end of the growing season and higher percentages of surviving and reproductive shoots (see term genet size in Table 2 for results obtained when the covariate was fitted first). When genet size was fitted after the mowing term, the covariate was not significant for any of the three demographic variables. Indeed, a split-plot ANOVA carried out in the same way as shown in Table 1, but with genet size as response variable, revealed that mowing strongly decreased genet size ($P < 0.05$). In addition, none of the slope parameters obtained separately for unmown and mown plots for

Table 2 Table of significances for mean shoot height per genet at the end of the growing season, percentage of surviving shoots per genet until the end of the growing season, and percentage of reproducing shoots per genet from 1988 to 1992 (120 genets from 1988 to 1989, 30 genets from 1990 to 1992). Significances are based on ANOVA (mean shoot height) or analysis of deviance (percentage of surviving and reproducing shoots). For each character two models, one unadjusted (left column) and one adjusted (right column) for the covariate genet size, were fitted

	Mean shoot height per genet		Percentage of surviving shoots per genet		Percentage of reproductive shoots per genet	
Source of variation	− cov.	+ cov.	− cov.	+ cov.	− cov.	+ cov.
Genet size		**		*		***
Mowing	*	*	–	–	*	(*)
Genet size × mowing		–		–		–
Genet treatments	*	*	***	**	*	*
Mowing × genet treatments	–	–	–	–	–	–
Genet	***	***	*	**	***	**
Year						
Year (linear)	***	***	*	(*)	***	*
Year (quadratic)	***	***	***	***	**	**
Mowing × year						
Mowing × year (linear)	*	–	–	–	–	–
Mowing × year (quadratic)	–	–	**	*	–	–
Genet treatment × year					–	–
Genet treatment × year (linear)	–	–	*	*	–	–
Genet treatment × year (quadratic)	–	–	–	–	–	–

– NS, (*) $P < 0.1$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

the relationship between genet size and the three demographic variables was significantly different from zero, suggesting that the observed decreases in within-genet shoot performance were due to the mowing treatment, which also reduced genet size, rather than to genet size *per se*.

SHOOT FLUX

Unmown plots in April 1989 contained approximately six genets per m^2. None of the 120 selected genets died between August 1987 and April 1989 and no new genets had appeared, and this estimated genet density was therefore taken as the basis for the calculation of overall shoot densities in each year.

To describe the flux of shoots in the study population, data from all genet treatments were pooled for mown and for unmown plots. In August 1987, at the start of the experiment, shoot densities for vegetative and sexual shoots were very similar in mown and unmown plots (Fig. 2). In unmown plots the ramet population increased over time, as shown by the increasing densities of both rhizomes and shoots (sum of rosettes, bolted shoots and sexual shoots) from 1987 to 1992 (Fig. 2). In August 1992, shoot density in unmown plots was 4.7 times as high as in August 1987. The annual growth rate of the shoot population (based on the last census date in each year) decreased from 1.70 (1987–88) to 1.11 (1991–92), thus slowly tending towards equilibrium. In 1988, 49.4% of all initiated rhizomes in unmown plots grew into shoots and this proportion increased to 96.6% in 1992. The proportion of rosettes in the overall shoot population (rosettes plus bolted shoots) in May of each year varied between 19% (1990) and 36% (1992) in unmown plots. Most rosettes died during the period when taller shoots were showing maximum growth (May–July), and although a few bolted none reached the reproductive stage. In contrast, shoots that had bolted by early May had a much higher probability of surviving until the end of the growing season than did rosettes. Between 36.9% (1989) and 50.7% (1988) of these bolted shoots in unmown plots reproduced each year (Fig. 2). Reproductive shoots never died before the end of the growing season (October). Very few shoots appeared between May and the end of the growing season, and the population thus consisted mainly of one cohort of shoots.

In mown plots rhizome density decreased over time, suggesting that mowing may be an effective control measure. However, the proportion of rhizomes growing into shoots increased over the years, while the shoot density increased from 1987 to 1988 and then remained roughly constant from 1988 to 1992 (Fig. 2). Of the shoots that had bolted by early May in mown plots, between 7.9% (1991) and 27.5% (1987) reached the reproductive stage.

