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Clonal Integration Affects Growth, Photosynthetic Efficiency and Biomass Allocation, but not the Competitive Ability, of the Alien Invasive *Alternanthera philoxeroides* under Severe Stress

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- *Background and Aims* Many notorious alien invasive plants are clonal, but little is known about some roles and aspects of clonal integration. Here, the hypothesis is tested that clonal integration affects growth, photosynthetic efficiency, biomass allocation and competitive ability of the exotic invasive weed *Alternanthera philoxeroides* (Amaranthaceae).
- *Methods* The apical parts of *Alternanthera* were grown either with or without the lawn grass *Schedonorus phoenix* (tall fescue) and their stolon connections to the basal parts grown without competitors were either severed or left intact.
- *Key Results* Competition greatly reduced the maximum quantum yield of photosystem II (F_v/F_m) and growth (biomass, number of ramets and leaves, total stolon length and total leaf area) of the apical *Alternanthera*, but not the biomass of *S. phoenix*. Stolon connections significantly increased F_v/F_m and growth of *Alternanthera*. However, such effects on growth were smaller with than without competition and stolon connections did not alter the relative neighbour effect of *Alternanthera*. Stolon connections increased *Alternanthera*'s biomass allocation to roots without competition, but decreased it with competition.
- *Conclusions* Clonal integration contributed little to *Alternanthera*'s competitive ability, but was very important for *Alternanthera* to explore open space. The results suggest that the invasiveness of *Alternanthera* may be closely related to clonal integration.

Key words: Alien species, alligator weed, *Alternanthera philoxeroides*, chlorophyll fluorescence, clonal invasive plants, competition, physiological integration, *Schedonorus phoenix*.

INTRODUCTION

Connected ramets of clonal plants can share water, carbohydrates and nutrients through clonal integration (Alpert and Mooney, 1986; Marshall, 1990; Stuefer *et al.*, 1994, 1996; Alpert, 1996, 1999; Wijesinghe and Hutchings, 1997). Many studies have shown that clonal integration facilitates establishment of newly produced ramets, improves survival, growth and/or reproduction of adult ramets in stressful environments, and helps genets to occupy open space (Hartnett and Bazzaz, 1985; Hester *et al.*, 1994; Brewer and Bertness, 1996; Jónsdóttir and Watson, 1997; Yu *et al.*, 2002, 2004; Lötscher, 2006). These positive effects of clonal integration may provide clonal plants with a competitive advantage over non-clonal plants or clonal plants with little integration. On the other hand, integration-mediated increases in performance of clonal plants may reduce the growth and reproduction of their competitors. As a result, clonal integration may influence species co-existence, community structure and ecosystem functioning (Oborny and Podani, 1995; Pyšek, 1997; Wilsey, 2002).

In past decades, plant invasion has become a great threat to global ecosystems (Mack *et al.*, 2000; Pimental *et al.*, 2000; Mitchell and Power, 2003). Many notorious alien invasive plants are clonal (Liu *et al.*, 2006). Some have vigorous clonal growth that enables them to invade local communities and to displace native plant species (Crawley, 1986; Blossey and Kamil, 1996; Liu *et al.*, 2006). For example, the alien invasive rhizomatous herb *Solidago gigantea* and the stoloniferous herb *Alternanthera philoxeroides* (alligator weed) form very dense stands, which exclude almost all other species (Julien and Bourne, 1988; Jakobs *et al.*, 2004). Some studies have suggested that the competitive ability, and thus the invasiveness, of alien clonal plants may be closely related to clonal traits such as clonal integration (Pyšek, 1997; Reichard, 1997; Maurer and Zedler, 2002; Pyšek *et al.*, 2003; Liu *et al.*, 2006). To date, however, very few studies have addressed how clonal integration affects growth of alien invasive clonal plants when competing with native species.

