

Clonal integration is beneficial for resource sharing in a creeping amphibian herb (*Alternanthera philoxeroides*)

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Received: 14 January 2016 / Revised: 00 Month 0000 / Accepted: 17 September 2017 / Published online: 27 November 2017
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Abstract Clonal integration facilitates the growth and reproduction of clonal plants by providing the ability to share resources among ramets in heterogeneous environments. The benefits of clonal integration for plant growth may depend on a contrast in resource availability and may encounter costs, especially when a young part of the clone is growing across a border between richer and poorer conditions than the old part. We studied a clonal amphibian plant growing across a border between an aquatic and a terrestrial ecosystem, which typically differ in the availability of resources. We asked whether the young part of the clone is supporting the old part with phosphorus and whether this support has costs. We performed an experiment with *Alternanthera philoxeroides* where plants grow from water to a terrestrial habitat. The terrestrial habitat had either a low or high phosphorus supply, and the connection between the old and young parts of the clone was either left intact or split.

We determined that the young part of the clone growing in a terrestrial habitat supported the old part with phosphorus when growing on a substrate rich in phosphorus. We have found no cost of this resource translocation; on the contrary, whole clones increased not only their accumulation of phosphorus, but also of nitrogen. Our study shows how an amphibian plant may profit from heterogeneous habitats by resource sharing in a clonal network.

Keywords Clonal integration · Heterogeneity · N uptake · P availability · Resource sharing

Introduction

The term habitat heterogeneity refers to a non-uniform spatial distribution of essential resources which limits the growth of plants in a natural ecosystem (Stuefer 1996; Ye et al. 2015). While non-clonal plants, which are restricted to a single rooting point, cannot always explore and exploit this type of heterogeneity (Stuefer 1998), many clonal plants can do it due to multiple rooting units connected by spacers (Stuefer et al. 1994; He et al. 2011). The spacers (e.g. stolons and rhizomes) allow sharing of resources such as water (Geng et al. 2006), photosynthates (Hartnett and Bazzaz 1983; Slade and Hutchings 1987) and mineral nutrients (Liu et al. 2016). This kind of reciprocal resource sharing, usually referred to as division of labour (Stuefer 1998; Ye et al. 2015), enables clonal plants to behave as a cooperative system (Hutchings 1999) and therefore improves survivorship, growth and reproduction of recipient rooting

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units (ramets) of clonal plants in resource-poor patches of heterogeneous habitats (Alpert and Mooney 1986; Lu et al. 2016). Therefore, clonal plants have a more efficient use of spatially scattered resources compared to non-clonal plants (Herben 2004).

There is no agreement whether resource sharing is costly for a plant (Salzman and Parker 1985; Xu et al. 2010). Many studies have shown benefits of resource sharing for the recipient ramets at no costs to the donor ramet (Alpert and Mooney 1986; Stuefer 1995; Yu et al. 2002; Liu et al. 2016; Lu et al. 2016). Other studies have reported costs to donor ramets (Caraco and Kelly 1991; Pauliukonis and Gough 2004; Luo et al. 2014) or even the cessation of support to recipient ramets in seriously impoverished site (Hartnett and Bazzaz 1983; Wolfer and Straile 2012). There are two important reasons for the inconsistency of results:

- (i) The benefit of resource sharing may vary with contrasting resource availability in different patches (Hutchings and Wijesinghe 2008). The underlying mechanism may be stronger functional specialization of ramets for uptake of a limiting resource with its increasing availability (Hartnett and Bazzaz 1983; Stuefer et al. 1994; Alpert 1999; Saitoh et al. 2002; Yu et al. 2002).
- (ii) Plants can more easily share resources in direction of their growth (acropetally), i.e. from established ramets with own root system to young ramets without roots (developmental division of labour – Stuefer 1998) than from young to old ramets (basipetally – Alpert and Mooney 1986; Jónsdóttir and Callaghan 1989). From preceding studies we know that the basipetal or acropetal direction of translocation primarily depends on the source-sink relationships of interconnected ramets (Hutchings and Wijesinghe 1997). For example, Lötscher and Hay (1997) report that phosphorus (P) can be transported basipetally in *Trifolium repens* under heterogeneous P supply, while Roiloa and Hutchings (2012) report prevailing acropetal resource sharing in *Glechoma hederacea*.

Although heterogeneity in resource availability can be found in numerous communities, in some of them it can be clearly observed. For example, in wetlands plants may be subjected to mosaic of aquatic and terrestrial patches that clonal plants can cross (Wolfer and Straile 2004; Wang et al. 2009). Clonal amphibian plants are often found in aquatic-

terrestrial ecotones, which typically differ by the availability of nutrients (Liu et al. 2016), oxygen (Frost-Christensen et al. 2003), carbon dioxide (Robe and Griffiths 2000), light (Etnier et al. 2017), etc. For example, the same P concentration differs in aquatic-terrestrial ecotones, where P concentrations in natural clean waters are relatively small compared with the amount of P used in soils (Barko et al. 1991; Sanyal and De Datta 1991). McRoy and Barsdate (1970) have reported that aquatic plant *Zostera marina* can obtain P from the sediment by roots and translocate to other parts of the plant. We thus predicted that ramets of clonal amphibian plants rooting within rich P soils also could absorb and translocate P to ramets floating in P-poor waters due to clonal integration. Therefore, we conducted an experiment using a creeping amphibian herb, *Alternanthera philoxeroides*, with representative clonal propagation from aquatic to terrestrial environments to explore the following three questions: (1) Can clonal integration improve the performance of basal ramets in a low P availability habitat by resource sharing supported by apical ramets in a high P habitat? (2) What might clonal integration cost the growth of apical ramets due to the basipetal translocation of P resources? (3) Can whole clonal fragments benefit more from soluble P compared to insoluble P due to greater contrasting levels of P availability between aquatic and terrestrial environments?

