Biol Invasions (2012) 14:1101–1110
DOI 10.1007/s10530-011-0141-5

ORIGINAL PAPER

Effects of fragmentation on the survival and growth of the invasive, clonal plant *Alternanthera philoxeroides*

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Received: 20 June 2011 / Accepted: 19 November 2011 / Published online: 26 November 2011

Abstract The capacity of small clonal fragments to survive and grow is a major factor in the spread of clonal plants, especially aquatic species. This study of the introduced, invasive, amphibious, stoloniferous herb *Alternanthera philoxeroides* in China tested the effects of fragment size, of loss of the stolon apex, and of the original position of a fragment within a clone before fragmentation on the survival and growth of fragments in a greenhouse experiment. The stolon internodes of plants consisting of one stolon with 5 ramets were severed in all 16 possible patterns, generating fragments of 1–5 ramets. These 16 fragmentation treatments were crossed with removal of the stolon apex. Fragmentation and apex removal did not affect total growth of plants, but more highly fragmented plants produced smaller, more numerous ramets. The survival of fragments consisting of one original ramet was about 85%, compared to 100% survival of fragments with 5 original ramets. Fragments consisting of the youngest ramets along the original stolon grew more than fragments of the same size that consisted of older ramets. These effects of fragmentation on growth provide new evidence for clonal integration of the rate at which connected ramets produce new ramets and novel evidence that fragments produced from different portions of clones have different potential for spread. They further suggest that detachment of small groups of distal ramets along stolons in the field might be very effective in spreading the species and that a trade-off between the number and the size of new ramets produced by fragments may represent an adaptive, plastic response to disturbance. Results do not recommend intentional fragmentation of clones as a means of controlling the rate of growth of this invasive species but suggest that incidental fragmentation may not increase its growth in mass, although it may increase its rate of spread.

Keywords Alligator weed · *Alternanthera philoxeroides* · Aquatic plant · Clone · Disturbance · Fragmentation · Invasiveness · Stolon apex

Introduction

Natural and human-caused disturbances and the senescence of internodes frequently fragment the groups of connected ramets formed by clonal plants into smaller groups of one to several ramets (Barrat-Segretain and Bornette 2000; Klimešová et al. 2008; Latzel and Klimešová 2009). The capacity of these

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small fragments to disperse, survive, and grow is a major factor in the spread of clonal plants (Klimeš et al. 1997; Barrat-Segretain and Bornette 2000). Establishment of small fragments is particularly important in the spread of aquatic and marine clonal species, including species of introduced, invasive plants and algae (Wright and Davis 2006; Jia et al. 2009; Okada et al. 2009). Understanding what determines the survival and growth of small clonal fragments is thus of both scientific and practical interest.

Previous studies of the survival and growth of small clonal fragments have contrasted the probability of establishment of seeds and fragments of the same species (e.g., Going et al. 2008) and found effects of such environmental factors as substratum, burial, and the orientation at which fragments lodge (Bimova et al. 2003; Di Carlo et al. 2005; Dong et al. 2010a; Xie et al. 2010). Although size of fragments is an obvious and likely factor, relatively few studies have explicitly tested its effects on survival or growth, and those that have reported different effects in different species (Cabaço et al. 2005; Truscott et al. 2006; Klimešová et al. 2008). One apparently unanswered question of particular interest is whether different degrees of fragmentation, such as might be caused by different intensities of disturbance, affect the total growth of clones. Knowing this might help predict the degree to which management practices that intentionally or inadvertently fragment clones are likely to reduce or increase the abundance and spread of invasive clonal species.

Two other understudied factors likely to determine the survival and growth of clonal fragments are the presence of a stolon or rhizome apex and the relative position within a clone of the ramets forming a fragment. Since the apex of a stem can inhibit the initiation of lateral buds, one might expect that the presence of a stolon apex could decrease the growth of fragments of stoloniferous plants. This has been tested a number of times (Birch and Hutchings 1994; Julien and Bourne 1986; McPhee et al. 1997) but rarely in combination with different levels of fragmentation (Cabaço et al. 2005). Finally, since nutrient levels in the external environment in which fragments develop before fragmentation can affect their survivorship (Puijalon et al. 2008), since presence of internodes with a store of resources can increase performance of fragments (Dong et al. 2010b; Stuefer and Huber 1999), and since relative position within a clone can partly determine the internal resource status of a fragment (e.g. Alpert 1996), it might be expected that differences in relative position within a clone before fragmentation could affect the fate of fragments. This appears not to have been investigated.