Several studies have addressed how clonal integration affects growth of clonal plants when they compete with neighbours (Hartnett and Bazzaz, 1985; Schmid and Bazzaz, 1987; Hartnett, 1993; Price and Hutchings, 1996; Pennings and Callaway, 2000; Peltzer, 2002; Březina *et al.*, 2006), but the results disagree. Clonal integration

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was not shown to affect growth of *Glechoma hederacea* (Price and Hutchings, 1996), *Panicum virgatum* (Hartnett, 1993), *Populus tremuloides* (Peltzer, 2002) or *Calamagrostis epigejos* (Březina *et al.*, 2006). Hartnett and Bazzaz (1985), however, found that the growth response of a *Solidago canadensis* ramet to a given neighbour species varied with the neighbour species encountered by its interconnected ramets, suggesting that clonal integration played an important role. Pennings and Callaway (2000) also found that clonal integration significantly increased growth of several salt marsh plants when they competed with neighbours for below-ground resources and tended to increase growth when they competed with neighbours for both above- and below-ground resources. However, none of these studies had investigated whether clonal integration reduced the growth of the neighbour plants (i.e. competitors).

Effects of clonal integration on photosynthetic efficiency of plants have not been widely studied (but see Hartnett and Bazzaz, 1983; Roiloa and Retuerto, 2005, 2006*a*, *b*). Photosynthetic efficiency can be estimated by measuring chlorophyll fluorescence (Schreiber *et al.*, 1998), and the maximum quantum yield of photosystem II (F_v/F_m) derived from the parameters of chlorophyll fluorescence is a sensitive indicator of plant photosynthetic performance (Björkman and Demmig, 1987; Johnson *et al.*, 1993; Roiloa and Retuerto, 2005, 2006*a*,*b*). F_v/F_m usually decreases when plants are exposed to environmental stress (Björkman and Demmig, 1987; Johnson *et al.*, 1993; Roiloa and Retuerto, 2005, 2006*a*, *b*). Because clonal integration may alleviate the competition-mediated stress on ramets, it may greatly reduce the negative effects of competition on F_v/F_m. However, no study has been conducted to test this hypothesis.

Many studies have investigated effects of clonal integration on biomass allocation of clonal plants (Salzman and Parker, 1985; Friedman and Alpert, 1991; Evans and Whitney, 1992; Birch and Hutchings, 1994; Stuefer *et al.*, 1994, 1996; Wijesinghe and Hutchings, 1997; Yu *et al.*, 2002; Roiloa *et al.*, 2007). In heterogeneous conditions consisting of a mixture of rich and poor resource patches, clonal integration can modify biomass allocation so that relatively more biomass is allocated to the organs (roots or leaves) to acquire more abundant resources, a phenomenon called 'division of labour' (Stuefer *et al.*, 1996; Alpert and Stuefer, 1997; Hutchings and Wijesinghe, 1997). This is in contrast with the pattern of non-clonal plants or clonal plants grown in homogeneous conditions (Birch and Hutchings, 1994; Stuefer *et al.*, 1996; Alpert and Stuefer, 1997; Hutchings and Wijesinghe, 1997). However, very few studies have been conducted to address how clonal integration affects biomass allocation of plants when they were grown with competitors, especially for exotic invasive clonal plants.

Alternanthera philoxeroides (hereafter referred to by the genus name only) is a stoloniferous alien invasive weed of the Amaranthaceae and originates from the Parana River region of South America (Gunasekera and Bonila, 2001). It is amphibious, growing both in riparian and in terrestrial habitats (Julien and Stanley, 1999). In terrestrial situations *Alternanthera* can displace native species (Julien and Bourne, 1988) and block irrigation and drainage systems of cropland; in riparian systems it can cover the entire water surface, reducing oxygen exchange, preventing flow and potentially increasing flood damage (Ma and Wang, 2005). In China, *Alternanthera* has invaded different ecosystems, including cropland, lawn, garden, marshes and lakes, and has caused great economic and environmental problems (Wang and Wang, 1988; Ma and Wang, 2005). It is one of the world's worst invasive weeds and one of the 16 worst alien invasive weeds in China (Julien *et al.*, 1995; Holm *et al.*, 1997; Ma and Wang, 2005).