Material and methods

Study species

Alternanthera philoxeroides (Mart.) Griseb. (Amaranthaceae) is a perennial amphibian species native to America that is rapidly spreading in China (Dong et al. 2010; Zhou et al. 2012). It occurs in a variety of wetland habitats due to its easy clonal multiplication by the fragmentation of branching creeping shoots (Sainty et al. 1997). Each node of the horizontal stem may produce a new branch, a potentially independent fragment of the clone (Geng et al. 2006).

Clonal fragments for an experiment using *A. philoxeroides* were collected from a single population distributed in a branch of the Yangtze River in Zhejiang, China (32°13' N, 119°28' E), where genetic diversity of *A. philoxeroides* is extremely low (Wang et al. 2005). Then, these clonal fragments were propagated in a greenhouse at Jiangsu University, China. The fragments were cultured in 0.5× Hoagland nutrient solutions

(Dai et al. 2016). After one month of culturing, similar-aged and -sized clonal fragments (24.81 ± 0.61 cm in length; mean \pm SE), with four nodes and one apex were used for the experiment.

Experimental design

Herein, the three oldest nodes of the clonal fragments are referred to as the ‘basal part’ of the clonal fragments, and the youngest node and one apex of the fragments are referred to as the ‘apical part’ (Fig. 1). The basal parts of the clonal fragments were placed into containers ($30 \times 20 \times 8$ cm; length \times width \times height) filled with a modified 0.5 \times Hoagland nutrient solution without additional nitrogen (N) and P to simulate low-P aquatic habitats (Table 1a) whereas the apical parts were planted in plastic pots (10 cm in diameter) filled with washed river sand (< 2 mm in diameter) to simulate high-P terrestrial habitats. The sand mixed with soluble P was treated with KH_2PO_4 , while that with insoluble P was treated with a mixture of inorganic P compounds and organic P compounds. The amount of P for each pot was 56.52 mg in both soluble and insoluble P treatments. Soluble P (orthophosphate ions) from soil solutions can be taken up by plants (Effendy et al. 2014); conversely, both inorganic P bound to metal cations and organic P are insoluble and cannot be directly acquired by plants (Vance et al. 2003; Richardson and Simpson 2011). Therefore, even though the quantities of soluble P and insoluble P are the same, compared to soluble P, the availability of insoluble P is lower for plants. The N amount was also 56.52 mg, provided by compounds of KNO_3 and NH_4Cl (M/M = 1:1) in each pot. Part of the

potassium was provided by the KH_2PO_4 which was used to supply P, and the rest of potassium was provided by adding KCl, while all other basal nutrients were supplied in constant (Table 1b), non-limiting amounts (Pearse et al. 2007).

When the apical parts had produced adventitious roots, half of the stolons were severed to prevent the integration of basal and apical parts, whereas for the other half, they were left connected to allow integration (Fig. 1). Each treatment was repeated five times. The experiment was performed in a greenhouse (temperature: $26 \pm 2^\circ\text{C}$; relative humidity: $62 \pm 2\%$, mean \pm SE; photosynthetic photon flux density (PPFD) during the day: approx. $300 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Each replicate was repositioned randomly every week to avoid the effects of possible environment patchiness within the greenhouse. The newly formed branches in the basal parts and apical parts outside the plastic pot were not allowed to root. An adequate amount of distilled water was supplied to the clonal fragments every two days. The modified Hoagland solutions were completely replaced every two weeks to maintain the same initial nutrient concentration.

Harvest and measurements

After nine weeks of culturing, the apical and basal parts of the clonal fragments of *A. philoxeroides* were harvested separately. The number of new nodes, total stolon length and the number of branches were counted for the apical parts or basal parts, respectively. The apical parts and basal parts of plants were divided into roots and shoots (including stems and leaves), and then dried at 70°C for

Fig. 1 Experimental design of this study. A clonal fragment of *Alternanthera philoxeroides*, each end consisting of three old/basal nodes floating in low-P water (white rectangles) and one young/apical node with a stolon apex (grey squares) planted in high-P sand (grey squares), with two different P available forms: soluble P (SP) and insoluble P (ISP). Stolons between the apical and basal parts were either connected (left) or severed (right)

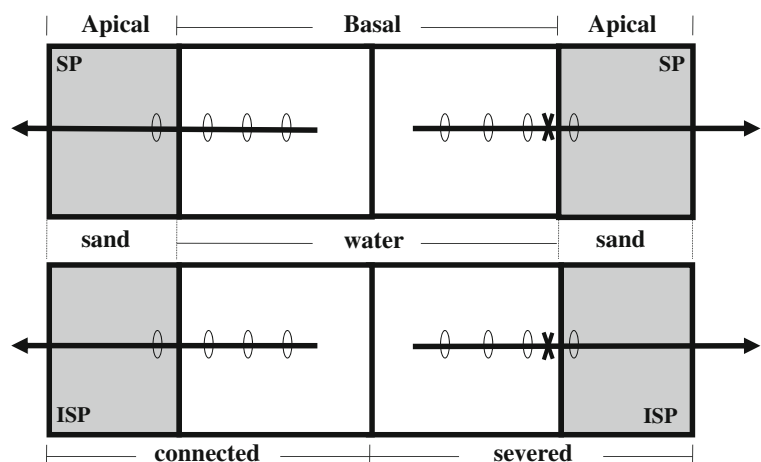


Table 1 Compositions of nutrient addition: **A** – main elements in water; **B** – elements in sand