We therefore tested the effects of these three relatively unexplored factors, size, presence of apex, and position within clone, on the survival and growth of fragments of a highly invasive, stoloniferous, aquatic plant species, *Alternanthera philoxeroides*. We specifically asked: (1) Does degree of fragmentation affect the total growth of clones? (2) Does the presence of a stolon apex decrease the growth of fragments? (3) Does fragment size or the presence of a stolon apex affect the survival rate of fragments? (4) Do fragments containing ramets that are more proximal along a stolon (i.e., farther from the apex and thus older) grow more than or less than fragments containing ramets that are more distal along the stolon (i.e., closer to the apex and thus younger)?

Materials and methods

Plant materials

Alternanthera philoxeroides (Mart.) Griseb., or alligator weed, is a perennial, amphibious herb native to South America (Julien et al. 1995; Holm et al. 1997; Sainty et al. 1998). It grows clonally via monopodial stolons up to 10 m long that can bear leaves, roots, and axillary stolons at each node; a node along a stolon with its leaves and roots thus corresponds to a ramet. Clones can form extensive networks of connected ramets within one growing season (Geng et al. 2006), and physiological integration between connected ramets can modify their individual and combined growth and spread (Wang et al. 2008, 2009; Yu et al. 2009; Dong et al. 2010a, b; Xu et al. 2010). Disturbances such as herbivory, mowing, and application of herbicides frequently fragment clones into pieces of different sizes, and even very small fragments such as ones consisting of a single ramet or highly stressed fragments such as in aquatic mats stranded over the winter on dried sediments can survive and produce new stolons and ramets (Liu and Yu 2009; Dong et al. 2010a, b; Dugdale et al. 2010). *A. philoxeroides* has been widely introduced outside its native range and is now considered to be one of the most invasive plant species in the world (Julien et al. 1995; Holm et al. 1997; Sainty et al. 1998). In southern China, *A. philoxeroides* is widespread in waterways and irrigation ditches and in adjacent, open terrestrial areas, including crop fields (Ma and Wang, 2005). *A. philoxeroides* in China has extremely low genetic diversity and may be derived from a single clone (Ye et al. 2003; Wang et al. 2005; Pan et al. 2007).

The experiment was conducted in a greenhouse at Forest Science Company, Ltd., of Beijing Forestry University. *A. philoxeroides* was propagated vegetatively in the greenhouse from a clone collected in Jiangxi Province in China and maintained at the Institute of Botany of the Chinese Academy of Science in Beijing. About 3,000 individual nodes were planted in a 1:1 (v:v) mixture of sand and peat and allowed to produce axillary stolons. After one month, 320 stolons that were approximately 20 cm long and that each bore five unrooted ramets (i.e., nodes with leaves) and a live apex were selected for use. Each of these one-stolon, 5-ramet units was detached and allowed to establish for six days in a container that was 32 cm long × 15 cm wide × 9 cm high and filled with a 1:1 mixture of sand and vermiculite. During establishment, each ramet was appressed to the soil surface with toothpicks so that all ramets rooted.

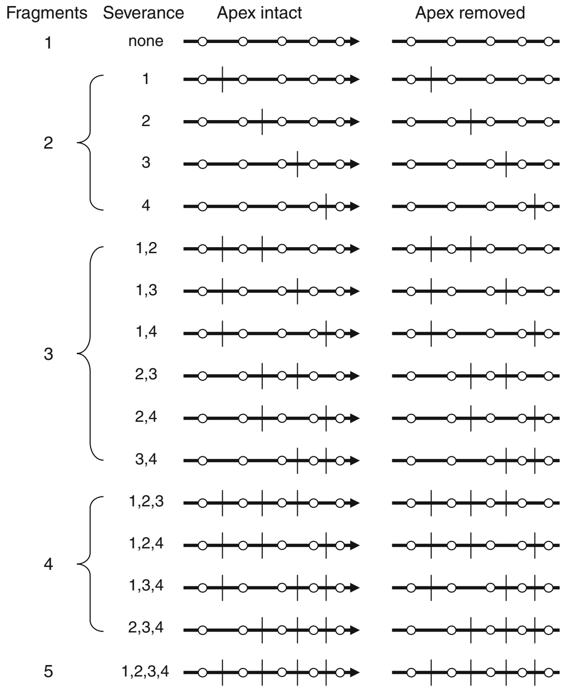

Fig. 1 Experimental design. Initial clonal units, referred to as "plants" and consisting of a stolon bearing five ramets (*circles*) and an apex (*arrow*) were divided into 1–5 groups of ramets, referred to as "fragments", by severing stolon internodes between ramets (*vertical lines*). Fragmentation treatments were crossed with apex removal. Severance gives the numbers of the internodes severed, with 1 being the oldest