To examine the effect of clonal integration on growth, photosynthetic performance, biomass allocation and thus competitive ability of exotic invasive clonal plants, we grew clonal fragments of *Alternanthera* in containers with two sections. The apical (with the apical parts of the *Alternanthera* clonal fragments) were grown either with or without a common lawn grass, *Schedonorus phoenix* (tall fescue), whereas the basal sections (with basal parts of the clonal fragments) were grown without competitors. Stolons connecting the two parts were either severed or left intact to test the effect of clonal integration. Specifically, we test the following hypotheses. (1) Stolon connections (clonal integration) will significantly improve growth and competitive ability of *Alternanthera*. (2) Clonal integration will buffer the decrease in F_v/F_m of *Alternanthera* grown with competitors. (3) Stolon connections will change biomass allocation of *Alternanthera* grown with competitors. According to the theory of labour division (Alpert and Stuefer, 1997; Hutchings and Wijesinghe, 1997), we predict that stolon connection will increase biomass allocation to leaves if the below-ground competition (for nutrients and/or water) is more severe and will increase that to roots if the above-ground competition (for light) is more severe. (4) Severing stolons of *Alternanthera* will increase growth of *S. phoenix*.

MATERIALS AND METHODS

Experimental design

The experiment used a factorial design involving competition (with or without) and stolon connection (intact or severed). The plants of *Alternanthera philoxeroides* (Mart.) Griseb. used in this experiment were 28 similar-sized clonal fragments (12·74 ± 0·29 cm in length; mean ± s.e.), each consisting of a stolon with six ramets. Each clonal fragment was classified into two parts, one termed as the 'basal part' consisting of four relatively old ramets (relatively proximal to their mother ramets) and the other as the 'apical part' consisting of two relatively young ramets (relatively distal to the mother ramets) and a stolon apex. Because previous studies have shown that all *Alternanthera* plants in China are genetically identical (Xu *et al.*, 2003; Wang *et al.*, 2005), the clonal fragments used in this experiment were derived only from a single clone collected from cropland in Yunnan Province, China.

The experimental containers were 35 plastic trays (50 × 37 × 15 cm; length × width × height), each having two separated sections (Fig. 1) – the basal section (16·7 cm long) and the apical section (33·3 cm long). Nutrients, water and roots in the two sections did not interfere with each other. The trays were filled with a mixture of sand and peat at a volume ratio of 4 : 1 and with 0·8 g L^{-1} of slow-release fertilizer (Osmocote 301, Scotts, USA) having an elemental ratio of 15 N : 11P : 13K : 2 Mg. On 25 November 2005, the apical sections of 21 trays were planted with the lawn grass *Schedonorus phoenix* (Scop.) Holub. (tall fescue, previously named *Festuca arundinacea* Schreb.), sown at a seed density of 30 g m^{-2} (approx. 12 228 $\pm$ 309·97 seeds m^{-2}; mean $\pm$ s.e., $n = 3$). The remaining 14 trays were kept with the apical sections unsown.

On 20 December, 28 clonal fragments of *Alternanthera* were positioned in 28 trays (14 with and 14 without the grass competitor). The remaining seven trays with grasses were used as a control for grass growth without competition. Each clonal fragment was arranged such that the four ramets of the basal part were placed within the basal section of a tray and the two ramets and the apex of the apical part were placed within the apical section of the same tray (see Fig. 1). At this time, the *S. phoenix* sward was 15·12 $\pm$ 0·27 cm (mean $\pm$ s.e.) high and at a density of 1·18 $\pm$ 0·07 plants cm^{-2}. The stolon of the apical ramets was anchored to the soil surface to facilitate rooting. On 10 January 2006, when the first three basal nodes of the apical ramets of all clonal fragments had rooted, the stolon connections between the apical and the basal parts were severed in 14 trays, whilst the other 14 trays were kept untreated (Fig. 1). The experiment was ended on 12 March 2006. During the experiment, new stolons and ramets derived from the basal (or apical) part of a clonal fragment were prevented from growing into the basal (or apical) section of the tray.

Both material preparation and experiment were conducted in a heated glasshouse (18–25 °C) at the Institute of Botany, Chinese Academy of Sciences in Beijing, China. During the experiment, artificial light was provided to ensure a lighting period of 12 h. All plants were watered two or three times a week, and sprayed twice during the experiment with fungicide against fungal infection. To avoid the effects of possible environmental patchiness within the glasshouse, the trays were systematically repositioned in the glasshouse every 2 weeks so that each tray experienced all possible conditions. To simulate mowing in a lawn ecosystem, all *S. phoenix* plants were clipped to 3 cm high on 12 January and 12 February 2006.