A		
Element	Content [mg/container (3 L)]	Compound
Mg	4.8	MgSO ₄ ·7H ₂ O
S	3.2	MgSO ₄ ·7H ₂ O
Fe	0.18	C ₁₀ H ₁₂ FeN ₂ NaO ₈
K	39	KCl
B		
Element	Content [mg/pot]	Compound
P	56.52	Soluble P: KH ₂ PO ₄ Insoluble P: 50% Ca ₅ (OH)(PO ₄) ₃ , 30% AlPO ₄ , 20% C ₆ H ₆ O ₂₄ P ₆ Na ₁₂
N	56.52	KNO ₃ :NH ₄ Cl = 1:1
K	135.75	KCl, KNO ₃ , KH ₂ PO ₄
Ca	60.86	CaCl ₂ , Ca ₅ (OH)(PO ₄) ₃
Mg	24	MgSO ₄ ·7H ₂ O
S	32.02	MgSO ₄ ·7H ₂ O, ZnSO ₄ ·7H ₂ O, MnSO ₄ ·4H ₂ O, CuSO ₄ ·5H ₂ O
Fe	5.6	C ₁₀ H ₁₂ FeN ₂ NaO ₈
Cu	0.01	CuSO ₄ ·5H ₂ O
B	0.27	H ₃ BO ₃
Mn	0.55	MnSO ₄ ·4H ₂ O
Mo	0.01	Na ₂ MoO ₄ ·2H ₂ O
Zn	0.03	ZnSO ₄ ·7H ₂ O

72 hours and weighed. The total biomass of apical parts or basal parts was the sum of the biomass of the root and the shoot. The number of new nodes, total stolon length, the number of branches, and the biomass of both basal parts and apical parts were also counted for the whole fragments. After a digestion procedure (Kjeldahl digestion method; 1 hour at 200°C and 2 hours at 340°C in a mixture of concentrated sulfuric acid and 30% hydrogen peroxide) (Fujita et al. 2010), the N and P concentrations in the leaves of apical and basal parts were determined colourimetrically using a UV-1200 spectrophotometer (MAPADA, Shanghai, China).

Data analysis

Two-way ANOVAs were used to test the effects of clonal integration (connected vs. severed) and P availability (soluble P vs. insoluble P) on the growth traits (i.e. biomass, number of new nodes, total stolon length, number of branches, and ratio of root to shoot), and stoichiometric nutrition (i.e. concentration and accumulation of N and P) of the apical or basal parts and whole clonal fragments. Values for the biomass of root and the number of branches of the basal parts were $\log(x + 1)$

transformed to satisfy requirements of normality and homogeneity of variance. Differences between individual means were tested with Bonferroni tests to examine the effects of the treatments, and the P values were adjusted by Bonferroni correction. All analyses were performed with SPSS Statistics 22.0 software (SPSS, Chicago, IL, USA).

Results

Performance of basal parts

Total stolon length, the number of new nodes, and the P concentration and N concentration in leaves of the basal parts were greatly affected by P availability whereas the other measures were not affected (Tables 2 and 3). Total stolon length and the number of new nodes of basal parts were greater when the stolons were connected with a soluble P treatment than with an insoluble P treatment (Fig. 2a,c), but the P concentration and N concentration in leaves of the basal parts were reversed (Fig. 3a,b).

Table 2 *P*-values of two-way analysis of variance (ANOVA) for stolon connection (C) and phosphorus form (P) and their interactions (C × P) on variables related to growth traits of apical and basal part. The *P* values were adjusted by the Bonferroni correction

Growth traits	Basal part			Apical part			Clonal fragment		
	Connection	Phosphorus	C × P	Connection	Phosphorus	C × P	Connection	Phosphorus	C × P
total stolon length	0.000	0.000	0.000	0.000	0.001	0.054	0.000	0.000	0.020
number of new nodes	0.000	0.000	0.000	0.000	0.000	0.013	0.000	0.000	0.006
number of branches	0.050	0.050	0.050	0.005	0.001	0.000	0.005	0.001	0.001
biomass of root	0.000	0.044	0.027	0.071	0.009	0.086	0.019	0.011	0.102
biomass of shoot	0.000	0.043	0.042	0.000	0.003	0.106	0.000	0.002	0.122
total biomass	0.000	0.126	0.143	0.000	0.000	0.127	0.000	0.000	0.127
ratio of root to shoot	0.000	0.008	0.001	0.001	0.134	0.042	0.001	0.127	0.057

P < 0.007

The growth of basal parts was greatly affected by stolon connection, except for the number of branches (Table 2, *P* < 0.007 and Table 3, *P* < 0.0125 with Bonferroni correction). Stolon connection significantly increased the biomass of the shoot, the biomass of the root, total biomass and the ratio of the root to the shoot of the basal parts (Fig. 2d,e; Fig. 2f; Fig. 4), and greatly increased the concentration and accumulation of P and N (Fig. 3).

There was a significant interaction effect of P availability by stolon connection on the ratio of the root to the shoot of the basal parts (Table 2). The ratio of the root to the shoot in insoluble P treatments was greater than that in soluble P treatments when the stolons were connected (Fig. 4).