Experimental design

The rooted, one-stolon, 5-ramet units were then subjected to 32 treatments, each of the 16 possible patterns of division of a unit into smaller groups of ramets crossed with removal of the stolon apex (Fig. 1). To assign units to treatments, they were first sorted into ten sets by length and thickness of the stolons. One unit within each set was randomly assigned to each treatment, giving ten replicates per treatment. The appropriate severances were then made (Fig. 1), each in the middle of the stolon internode between two ramets. To help prevent limitation of growth by water or nutrients during the experiment, all ramets were watered daily with enough tap water to keep the soil surface moist throughout the day, and watered weekly with a nutrient solution of 0.30 g L^{-1} soluble fertilizer (Peters Professional, Scotts-Sierra Horticultural Products Co., Marysville, Ohio, USA; 20% N, 20% P, 20% K). The experiment began on 13 August 2009 and ended after 12 weeks, on 3–6 November.

At the end of the experiment, the numbers of surviving groups of ramets were recorded. A group was considered not to have survived if all of the ramets in the group had died. The number and total leaf area (WinFOLIA Pro 2004a, Regent Instruments, Inc., Québec, Canada) of the new ramets produced by each surviving group were measured, along with the total length of the new stolons produced by the group. Each group was then separated into the original ramets present at the start of the experiment and the new stolons and ramets produced during the experiment, dried at 70°C for 48 h, and weighed. The leaves of the original ramets had all senesced and fallen off by the end of the experiment.

To simplify terms in the Results and Discussion, we will refer to each of the initial, one-stolon, 5-ramet units plus its new ramets and stolons as a "plant", regardless of whether it was fragmented into smaller groups. We will refer to each of the groups derived from a plant by severing its internodes as a "fragment". In the treatments where none of the internodes of the original stolon of a plant were severed and there was thus one fragment per plant, "fragment" becomes synonymous with "plant". In the treatments where all of the original internodes of a plant were severed, "fragment" becomes synonymous with "a single original ramet plus its new stolons and ramets" (Fig. 1). We kept track of which fragments belonged to which plants so that we could calculate the total final mass and size of each plant by summing the values for the fragments of the plant. We characterized the position of a fragment within a plant on the basis of the position along the original stolon of the plant of the original ramets contained in the fragment. For example, a fragment with two original ramets might occupy any one of four positions: the two original ramets closest to the apex of an original stolon (and thus the two most distal and youngest original ramets of a plant), the second and third closest, the third and fourth closest, or the fourth and fifth closest (and thus the two oldest and most proximal original ramets of a plant). We numbered the original ramets in a plant on the basis of position, with 1 being the oldest and most proximal, and 5 being the youngest and most distal, similarly to the way we numbered internodes (Fig. 1).

Data analysis

Effects of treatments on growth were analyzed with ANOVAs. To test effects of treatments on whole plants, we used a two-way ANOVA model with fragmentation (division into 1, 2, 3, 4, or 5 fragments, with division into 1 fragment being the same as no division) and stolon apex (present or removed) as fixed effects. To test effect of the position of a fragment within a plant, we used a one-way ANOVA model with position as fixed effect. Only plants with the apex removed were included in this test, because fragments in most positions were necessarily severed from the apex of the original stolons; fragments in which all ramets died were excluded. Effect of position was tested separately for two- and for three-ramet fragments.

To more specifically test for an interactive effect of the removal of the apex and fragment size, we used a two-way ANOVA model with apex (present or removed) and size of fragment (1, 2, 3, 4, or 5 original ramets) as fixed effects. Only fragments containing the youngest original ramet were included, and fragments in which all ramets died were excluded.