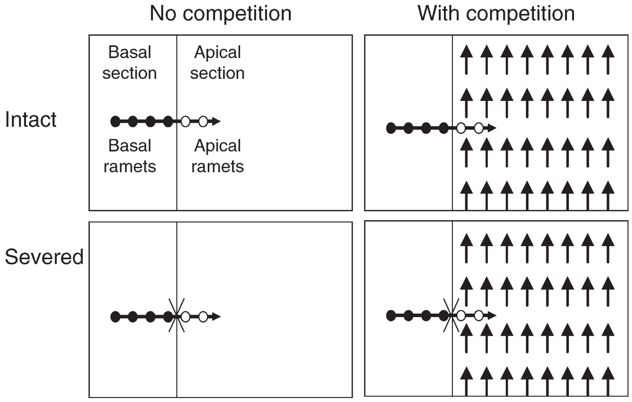

FIG. 1. Schematic representation of the experimental design. The clonal fragments of *Alternanthera*, each consisting of four basal ramets (filled circles) and two apical ramets (open circles) with a stolon apex (horizontal arrow), were grown either with (left) or without (right) competitors (*Schedonorus phoenix*, vertical arrows) and with stolon connections between basal and apical ramets either intact (top) or severed (bottom).

Measurements

Between 1930 h and 2030 h on 8 March 2006, after a dark adaptation of at least 1·5 h sufficient for the photosystem II (PSII) reaction centres to open, the minimal (F_0) and the maximum fluorescence yield (F_m) were measured for a fully developed, healthy leaf on the second-youngest *Alternanthera* ramet in each apical part using a portable chlorophyll fluorometer (PAM-2100, Walz, Effeltrich, Germany) with the saturation pulse method (Schreiber *et al.*, 1998). The maximum quantum yield of PSII (F_v/F_m) was calculated as $(F_\text{m} - F_0)/F_\text{m}$ (Björkman and Demmig, 1987; Johnson *et al.*, 1993; Maxwell and Johnson, 2000; Roiloa and Retuerto, 2006*a*, *b*).

At harvest, the number of ramets, leaves and stolons were counted, and stolon length and total leaf area of *Alternanthera* were measured for the apical section of each tray. Then *Alternanthera* in the apical sections were harvested and separated into leaves, stolons and roots and their biomass was determined after drying at 70 °C for 48 h. Above-ground parts of *S. phoenix* plants in the apical section of each tray were also harvested and their root biomass was obtained based on the dry mass measured in five systematically sampled soil cores (4·5 cm in diameter). The biomass of *S. phoenix* clipped on the two dates (see above) was also measured.

Data analysis

Two-way analysis of variance (ANOVA) was used to test the effect of stolon connection (clonal integration) and competition on F_v/F_m of *Alternanthera* in the apical sections (Sokal and Rohlf, 1981). Two-way multivariate analysis of variance (MANOVA) was employed to investigate the global effects of stolon connection and competition on growth and percentage biomass allocation of *Alternanthera*, and corresponding univariate analyses were also conducted. One-way ANOVA followed by Student–Newman–Keuls (SNK) tests were used to assess whether biomass of *S. phoenix* in the apical sections differed among the three treatments (no competition; with competition with severed stolon connection of *Alternanthera*; with competition with intact stolon connection).

The index of the relative neighbour effect (RNE) was calculated to measure the competitive intensity of *S. phoenix* on *Alternanthera* (Kikvidze *et al.*, 2006). The RNE of *Alternanthera* was calculated as $(C–A)/\max(C, A)$, where A is the average biomass of *Alternanthera* across replicates without competition, C is biomass of *Alternanthera* with competition, and $\max(C, A)$ is the larger value between A and C. Under conditions of competition (not facilitation), the RNE values range between −1 and 0; the greater the RNE values are, the smaller the neighbour's competition effect is. A *t*-test was conducted to investigate whether stolon connection affected the RNE of *Alternanthera*. A significantly larger RNE with than without stolon connection would indicate that clonal integration improves *Alternanthera*'s competitive ability. The RNE of *S. phoenix* was not considered because a significant competition effect was not observed (see Results). The main stolon tip of one *Alternanthera* clonal fragment was damaged during the experiment, so data relevant to this plant were excluded from all analyses. The software package SPSS 13·0 (SPSS, Chicago, IL, USA) was used for all analyses.