Performance of apical parts

Most measures of apical parts were greatly affected by P availability, except for the biomass of the root, and the ratio of the root to the shoot (Tables 2 and 3). Total biomass, total P accumulation and total N accumulation

Table 3 *P* values of two-way analysis of variance (ANOVA) for stolon connection (C) and phosphorus form (P) form and their interactions (C × P) on variables related to concentration and

	Basal part			Apical part		
	Connection	Phosphorus	C × P	Connection	Phosphorus	C × P
P concentration in leaves	0.000	0.000	0.000	0.001	0.000	0.034
N concentration in leaves	0.000	0.000	0.000	0.005	0.004	0.003
Total P accumulation	0.000	0.087	0.083	0.081	0.000	0.213
Total N accumulation	0.000	0.196	0.187	0.000	0.000	0.023

P < 0.0125

of the apical parts were significantly greater in soluble P treatments than those in insoluble P treatments (Fig. 2f; Fig. 3c,d). Stolon connection made total stolon length, the number of new nodes and the N concentration in leaves of the apical parts significantly greater in soluble P treatments than those in insoluble P treatments (Fig. 2a,c; Fig. 3b), but the number of branches, biomass of the shoot and the P concentration in leaves of the apical parts exhibited no significant difference between soluble and insoluble P treatments (Fig. 2b,d; Fig. 3a).

The growth of apical parts was also greatly affected by stolon connection, except for the biomass of root and the total P accumulation (Tables 2 and 3). Stolon connection significantly increased total stolon length, the number of new nodes, biomass of the shoot, total biomass and total N accumulation of the apical parts (Fig. 2a,c,d,f; Fig. 3d).

Performance of whole clonal fragments

P availability and stolon connection significantly affected all the growth measures except for biomass

accumulation of phosphorus and nitrogen for apical and basal parts. The *P*-values were adjusted by the Bonferroni correction

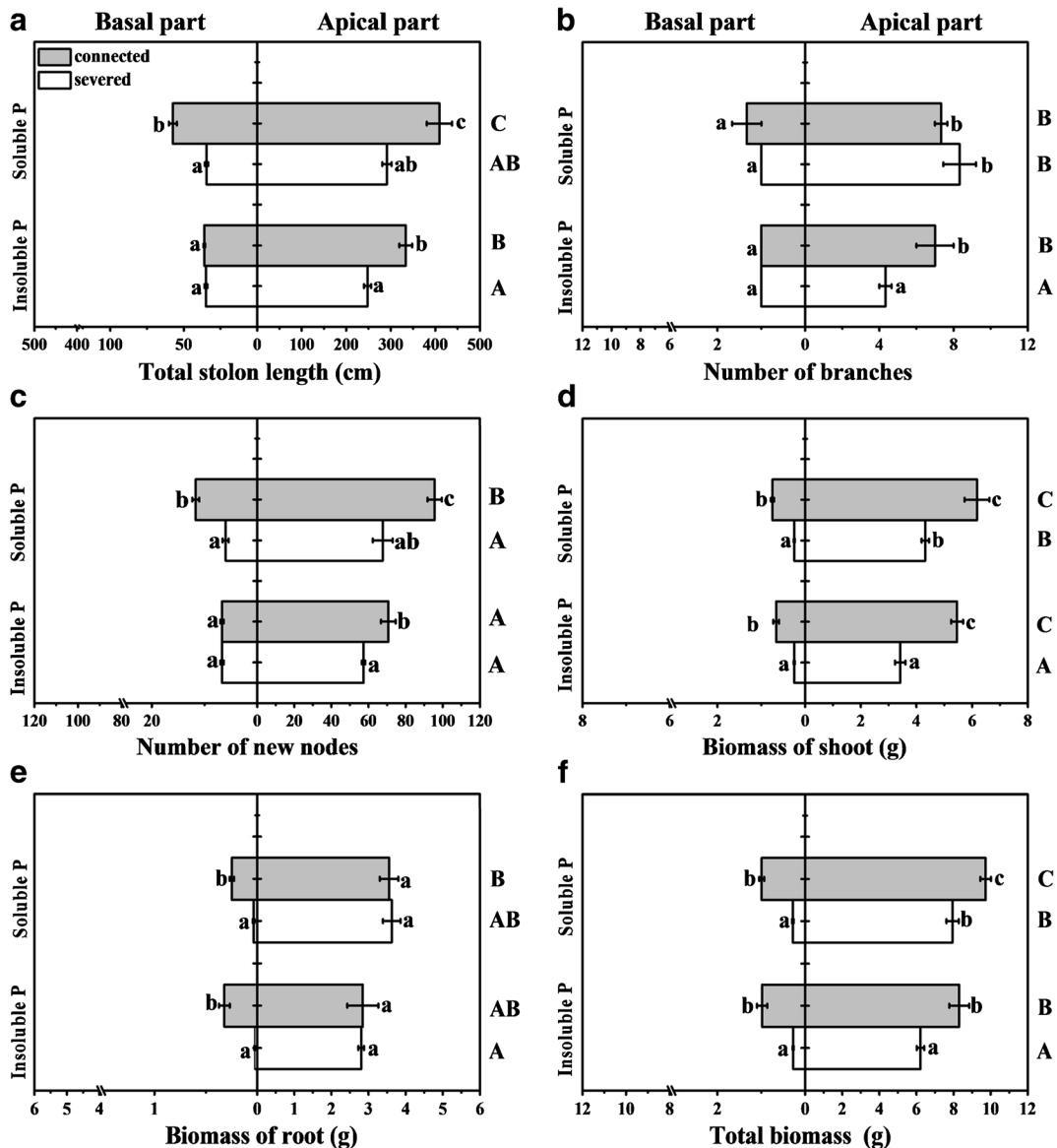


Fig. 2 Lateral extension and biomass of *Alternanthera philoxeroides* subjected to soluble P or insoluble P treatments. Stolons connecting apical and basal parts were either connected (grey) or severed (open). The left horizontal bars represent the basal parts whereas the right horizontal bars represent the apical parts. The sums of the basal part and the apical part indicate the