In the above analyses, separate ANOVAs were run for each of six measures of growth: final dry biomass of new stolons and ramets, leaf area of new ramets, length of new stolons, and number of new ramets per plant or per fragment; and mass or leaf area per new ramet. Duncan tests were used to compare individual means. Data were transformed before analysis as needed to improve homoscedasticity; figures show untransformed data.

Effects of fragment size and apex removal on the survival of fragments were tested with a logistic regression. This test included the treatments used in the above test for interactive effect of removal of apex and size of fragment. All analyses were conducted in SPSS 16.0 (SPSS, Chicago, Illinois, USA).

Results

Degree of fragmentation did not affect the final dry biomass of new stolons and ramets, the final leaf area of new ramets, or the total length of new stolons produced by plants (Fig. 2a, c, e; Table 1). However, fragmentation did produce an apparent trade-off between size and number of new ramets. More highly fragmented plants produced new ramets that were smaller in mass and leaf area but greater in number (Fig. 2b, d, f; Table 1). Accordingly, the number of new ramets produced by a plant showed a negative relationship to the mass and the leaf area per new ramet (Fig. 3).

Contrary to the expectation that presence of the stolon apex would decrease total growth, removal of the apex of the original stolon did not affect the total mass or size of new stolons and ramets produced by plants nor the mean mass or size of new ramets, nor was there an interactive effect of fragmentation and removal of the apex of the stolon (Table 1). A more specific test for effect of removal of the apex, which compared growth of distal one- to five-ramet fragments with and without the apex of the original stolon (see Methods), likewise showed no effect of apex or interactive effect of apex and fragment size on any measure of growth (data not shown; each $P > 0.18$).

Smaller fragments had a lower survival rate than larger ones (Fig. 4). All fragments containing five