RESULTS

Photosynthetic performance of Alternanthera

Both competition with the lawn grass, *S. phoenix*, and severing the stolon markedly reduced the value of F_v/F_m of *Alternanthera* in the apical sections (competition effect: $F_{1,23} = 72·8$, $P < 0·001$; stolon connection effect: $F_{1,23} = 7·6$, $P = 0·011$; Fig. 2). However, the effect of stolon connection tended to be larger when *Alternanthera* was grown with rather than without competition (interaction effect: $F_{1,23} = 3·8$, $P = 0·058$; Fig. 2).

Growth and competitive intensity of Alternanthera

Overall, stolon connection, competition and the interaction had significant effects on growth of *Alternanthera* in the apical sections (Table 1A). Competition greatly reduced biomass, number of ramets and leaves, total stolon length and total leaf area of *Alternanthera* (Table 1B, Figs 3A and 4). Severing stolons also significantly reduced these growth traits (Table 1B, Figs. 3A and 4), but such effects were, or tended to be, smaller when *Alternanthera* was grown with, rather than without, competition (Table 1B, Figs. 3A and 4). The relative neighbour effect of *Alternanthera* was −0·91 ± 0·02 (mean ± s.e.) when the stolons were kept intact and −0·92 ± 0·01 when they were severed; stolon connections had no effect ($t_{11} = 0·14$, $P = 0·89$).

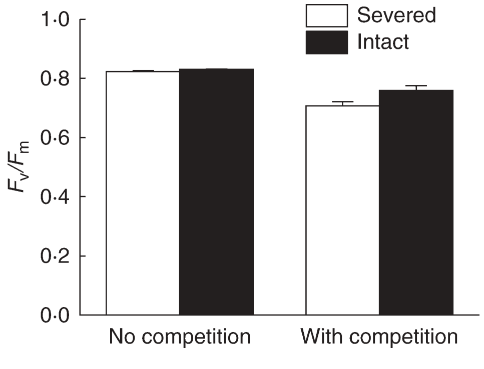

FIG. 2. The maximum quantum yield of photosystem II (F_v/F_m, ± 1 s.e.) of *Alternanthera* in the apical sections, grown either with or without competitors and with stolon connections either severed or kept intact.

TABLE 1. *Summary of MANOVA for effects of stolon connection, competition and their interaction on growth measures of* Alternanthera *in the apical sections*

(A) Multivariate test statistics and exact F-statistics

Effect	Wilk's Lambda	*F*	d.f.	*P*
Stolon connection	0·371	6·46	5,19	<0·001
Competition	0·043	84·01	5,19	<0·001
SC × C	0·207	14·52	5,19	<0·001

(B) Univariate test statistics

		Stolon connection		Competition		SC × C	
Trait	d.f.	*F*	*P*	*F*	*P*	*F*	*P*
Total biomass	1, 23	21·91	<0·001	175·56	<0·001	15·24	<0·001
Total leaf area	1, 23	11·78	0·002	131·42	<0·001	3·97	0·058
Total stolon length	1, 23	8·81	0·007	132·01	<0·001	4·89	0·037
Number of leaves	1, 23	6·51	0·018	182·30	<0·001	3·50	0·074
Number of ramets	1, 23	6·45	0·018	174·66	<0·001	4·52	0·045

Biomass allocation of Alternanthera

Stolon connection, competition and the interaction significantly affected biomass allocation of *Alternanthera* in the apical sections (Table 2A). Severing stolons increased biomass allocation to the leaves and decreased that to the roots when *Alternanthera* was grown without competition, whereas it decreased biomass allocation to the leaves and increased that to the roots when *Alternanthera* was grown with competition (Table 2B; Fig. 3B, D). Biomass allocation to the stolons was not affected by stolon connection, but was significantly larger when the apical ramets were grown with rather than without competition (Table 2B; Fig. 3C).

Growth of S. phoenix

Biomass of *S. phoenix* in the apical sections grown without interspecific competition (no *Alternanthera*) was 63·6 ± 1·6 g (mean ± s.e.), not significantly different from that when grown with *Alternanthera* with intact (66·4 ± 3·0 g) or severed (68·7 ± 1·4 g) stolon connections ($F_{2,17} = 1·05$, $P = 0·37$).