In 1989, mortality of shoots was much higher than in other years, most likely because of the drought periods in May and July. Thus, about half of all shoots that had bolted in early May 1989 died before the end of July and a relatively small proportion of

Table 3 (a) Mean shoot height in cm per genet at the end of the growing season, (b) percentage of surviving shoots per genet at the end of the growing season, and (c) percentage of sexually reproducing shoots per genet. Predicted means from the linear (a) or logistic model (b and c, unadjusted for the covariate genet size), together with number of genets available for analysis (in parentheses; one genet was wrongly assigned to the control instead of the severing treatment)

	Year	Rhizomes severed	Control	Neighbours removed
(a) Shoot height in cm				
Unmown	1988	118 (23)	125 (25)	129 (12)
	1989	60 (23)	76 (24)	86 (12)
	1990	109 (6)	108 (7)	127 (3)
	1991	95 (6)	84 (7)	94 (3)
	1992	97 (6)	90 (7)	95 (3)
Mown	1988	78 (24)	89 (24)	82 (12)
	1989	40 (20)	50 (20)	53 (12)
	1990	34 (5)	50 (5)	67 (2)
	1991	45 (5)	54 (5)	60 (2)
	1992	55 (5)	69 (5)	73 (2)
(b) % surviving shoots				
Unmown	1988	53 (23)	59 (25)	65 (12)
	1989	48 (23)	51 (25)	65 (12)
	1990	58 (6)	50 (7)	60 (3)
	1991	55 (6)	49 (7)	68 (3)
	1992	43 (6)	36 (7)	68 (3)
Mown	1988	64 (24)	68 (24)	74 (12)
	1989	38 (24)	44 (24)	55 (12)
	1990	79 (5)	62 (5)	57 (2)
	1991	60 (5)	41 (5)	41 (2)
	1992	64 (5)	44 (5)	59 (2)
(c) % reproductive shoots				
Unmown	1988	55 (23)	67 (25)	70 (12)
	1989	37 (23)	56 (24)	63 (12)
	1990	49 (6)	61 (7)	86 (3)
	1991	47 (6)	38 (7)	68 (3)
	1992	42 (6)	32 (7)	54 (3)
Mown	1988	24 (24)	37 (24)	35 (12)
	1989	9 (20)	26 (20)	18 (12)
	1990	4 (5)	10 (5)	19 (2)
	1991	7 (5)	11 (5)	7 (2)
	1992	11 (5)	18 (5)	25 (2)

them reached the reproductive stage (36.9% in unmown and 11.9% in mown plots). Further, a large number of 'replacement shoots' emerged from May–September 1989 (Fig. 2), particularly in unmown plots.