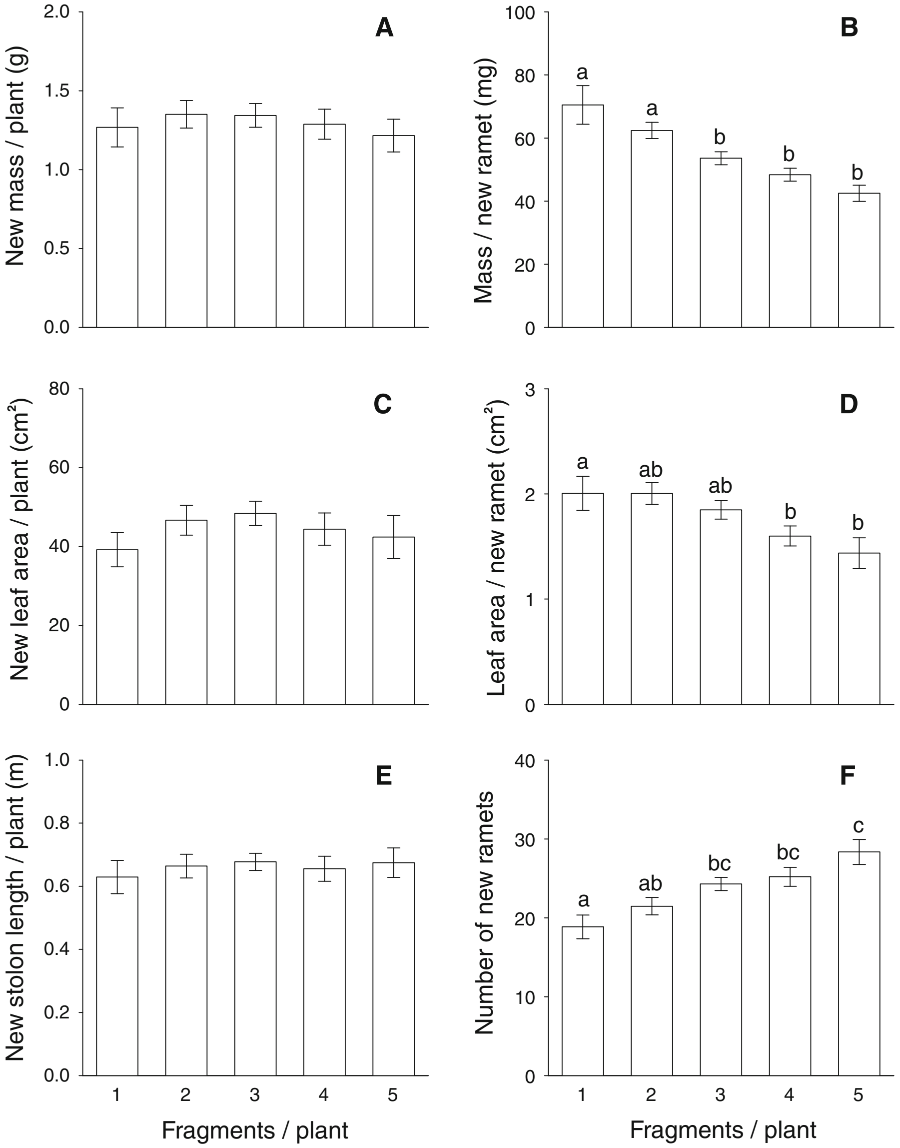

Fig. 2 Effect of fragmentation (division of plants containing 5 ramets into 1 to 5 fragments) on (**a**) mass of new stolons and ramets per plant, (**b**) mass per new ramet, (**c**) leaf area of new ramets per plant, (**d**) leaf area per new ramet, (**e**) total length of new stolons per plant and (**f**) number of new ramets per plant of *Alternanthera philoxeroides*. Values are means ± SE. For measures affected by fragmentation ($P < 0.05$; see Table 1 for ANOVAs), letters above bars show which treatments differed within a measure (Duncan test, $P < 0.05$)

original ramets (i.e., plants that were not fragmented) survived; about 85% of one-ramet fragments survived. Removal of the apex did not affect the survival of fragments (Fig. 4).

Among fragments with two original ramets, those with the two youngest original ramets in a plant grew more than those with the two oldest original ramets. For example, fragments with original ramets 4 and 5 (the two youngest, most distal of the five original ramets in a plant) had greater final dry mass and leaf area of new stolons and ramets than two-ramet fragments from the other three possible positions in a plant, i.e., with original ramets 1 and 2 (the oldest in a plant), 2 and 3, or 3 and 4 (Fig. 5a, c; Table 2).

Table 1 Analyses of variance due to effects of fragmentation and presence of a stolon apex in characteristics of final dry biomass and size of new stolons and ramets produced by plants of *Alternanthera philoxeroides*

	Fragmentation		Apex		Interaction	
	$F_{4,300}$	P	$F_{1,300}$	P	$F_{4,300}$	P
New mass/plant	0.30	0.9	0.28	0.9	1.50	0.20
New leaf area/plant	0.46	0.8	0.08	0.8	1.45	0.22
New stolon length/plant	0.28	0.9	1.79	0.18	1.34	0.25
Number of new ramets	**4.26**	**0.002**	1.71	0.19	0.98	0.4
Mass/new ramet	**7.38**	**< 0.001**	1.89	0.17	1.58	0.18
Leaf area/new ramet	*3.23*	*0.013*	0.96	0.3	0.73	0.6