of the root (Table 2). Compared with insoluble P treatments, when stolons were connected, total stolon length, the number of new nodes and total biomass of whole clonal fragments in soluble P treatments were significantly greater (Fig. 2a,c,f). Stolon connection significantly increased total stolon length, biomass of the shoot and total biomass of whole clonal fragments (Fig. 2a,d,f).

lateral extension and biomass for a whole clonal fragment. Bars and vertical lines represent the means and standard errors ($n = 5$). For the basal parts and the apical parts, respectively; horizontal bars sharing the same lowercase letter are not significantly different at $P = 0.05$. For the whole clonal fragment, horizontal bars sharing the same capital letter are not different at $P = 0.05$

Discussion

Clonal integration was advantageous for both basal and apical part of the clone growing in aquatic versus terrestrial conditions and more so when availability of P was high. Therefore, we observed costs due to resource sharing neither for donor part of the clone nor for whole-clone performance.

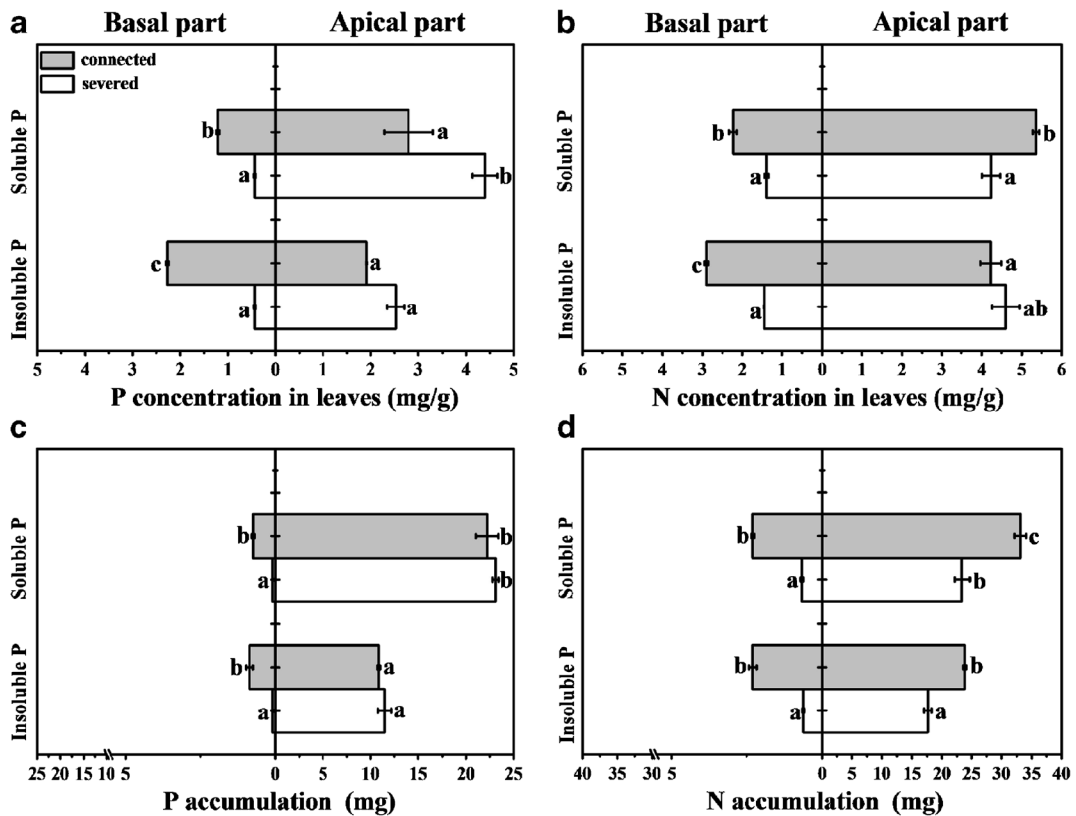


Fig. 3 P and N uptake of the apical and basal parts of *Alternanthera philoxeroides* subjected to soluble P or insoluble P treatments. Stolons connecting apical and basal parts were either connected (grey) or severed (open). (A) P concentration in leaves;

(B) N concentration in leaves; (C) P accumulation; and (D) N accumulation. Bars and vertical lines represent the means and standard errors ($n = 5$). Bars with the same letters are not significantly different at $P = 0.05$.

Basipetal translocation of resources

In the present experiments, stolon connection significantly increased the biomass and the P and N accumulation of the basal parts of the clonal amphibian herb *A. philoxeroides* regardless of P availability. This result suggests that clonal integration facilitates the survivorship and growth of old ramets growing in nutrient-poor water due to basipetal translocation of resources.