DISCUSSION

Integration effects on photosynthetic efficiency of Alternanthera

For several species in favourable conditions, the normal range for F_v/F_m values is between 0·75 to 0·85 (Butler and Kitajima, 1975; Björkman and Demmig, 1987; Demmig and Björkman, 1987). Without competition, F_v/F_m values of both connected and severed ramets of *Alternanthera* in the apical parts are within the normal

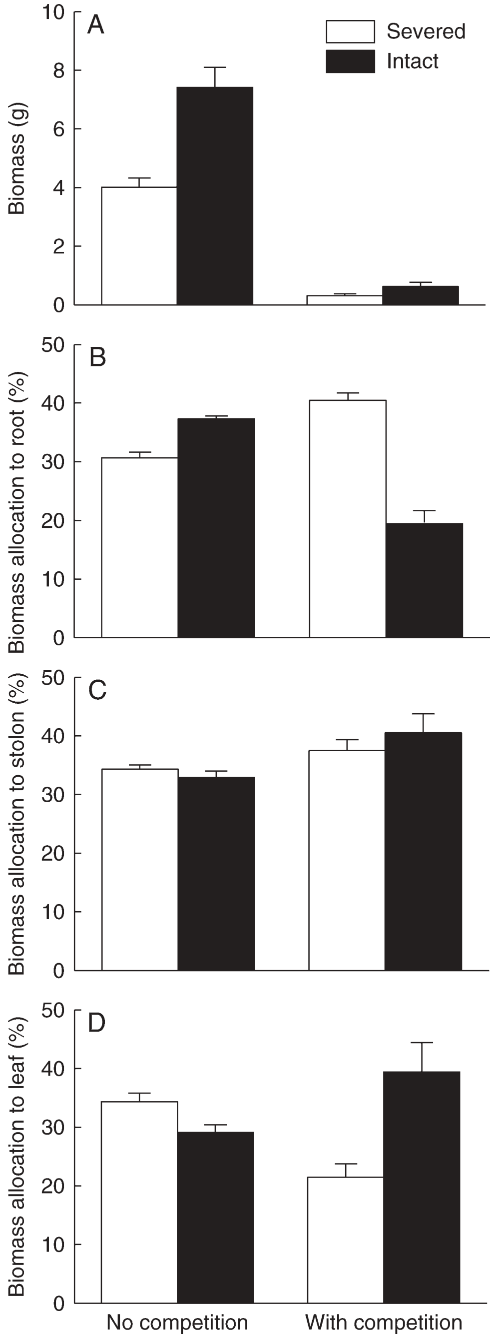

FIG. 3. (A) Biomass and (B, C, D) percentage biomass allocation (± 1 s.e.) of *Alternanthera* in the apical sections, grown either with or without competitors and with stolon connections either severed or kept intact.