Values are in bold where $P < 0.01$ and in italics where $P = 0.01$–0.05

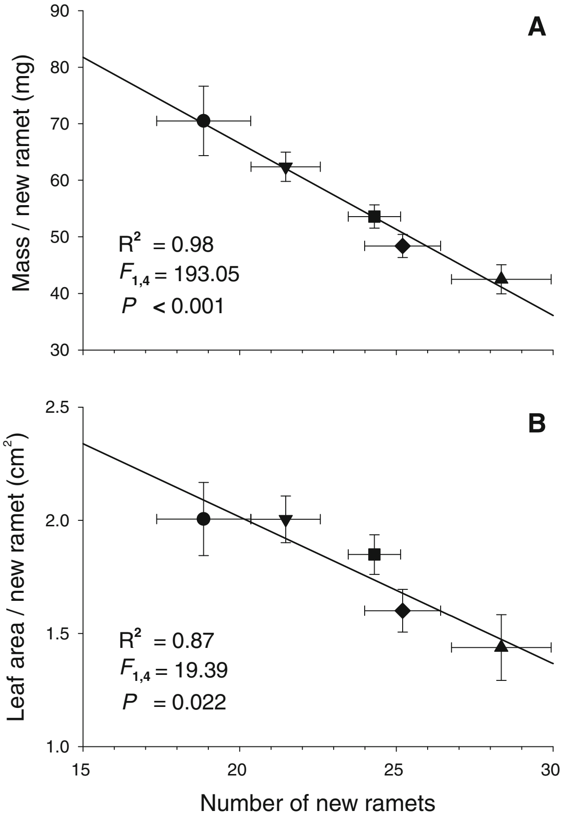

Fig. 3 Relationships between number of new ramets and (**a**) dry biomass per new ramet or (**b**) leaf area per new ramet of *A. philoxeroides* subjected to different degrees of fragmentation (division of a plant consisting of five ramets into 1 (*filled circle*), 2 (*filled invert triangle*), 3 (*filled square*), 4 (*filled rhombus*), or 5 (*filled triangle*) fragments). Values are means across treatments within each level of fragmentation. *Error bars* show ± SE. Lines and statistics are from linear regressions

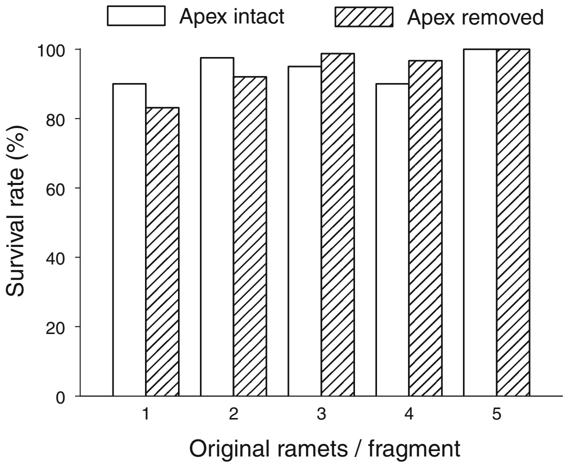

Fig. 4 Effects of removal of the stolon apex and of the size of fragments (the number of original ramets in the fragment) on their survival. Size affected survival (logistic regression: $\chi^2_4 = 9.79$; $P = 0.04$) but removal of the apex did not ($\chi^2_1 < 0.001$; $P > 0.9$); effects did not interact ($\chi^2_4 = 3.62$; $P = 0.5$)

Fragments with original ramets 4 and 5 also had relatively large new ramets compared to two-ramet fragments from other positions in a plant (Fig. 5b, d; Table 2). Position within a plant did not significantly affect the total length of new stolons or the number of new ramets produced by a two-ramet fragment (Fig. 5e, f; Table 2). Three-ramet fragments showed qualitatively similar patterns (data not shown), though effect of position was significant ($P < 0.05$) only for leaf area per ramet (Table 2).