Typically, resources move from older to younger ramets (acropetal translocation) (Alpert and Mooney 1986; Jónsdóttir and Callaghan 1989). For example, the growth of *Glechoma hederacea* is significantly greater in acropetal treatments than in basipetal treatments (Roiloa and Hutchings 2012). Sharing of nutrients in our experiment was thus driven mainly by the source-sink relationship among ramets. Basipetal translocation of resources driven by source-sink relationship is also common in many other clonal plants, such as *Trifolium repens*, *Fragaria orientalis* and *Sasa palmata*

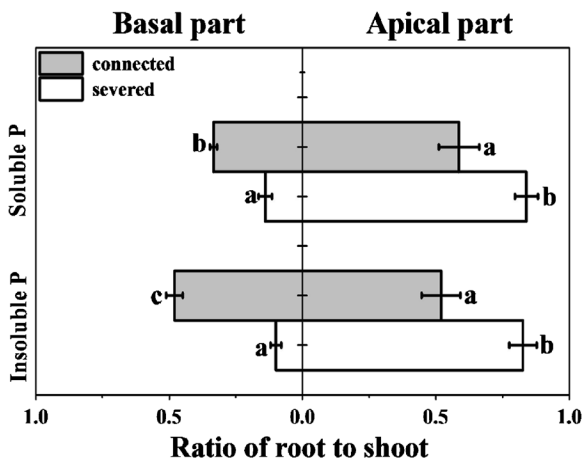


Fig. 4 Ratio of root to shoot of the apical and basal parts of *Alternanthera philoxeroides* subjected to soluble P or insoluble P treatments. Stolons connecting apical and basal parts were either connected (grey) or severed (open). Bars and vertical lines represent the means and standard errors ($n = 5$). Bars with the same letters are not significantly different at $P = 0.05$

(Lötscher and Hay 1997; Saitoh et al. 2006; Zhang and Zhang 2013). For instance, under heterogeneous P supply, 50% of ^{32}P exported from a high-P patch is transported basipetally in the small-leaved *Trifolium repens* (Lötscher and Hay 1997).

Further, persistence of stolon connections significantly increased the root to shoot ratio of the basal parts but significantly decreased the root to shoot ratio of the apical parts (Table 2 and Fig. 4) in comparison with split treatments. It was probably due to necessity to build own root system for separated apical parts but not for integrated apical parts due to developmental division of labour (Stuefer 1998; Zhang and Zhang 2013). Apical parts of clones lacking roots are usually a source of carbon for older part of a clone, which is a source of water (Marshall 1990; Stuefer et al. 1994; Jónsdóttir and Watson 1997) and dissolution products of relatively abundant salts (i.e. potassium and calcium – Barko et al. 1991).

Contrary to other studies considering the benefits to recipient ramets and the costs to donor ramets (Wang et al. 2009; Xu et al. 2010), our study found that clonal integration did not cost any growth to donor parts but increased whole clonal fragments. The main reason for the lack of costs incurred by the apical parts in the experiment is the fact that only surplus P and N resources may be transported from the apical parts to the basal parts (Table 3, Fig. 3c and d). Therefore, surplus resource supplies for recipient ramets do not limit the normal growth of donor ramets (Yu et al. 2002; Liu et al. 2016). However, the maintenance of stolon connections significantly decreased the P concentration in leaves of the apical parts. One possible reason is that the growth rate of the apical parts is greater than their rate of P uptake, which is causing the dilution of P in plant tissues (Jarrell and Beverly 1981).

Contrasting levels of P availability

Growth parameters were enhanced in treatment with soluble P in comparison with insoluble P and this is in agreement that resource sharing is more beneficial when there are greater contrasts in resource availability (Hutchings and Wijesinghe 2008; Richardson and Simpson 2011). Resource contrast between heterogeneous environments plays important role as the main external driving force behind integration effects (Caraco and Kelly 1991). The benefits of clonal integration are enhanced under higher levels of contrast, for instance, drought-stressed ramets gain more benefits in a high-contrast environment than in a lower-contrast environment (Zhang et al. 2009).

Our results also show that the N concentration in leaves and total N accumulation were significantly higher in our soluble P treatments than those in our insoluble P treatments when the stolons were connected (Fig. 3b and d; Table 3). It suggests that both P availability and clonal integration significantly facilitate N assimilation, as shown in other studies (Treseder and Vitousek 2001; Güsewell et al. 2003). Due to higher availability of P, plants have higher biotic N demands to avoid elemental imbalance (Treseder and Vitousek 2001). Therefore, it may be expected that P availability can alter N assimilation in plants (Rufy et al. 1990).

Conclusion

Resource sharing by clonal integration is an important strategy that allows the survivorship and expansion of clonal amphibian plants *A. philoxeroides* in aquatic-terrestrial ecotones, which typically differ in the availability of resources. The higher was the level of resource contrast responsible for the establishment of source-sink relationships between interconnected ramets, the greater was the benefit of resource sharing. In addition, N assimilation was enhanced under more contrasting levels of P availability. Therefore, resource contrast will be one of most important driving factors to affect the expansion of *A. philoxeroides* in aquatic-terrestrial ecotones, especially in the context of anthropogenic nutrient input and resource eutrophication.

Acknowledgements This work was supported by the National Natural Science Foundation of China (31570414), the Natural Science Foundation of Jiangsu (BK20150503, BK20150504), the Research and Innovation Project for College Graduates of Jiangsu Province (KYLX15_1088 15A316), the Natural Science Research Project of Higher Education of Jiangsu (14KJB610005), the Jiangsu Planned Projects for Postdoctoral Research Funds (1501028B), the Priority Academic Program Development of Jiangsu Higher Education Institutions (PAPD), the Jiangsu Collaborative Innovation Center of Technology and Material of Water Treatment, and the State Key Research Development Program of China (2017YFC1200103, 2016YFC0502002).