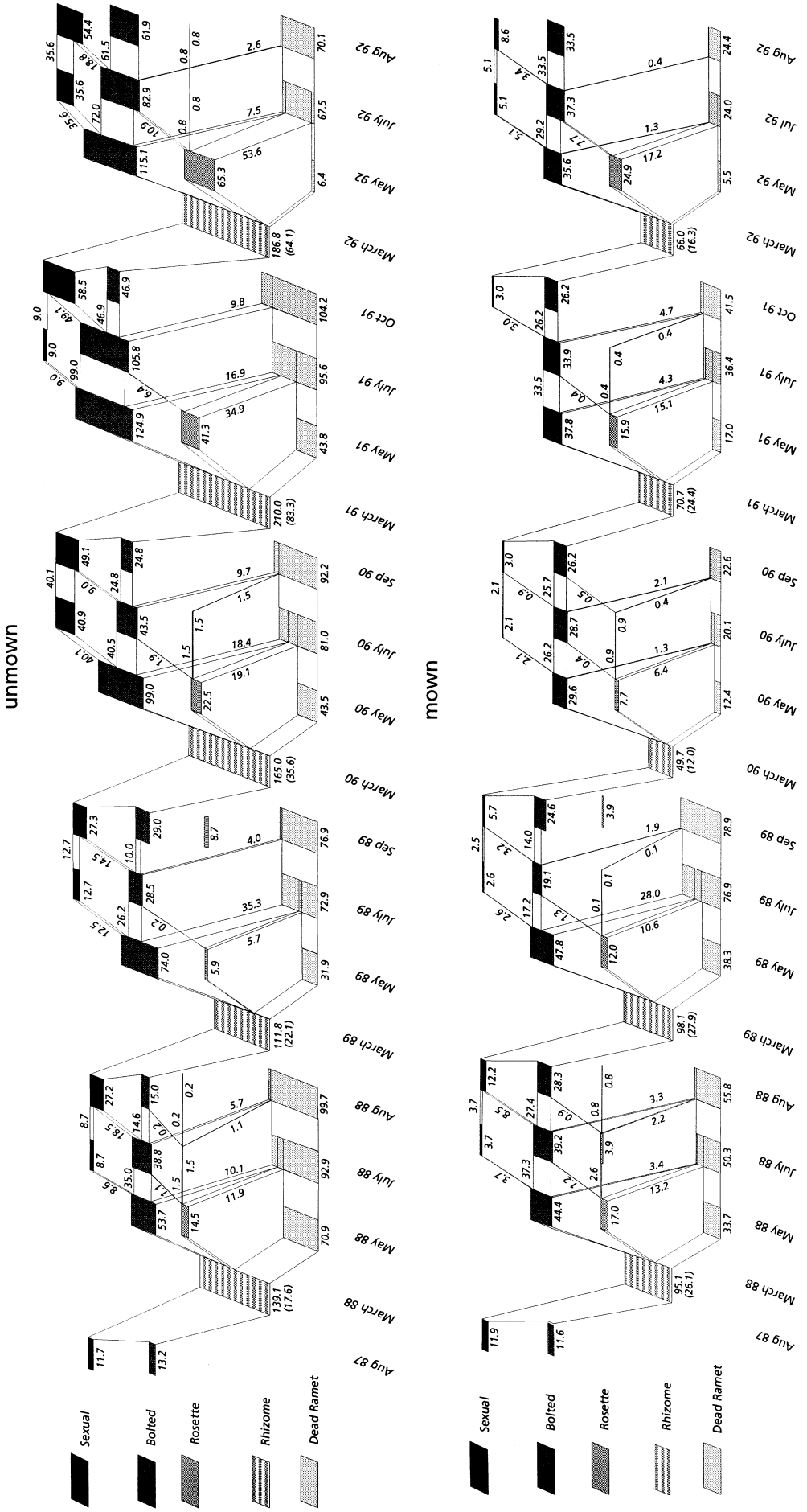
Discussion

INVADING *S. ALTISSIMA*: THE UNDERLYING DEMOGRAPHIC PROCESSES

This study looked at changes in demographic parameters of shoots over time during succession, and thereby explicitly considered the size of the parent genet as a covariable. Earlier work, however, compared populations of *S. altissima* of different successional age (e.g. Maddox *et al.* 1989). By experimentally manipulating demographic processes in the field we have shown that *S. altissima* is capable of producing dense stands of shoots by vegetative propagation even under stressful conditions.

By the final year of the study, when the population was in its eighth year, the density of more than 100 shoots per m^2 may represent the carrying capacity of the site for *S. altissima*. It may be a general pattern that populations of *S. altissima* that invade old-fields grow rapidly for a few years before they reach an upper density limit (Hartnett & Bazzaz 1985; Maddox *et al.* 1989).

There were distinct changes in demographic parameters during the early stages of old-field succession. Mean shoot height decreased, even if no experimental manipulations were applied, suggesting either that the resources of the habitat were being depleted or that the genets changed their allocation patterns during succession (Maddox *et al.* 1989). A change in allocation pattern is to be expected if clonal species with a compact growth form (such as *S. altissima*) are to avoid the problem of ramet crowding at the periphery



of genets as they increase in size (Sackville Hamilton *et al*. 1987).

Shoot survival decreased, again even if no experimental manipulations were applied (Table 3b). This suggests that support via rhizome connections reduces with increasing genet age, and rhizome systems are known to decay after 3–4 years (Meyer 1992; see also Hartnett & Bazzaz 1983). Moreover, the increasing shoot density may have led to increased competition between shoots as most shoot deaths occurred during the time when surviving shoots were growing fastest (Sarukhán & Harper 1973; Harper 1977; Noble *et al*. 1979; Bartlett & Noble 1985; Dickerman & Wetzel 1985; Cain 1990).

The proportion of shoots within a genet that allocated resources to sexual reproduction also decreased with succession. Although this observation supports some previous predictions (Abrahamson 1980), Bradbury (1981) observed lower proportions of flowering shoots in an invading than in an established population of *S. canadensis*. The compact rhizome architecture of *S. altissima* might suggest that resources will need to be invested in sexual reproduction rather than clonal growth as genets grow large (Sackville Hamilton *et al*. 1987). However, repeated mapping of rhizome systems in the study population showed that such constraints can be at least partly avoided by increased rhizome length (Meyer & Schmid 1999).