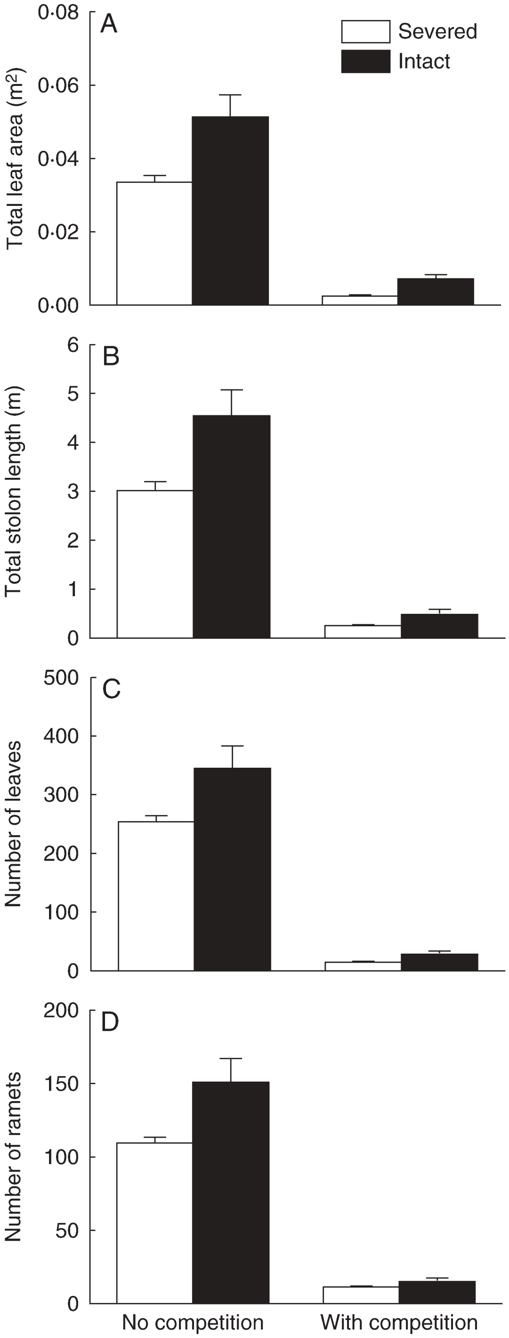

FIG. 4. (A) Total leaf area, (B) total stolon length, (C) number of leaves, and (D) number of ramets (± 1 s.e.) of *Alternanthera* in the apical sections, grown either with or without competitors and with stolon connections either severed or kept intact.

range for healthy plants (Fig. 2). Growing with *S. phoenix* decreased F_v/F_m of *Alternanthera* to the degree that was outside this range (Fig. 2), suggesting that competition imposed severe stress on *Alternanthera* (Maxwell and Johnson, 2000). However, the decrease in F_v/F_m of *Alternanthera* was greatly alleviated by stolon connections, and clonal integration allowed the ramets with competition to maintain their F_v/F_m values within the normal range (Fig. 2). The results, therefore, support our hypothesis and suggest that clonal integration markedly reduced the stress imposed by competition and significantly increased the photosynthetic activity of *Alternanthera.* Roiloa and Retuerto (2006*a*) also found that clonal integration significantly buffered the decrease in F_v/F_m of the offspring ramets of *Fragaria vesca* grown in soils contaminated by

TABLE 2. *Summary of MANOVA for effects of stolon connection, competition and their interaction on percentage biomass allocation of* Alternanthera *in the apical sections*

(A) Multivariate test statistics and exact F-statistics

Effect	Wilk's Lambda	*F*	d.f.	*P*
Stolon connection	0·410	15·81	2, 22	<0·001
Competition	0·575	8·13	2, 22	0·002
SC × C	0·178	50·72	2, 22	<0·001

(B) Univariate test statistics

		Stolon Connection		Competition		SC × C	
Trait	d.f.	*F*	*P*	*F*	*P*	*F*	*P*
Biomass allocation to leaves (%)	1, 23	26·61	<0·001	1·10	0·305	88·68	<0·001
Biomass allocation to stolons (%)	1, 23	0·20	0·660	8·39	0·008	1·48	0·235
Biomass allocation to roots (%)	1, 23	7·12	0·014	2·27	0·146	26·49	<0·001

heavy metals. As a result, clonal integration improved growth of *Alternanthera* when it was grown with competitors. However, repeated measurements at different time points are required for a full understanding of the integration effects on F_v/F_m.

Integration effects on growth and competitive ability of Alternanthera

Without competition, stolon connections markedly increased growth of *Alternanthera* in the apical sections. This is probably because the established adult ramets of *Alternanthera* in the basal sections supported the growth of the interconnected young, apical ramets and also facilitated the production of new meristems, probably by acropetal (i.e. from older to younger ramets) translocation of carbohydrates through clonal integration. A positive effect of clonal integration on the survival and/or growth of newly produced ramets has also been reported in several other clonal species, including *Solidago canadensis* (Hartnett and Bazzaz, 1983), *Holcus lanatus* (Bullock *et al.*, 1994), *Psammochloa villosa* (Dong, 1999; Dong and Alaten, 1999), *Hedysarum laeve* (Zhang *et al.*, 2002) and *Calamagrostis epigejos* (Březina *et al.*, 2006). The results suggest that clonal integration is very important for *Alternanthera* to explore open space and thus increase its invasiveness in natural habitats.