References

- Alpert P (1999) Clonal integration in *Fragaria chiloensis* differs between populations: Ramets from grassland are selfish. *Oecologia* 120:69–76
- Alpert P, Mooney HA (1986) Resource sharing among ramets in the clonal herb, *Fragaria chiloensis*. *Oecologia* 70:227–233

- Barko JW, Gunnison D, Carpenter SR (1991) Sediment interactions with submersed macrophyte growth and community dynamics. *Aquatic Bot* 41:41–65
- Caraco T, Kelly CK (1991) On the adaptive value of physiological integration in clonal plants. *Ecology* 72:81–93
- Dai ZC, Fu W, Qi SS, Zhai DL, Chen SC, Wan LY, Huang P, Du DL (2016) Different responses of an invasive clonal plant *Wedelia trilobata* and its native congener to gibberellin: Implications for biological invasion. *J Chem Ecol* 42:85–94
- Dong BC, Zhang MX, Alpert P, Lei GC, Yu FH (2010) Effects of orientation on survival and growth of small fragments of the invasive, clonal plant *Alternanthera philoxeroides*. *PLoS ONE* 5: e13631
- Effendy J, Woodfield D, Caradus J, McManus MT (2014) Responses to low P-supply in breeding lines of white clover (*Trifolium repens* L.) reveals two tiers of responses. *J Pl Nutr* 37:1441–1454
- Etnier SA, Villani PJ, Ryan TJ (2017) Influence of light quality and quantity on heterophylly in the aquatic plant *Nymphaea odorata* subsp. *tuberosa* (Nymphaeaceae). *NE Naturalist* 24: 152–164
- Frost-Christensen H, Jorgensen LB, Floto F (2003) Species specificity of resistance to oxygen diffusion in thin cuticular membranes from amphibious plants. *Pl Cell Environ* 26: 561–569
- Fujita Y, Robroek BJM, De Ruiter PC, Heil GW, Wassen MJ (2010) Increased N affects P uptake of eight grassland species: The role of root surface phosphatase activity. *Oikos* 119: 1665–1673
- Geng YP, Pan XY, Xu CY, Zhang WJ, Li B, Chen JK (2006) Phenotypic plasticity of invasive *Alternanthera philoxeroides* in relation to different water availability, compared to its native congener. *Acta Oecol* 30:380–385
- Güsewell S, Bollens U, Ryser P, Klötzli F (2003) Contrasting effects of nitrogen, phosphorus and water regime on first- and second-year growth of 16 wetland plant species. *Funct Ecol* 17:754–765
- Hartnett DC, Bazzaz FA (1983) Physiological integration among intracolonial ramets in *Solidago canadensis*. *Ecology* 64:779–788
- He WM, Alpert P, Yu FH, Zhang LL, Dong M (2011) Reciprocal and coincident patchiness of multiple resources differentially affect benefits of clonal integration in two perennial plants. *J Ecol* 99:1202–1210
- Herben T (2004) Physiological integration affects growth form and competitive ability in clonal plants. *Evol Ecol* 18:493–520
- Hutchings M (1999) Clonal plants as cooperative systems: Benefits in heterogeneous environments. *Pl Spec Biol* 14:1–10
- Hutchings MJ, Wijesinghe DK (1997) Patchy habitats, division of labour and growth dividends in clonal plants. *Trends Ecol Evol* 12:390–394
- Hutchings MJ, Wijesinghe DK (2008) Performance of a clonal species in patchy environments: Effects of environmental context on yield at local and whole-plant scales. *Evol Ecol* 22:313–324
- Jarrell WM, Beverly RB (1981) The dilution effect in plant nutrition studies. *Advances Agron* 34:197–224
- Jónsdóttir IS, Callaghan TV (1989) Localized defoliation stress and the movement of ^{14}C between tillers of *Carex bigelowii*. *Oikos* 54:211–219
- Jónsdóttir IS, Watson MA (1997) Extensive physiological integration: an adaptive trait in resource-poor environments? In de Kroon H and van Groenendael J (eds) *The ecology and evolution of clonal plants*. Backhuys Publishers, Leiden, pp 109–136
- Liu L, Lin HF, Dong BC (2016) Clonal integration enhances expansion ability of *Ipomoea aquatica* in aquatic-terrestrial ecotones. *Aquatic Bot* 128:33–40
- Lötscher M, Hay MJM (1997) Genotypic differences in physiological integration, morphological plasticity and utilization of phosphorus induced by variation in phosphate supply in *Trifolium repens*. *J Ecol* 85:341–350
- Lu HZ, Song L, Liu WY, Xu XL, Hu YH, Shi XM, Li S, Ma WZ, Chang YF, Fan ZX, Lu SG, Wu Y, Yu FH (2016) Survival and growth of epiphytic ferns depend on resource sharing. *Frontiers Pl Sci* 7:416
- Luo FL, Chen Y, Huang L, Wang A, Zhang MX, Yu FH (2014) Shifting effects of physiological integration on performance of a clonal plant during submergence and de-submergence. *Ann Bot (Oxford)* 113:1265–1274
- Marshall C (1990) Source-sink relations of interconnected ramets. In van Groenendael J and de Kroon H (eds) *Clonal growth in plants: regulation and function*. SPB Academic Publishing, The Hague, pp 23–41
- Mcroy CP, Barsdate RJ (1970) Phosphate absorption in eelgrass. *Limnol Oceanogr* 15:6–13
- Pauliukonis N, Gough L (2004) Effects of the loss of clonal integration on four sedges that differ in ramet aggregation. *Pl Ecol* 173:1–15
- Pearse SJ, Veneklaas EJ, Cawthray G, Bolland MDA, Lambers H (2007) Carboxylate composition of root exudates does not relate consistently to a crop species' ability to use phosphorus from aluminium, iron or calcium phosphate sources. *New Phytol* 173:181–190
- Richardson AE, Simpson RJ (2011) Soil microorganisms mediating phosphorus availability update on microbial phosphorus. *Pl Physiol* 156:989–996
- Robe WE, Griffiths, H (2000) Physiological and photosynthetic plasticity in the amphibious, freshwater plant, *Littorella uniflora*, during the transition from aquatic to dry terrestrial environments. *Pl Cell Environ* 23:1041–1054
- Roiloa SR, Hutchings MJ (2012) The effects of rooting frequency and position of rooted ramets on plasticity and yield in a clonal species: An experimental study with *Glechoma hederacea*. *Ecol Res* 27:145–152
- Rufty TW, MacKown CT, Israel DW (1990) Phosphorus stress effects on assimilation of nitrate. *Pl Physiol* 94:328–333
- Sainty G, McCorkelle G, Julien M (1997) Control and spread of alligator weed *Alternanthera philoxeroides* (Mart.) Griseb., in Australia: lessons for other regions. *Wetlands Ecol Managem* 5:195–201
- Saitoh T, Seiwa K, Nishiwaki A (2002) Importance of physiological integration of dwarf bamboo to persistence in forest understorey: a field experiment. *J Ecol* 90:78–85
- Saitoh T, Seiwa K, Nishiwaki A (2006) Effects of resource heterogeneity on nitrogen translocation within clonal fragments of *Sasa palmata*: An isotopic (^{15}N) assessment. *Ann Bot (Oxford)* 98:657–663
- Sanyal SK, De Datta SK (1991) Chemistry of phosphorus transformations in soil. *Advances Soil Sci (New York)* 16:1–120
- Salzman AG, Parker MA (1985) Neighbors ameliorate local salinity stress for a rhizomatous plant in a heterogeneous environment. *Oecologia* 65:273–277