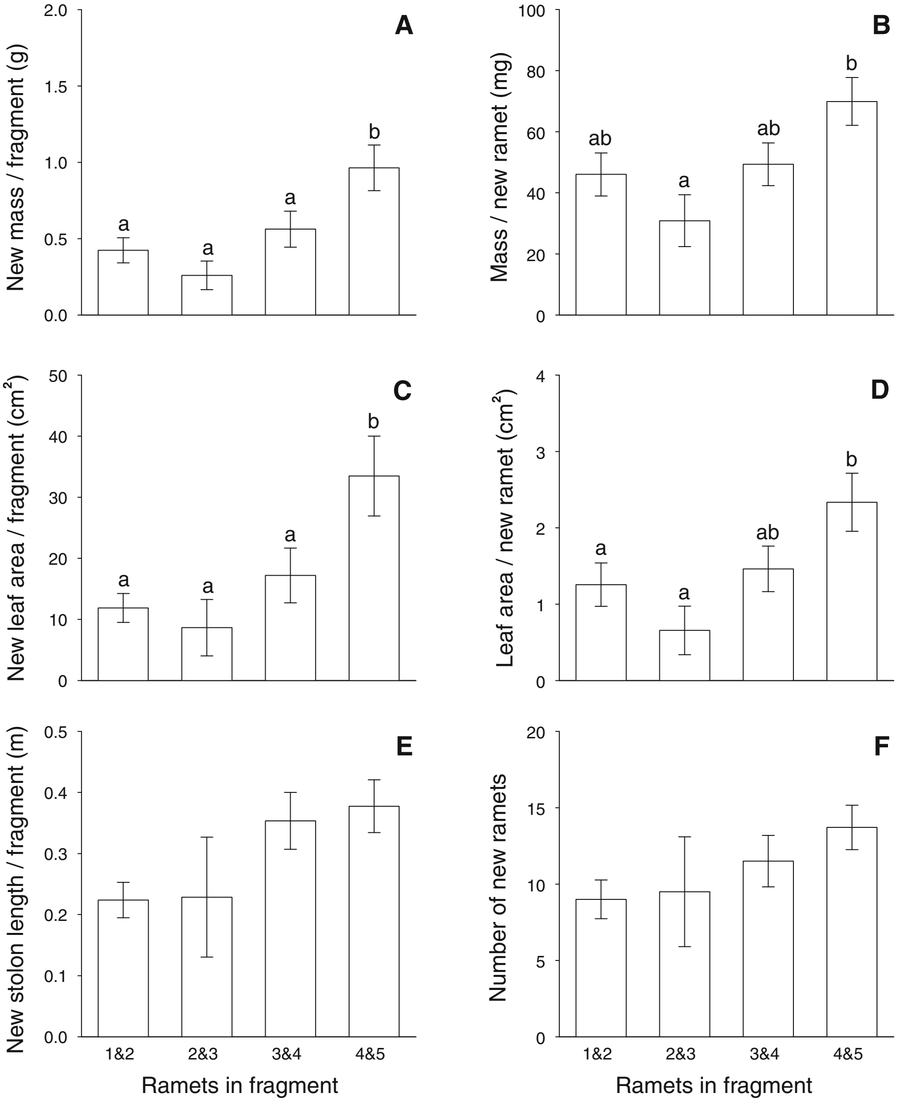

Fig. 5 Effect of position before fragmentation within a plant of *A. philoxeroides* consisting of one stolon bearing five ramets on (**a**) mass of new stolons and ramets per fragment, (**b**) mass per new ramet, (**c**) leaf area of new ramets per fragment, (**d**) leaf area per new ramet, (**e**) total length of new stolons per fragment and (**f**) number of new ramets per fragment in two-ramet fragments. Position is identified by order of ramets along the original stolon: 1 is the oldest, most proximal ramet and 5 is the youngest, most distal ramet. Values are means ± SE. For measures affected by fragmentation ($P < 0.05$; see Table 2 for ANOVAs), letters above *bars* show which treatments differed within a measure (Duncan test, $P < 0.05$)

Discussion

Results suggest that fragmentation of a clone of *A. philoxeroides* into very small groups of ramets, even complete fragmentation into single ramets, does not significantly affect its growth in mass or size. Disturbance that breaks stolon internodes is thus unlikely to either increase or control the growth of the species. This might not hold in environments that differ from the experimental conditions, in which water was not limiting and levels of light and nutrients were high and uniform. However, these conditions probably approximate those found in many of the crop fields and irrigation ditches where *A. philoxeroides* is of particular management concern in China. Size of fragments does appear to have effects on their individual growth in some clonal species, though effects may be positive in some species and negative in others. Truscott et al.

Table 2 Analyses of variance due to effect of position in characteristics of final dry biomass and size of new stolons and ramets produced by two- and three-ramet fragments of *A. philoxeroides*

	Two-ramet fragments		Three-ramet fragments	
	$F_{3,21}$	P	$F_{2,15}$	P
New mass/fragment	**5.50**	**0.006**	1.92	0.18
New leaf area/fragment	*4.65*	*0.012*	2.03	0.17
New stolon length/fragment	2.42	0.095	2.42	0.12
Number of new ramets	1.33	0.3	1.57	0.24
Mass/new ramet	*3.92*	*0.023*	1.91	0.18
Leaf area/new ramet	*3.85*	*0.024*	*5.87*	*0.013*

Values are in bold where $P < 0.01$ and in italics where $P = 0.01$–0.05

(2006) found that shoot fragments of *Mimulus guttatus* with 1–3 nodes grew faster and more than those of 4–6 nodes, while Cabaço et al. (2005) found that fragments of *Zostera noltii* with 1–2 ramets grew less than larger ones.

Fragment size did affect survival; survival rate of the smallest fragments was about 15% lower than that of the largest, which was 100%. It is possible that this effect was simply due to the fact that larger fragments had more original ramets, rather than to a lower probability of survival of individual ramets within smaller fragments. The high survival rate was similar to that observed for fragments of *M. guttatus* by Truscott et al. (2006).