When the apical parts of *Alternanthera* were grown with the common lawn grass *S. phoenix*, its biomass decreased sharply to 8·4–8·7 % of those without competition and ramet and stolon production to 6·3–14·2 %, suggesting that interspecific competition in the present experiment imposed very strong stress on *Alternanthera*. Unexpectedly, although stolon connection increased growth of *Alternanthera* with competition, such beneficial effects of clonal integration were much smaller as compared with those without competition. In addition, stolon connection did not affect the relative neighbour effect, suggesting that clonal integration did not affect the competitive ability of *Alternanthera* (Callaway *et al.*, 2002; Kikvidze *et al.*, 2006). In a south-eastern USA salt marsh, Pennings and Callaway (2000) also found that clonal integration was of little importance for the plants to compete with neighbours for both above- and below-ground resources. Similarly, clonal integration has not been found to influence the competitive ability of several other clonal plants (Schmid and Bazzaz, 1987; Hartnett, 1993; Price and Hutchings, 1996; Peltzer, 2002; Březina *et al.*, 2006). Therefore, clonal integration may be of most importance for clonal plants to explore open, stressful habitats, to better use resource patches and to flourish in low-productivity habitats (Jónsdóttir and Watson, 1997; Pennings and Callaway, 2000; Peltzer, 2002), but may contribute little to their competitive ability under severe stress (Pennings and Callaway, 2000; Peltzer, 2002).

Integration effects on biomass allocation of Alternanthera

Clonal integration significantly modified biomass allocation of *Alternanthera*, agreeing with previous findings on many other clonal plants (Salzman and Parker, 1985; Friedman and Alpert, 1991; Evans and Whitney, 1992; Birch and Hutchings, 1994; Stuefer *et al.*, 1994, 1996; Wijesinghe and Hutchings, 1997; Roiloa *et al.*, 2007). Without competition, clonal integration increased *Alternanthera*'s biomass allocation to roots at the expense of that to leaves. This is most likely because without competition soil resources (i.e. nutrients and water) were relatively more limiting for the quick spreading of *Alternanthera* ramets and stolons in the apical sections. For the connected apical ramets, the required carbohydrates could be transported efficiently from the basal ramets so that relatively more biomass could be allocated to roots in order to increase the growth of the whole ramet system in the apical parts. With competition, however, clonal integration significantly increased biomass allocation to leaves and decreased that to roots. This may be because, under severe competition, allocating more biomass to leaves allowed the connected apical *Alternanthera* ramets to be more easily placed above the canopy of the dense swards of *S. phoenix*, thus allowing them to harvest the relatively more abundant light resources at that level, whereas relatively scarce soil resources (due to the abundant roots of *S. phoenix*) could be compensated for by transport from the basal ramets grown without competition. This explanation was supported by the observation that stolons of *Alternanthera* plants could turn upright when they were grown with the dense swards. Biomass allocation of *Alternanthera* under competition agrees with the theory of labour division in clonal plants (Alpert and Stuefer, 1997; Hutchings and Wijesinghe, 1997). Thus, effects of clonal integration on the biomass allocation pattern may potentially improve the uptake of resources and enhance the invasiveness of *Alternanthera*.

Integration effects on the growth of S. phoenix

Unexpectedly, biomass of *S. phoenix* was not affected by the presence of *Alternanthera*, suggesting that competition treatments used in the experiment did not impose severe stress on *S. phoenix*. In addition, clonal integration did not suppress the growth of *S. phoenix*, in contrast to our prediction. This is probably because in the present experiment the density of *S. phoenix* was too high to allow an efficient invasion by *Alternanthera* apical parts (Brown and Fridley, 2003). This view was supported by the fact that with competition, biomass of *Alternanthera* in the apical sections was reduced to less than 10 % (8·4–8·7 %) as compared with that recorded without competition. Under such severe competition, even though clonal integration contributed significantly to the growth of *Alternanthera* in the apical sections, the negative effects of severe competition were still substantial due to the relatively short experimental duration (9 weeks). Thus, roles of clonal integration may be more important if the experiment had lasted longer.

CONCLUSIONS

When *Alternanthera* was grown with dense swards of *S. phoenix*, clonal integration contributed little to its competitive ability, even though clonal integration greatly benefited its photochemical activity. However, clonal integration was very important for *Alternanthera* to explore open space. We hypothesize that the effects of clonal integration on the competitive ability of *Alternanthera* and *S. phoenix* would be more pronounced if the density of *S. phoenix* was reduced and/or the duration of the experiment was prolonged. The results suggest that the invasiveness of *Alternanthera* may be closely related to clonal integration. To allow a generalization and robust extrapolation, more studies are needed.

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