- Slade AJ, Hutchings MJ (1987) An analysis of the costs and benefits of physiological integration between ramets in the clonal perennial herb *Glechoma hederacea*. *Oecologia* 73:425–431
- Stuefer JF (1995) Separating the effects of assimilate and water integration in clonal fragments by the use of steam-girdling. *Abstr Bot* 19:75–81
- Stuefer JF (1996) Potential and limitations of current concepts regarding the response of clonal plants to environmental heterogeneity. *Pl Ecol* 127:55–70
- Stuefer, JF (1998) Two types of division of labour in clonal plants: benefits, costs and constraints. *Perspect Pl Ecol Evol Syst* 1:47–60
- Stuefer JF, During HJ, de Kroon H (1994) High benefits of clonal integration in two stoloniferous species, in response to heterogeneous light environments. *J Ecol* 82:511–518
- Treseder KK, Vitousek PM (2001) Effects of soil nutrient availability on investment in acquisition of N and P in Hawaiian rain forests. *Ecology* 82:946–954
- Vance CP, Uhde-Stone C, Allan DL (2003) Phosphorus acquisition and use: critical adaptations by plants for securing a nonrenewable resource. *New Phytol* 157:423–447
- Wang BR, Li WG, Wang JB (2005) Genetic diversity of *Alternanthera philoxeroides* in China. *Aquatic Bot* 81:277–283
- Wang N, Yu FH, Li PX, He WM, Liu J, Yu GL, Song YB, Dong M (2009) Clonal integration supports the expansion from terrestrial to aquatic environments of the amphibious stoloniferous herb *Alternanthera philoxeroides*. *Pl Biol* 11:483–489
- Wolfer SR, Straile D (2004) Spatial and temporal dynamics of clonal architecture in *Potamogeton perfoliatus* L. *Aquatic Bot* 78:307–318
- Wolfer SR, Straile D (2012) To share or not to share: clonal integration in a submerged macrophyte in response to light stress. *Hydrobiologia* 684:261–269
- Xu CY, Schooler SS, Van Klinken RD (2010) Effects of clonal integration and light availability on the growth and physiology of two invasive herbs. *J Ecol* 98:833–844
- Ye X, Gao S, Liu Z, Zhang Y, Huang ZY, Dong M (2015) Multiple adaptations to light and nutrient heterogeneity in the clonal plant *Leymus secalinus* with a combined growth form. *Flora* 213:49–56
- Yu FH, Chen YF, Dong M (2002) Clonal integration enhances survival and performance of *Potentilla anserina*, suffering from partial sand burial on Ordos plateau China. *Evol Ecol* 15:303–318
- Zhang Y, Zhang Q (2013) Clonal integration of *Fragaria orientalis* in reciprocal and coincident patchiness resources: Cost-benefit analysis. *PLOS ONE* 8:e80623
- Zhang Y, Zhang Q, Luo P, Wu N (2009) Photosynthetic response of *Fragaria orientalis* in different water contrast clonal integration. *Ecol Res* 24:617–625
- Zhou J, Dong BC, Alpert P, Li HL, Zhang MX, Lei GC, Yu FH (2012) Effects of soil nutrient heterogeneity on intraspecific competition in the invasive clonal plant *Alternanthera philoxeroides*. *Ann Bot (Oxford)* 109:813–818