Fragmentation produced a pronounced trade-off between size and number of new ramets in *A. philoxeroides*. More highly fragmented plants produced more but smaller new ramets, such that total mass per plant was similar between levels of fragmentation. Stuefer et al. (2002) reported an analogous, apparent trade-off between ramet size and number between genotypes in a different species, but the present study may be the first report of such a trade-off within a genotype.

This trade-off has interesting physiological and ecological implications. The effect of fragmentation on the number of new ramets indicates that control of ramet production is physiologically integrated between connected ramets, such that connection to other ramets inhibits clonal reproduction. A number of earlier studies concluded that clones of various species avoid self-competition through self-inhibition of ramet production in groups of connected ramets (De Kroon and Kalliola 1995; Rivera and Scrosati 2008), suggesting that clonal integration of signals for initiation of new stolons or ramets may be fairly common in clonal plants. The mechanism remains untested.

Ecologically, it is tempting to interpret a trade-off between ramet size and number in response to fragmentation as being analogous to the well-known trade-off between seed size and number (e.g. Guo et al. 2010). Under such an interpretation, when levels of disturbance and thus fragmentation are high, plants produce a large number of small ramets and spread rapidly, much as the production of a large number of small seeds increases the dispersal ability of plants associated with high disturbance. When disturbance and fragmentation are low, plants produce a small number of large ramets that compete well in established vegetation, much as the production of a relatively small number of large seeds is associated with growth in habitats where disturbance is low and competition is high. Unlike in seeds, the trade-off between number and size of ramets in *A. philoxeroides* is phenotypically plastic and may be an example of adaptive plasticity. It would now be useful to test this hypothesis and to look for trade-offs between ramet size and number in other species.

Removal of the stolon apex had no evident effect on the survival or growth of plants or fragments of *A. philoxeroides*. Removing the apical shoot of fragments of *Z. noltii* greatly decreased their survival and growth (Cabaço et al. 2005). However, removing the stolon apex of plants of *Trifolium repens* or *Glechoma hederacea* did not affect their growth or architecture (Birch and Hutchings 1994; McPhee et al. 1997), removing the apical buds of fragments of *Salvinia molesta* had little effect except to slightly decrease the production of ramets, and mowing that removes shoot tips does not slow growth in *A. philoxeroides* (Wilson et al. 2007). In conjunction with the observed trade-off between ramet size and number, these present and previous results suggest that the stolon apex may often have little influence on the growth of other parts of a clone, in contrast to the apical dominance common in the shoots of non-clonal plants (e.g. Gonzáles-Teuber and Gianoli 2008).

Fragments containing the youngest, most distal of the original ramets of plants of *A. philoxeroides* grew more than fragments of the same size that contained older, more proximal ramets. This may be the first published example of an effect of position within a clonal plant on the subsequent growth of fragments. One might expect older ramets to be larger and therefore to support more new growth after fragmentation. On the other hand, acropetal transport of nutrients, as observed in some clonal species (e.g. Alpert 1996), might provide younger ramets with greater resources for new growth, and older ramets of some clonal species have diminished ability for growth (e.g. D'Hertefeldt and Jónsdóttir 1999). This effect may thus vary between clonal species, depending upon their patterns of physiological integration and clonal life history.

Knowledge of the effects of fragmentation on the growth of clonal plants under controlled conditions can suggest tests of the physiological mechanisms of clonal integration, complement observations of actual patterns of fragmentation in the field, and point to potential methods for the management of the growth of clonal species, including the control of invasive, introduced species. In *A. philoxeroides*, effects of fragmentation on growth provide evidence for clonal integration of rates of production of new ramets, suggest that detachment of small groups of distal ramets along stolons in the field might be very effective in spreading the species, suggest that a trade-off between ramet number and size may represent an adaptive, plastic response to disturbance, and do not recommend intentional fragmentation of clones as a means of managing the rate of growth of this invasive species.

Acknowledgments We thank Guo-Lei Yu, Wei Wu and Huan Li for research assistance. This study was supported by the Forestry Commonwealth Project (Grant 201004078), the Fundamental Research Funds for the Central Universities (Grant JC2011-4), the Specific Programs in Graduate Science and Technology Innovation of Beijing Forestry University (Grant BLYJ201104), and the External Cooperation Program of the Chinese Academy of Sciences (Grant GJHZ0904). This material was based in part on work supported by the U.S. National Science Foundation, while working at the Foundation, but does not necessarily reflect the views of the Foundation.

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