THE EFFECTS OF EXPERIMENTAL TREATMENTS

Mowing

Mowing prevented net population growth, but only after the first year of the 5-year observation period. This was due to a decrease in the production of new rhizomes rather than an effect on shoot survival. Large amounts of carbon and nitrogen accumulate in the shoots of *S. altissima* during August and September (Egli & Schmid 1991), and control by mowing (and subsequent removal of the cut material) is therefore most likely to be effective late in the season. Such repeated removal of resources should lead to decreases in both shoot number and height in subsequent seasons. In an experiment to control another clonal rhizomatous species, bracken, Lowday & Marrs (1992) demonstrated the importance of continued treatment if population recovery is to be avoided.

Reproduction was also inhibited by mowing. Although control is likely required to involve regular cutting before seed set, reduction in potential seed output could be important in delaying recovery if mowing is temporarily discontinued. Seed dispersal distance might also be reduced because of the reduction in shoot height. Previously suppressed plant species might recover after mowing and compete more strongly with *S. altissima* (Cornelius & Faensen-Thiebes 1990; Brown 1994; Joshi & Matthies 1996).

Mowing was especially successful in reducing the density of shoots in the drought year (1989). Continued mowing may therefore lead to the further spread of *S. altissima* being controlled by a combination of natural and artificial stress factors.

Clonal integration and effects of genet size

Although clonal support of ramets is thought to be beneficial for the entire genet under certain environmental conditions (Cook 1983; Pitelka & Ashmun 1985; Bullock *et al*. 1994b), support for new ramets tends to decrease with ramet age (Hartnett & Bazzaz 1983; Alpert & Mooney 1986; Bullock *et al*. 1994b). We found that rhizome severing had only a small effect. However, the severed connections were more than 1 year old and had already produced a fully established shoot, so that the ramets might well no longer be strongly integrated. Also, clonal integration might act only over short distances (i.e. between close neighbour ramets forming small integrated physiological units; *sensu* Watson & Casper 1984).

Disintegrated genets of *S. altissima* tended to suffer more from resource deprivation than if they were still intact, as shown by the reduced growth and probability of reproduction of shoots in genets with cut rhizomes (Table 3a, c). Schmid *et al*. (1988b) have demonstrated that divided genets of *S. altissima* also react more strongly to simulated herbivory than connected ones.

The relatively minor role played by clonal integration was further emphasized by the strong influence of genet size on shoot life history. Even if large genets were cut into several groups of shoots, these portions still performed better than small genets. Larger genets, whether connected or disconnected, produced larger shoots, possibly because they contained more starting capital, even after rhizome cutting, than smaller shoots of smaller genets of the same age did. In addition, it is conceivable that the

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Fig. 2 Flux of ramets (rhizomes and shoots) in a population of *S. altissima* in unmown and mown plots from August 1987 to 1992. Shoots are divided into rosettes, bolted vegetative shoots and sexual (reproducing) shoots. Numbers denote densities of rhizomes or shoots, with densities of rhizome buds in parentheses (all densities expressed per m^2). The sizes of the shaded areas reflect the densities of the different categories at specific census dates, and white bands denote transitions from one category to another. Shoots that developed after mowing are not shown, although new shoots produced during the later part of the growing season, mainly in response to disturbance, are indicated by rectangles that are either not connected to any other rectangle or that are wider than the sum of the widths of their contributory white bands.

larger genets occurred in better microenvironmental patches than the smaller genets.

Competition

The regulation of shoot density within genets of *S. altissima* can happen through changes in shoot production, shoot survival, or both. The increased shoot density by the end of the study period in genets around which neighbours had been removed was largely due to increased shoot survival. In a glasshouse experiment with *S. altissima*, Hartnett & Bazzaz (1983) showed that stressed shoots were initially supported but a withdrawal of resources was then possible. Shoots with a prolonged negative carbon balance should be identified and abandoned by the genet through active resource removal (Pitelka & Ashmun 1985; Schmid 1990). Here, such competition between shoots within genets seemed to be decreased after the removal of neighbours.

Our neighbour-removal treatment showed that the spread of *S. altissima* can also be restricted in established populations by competition from other plant species. Lack of competition, in contrast, will lead to very dense genets that further prevent the establishment of other species. Thus *S. altissima* has a very high potential for building dense stands of shoots.

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