Facilitation of amphibious habit by physiological integration in the clonal, perennial, climbing herb

1. Introduction

Clonal growth in plants is the asexual production of new potentially self-sufficient units, or ramets, that remain attached to the parent at least until they establish (de Kroon and van Groenendael 1997). Connected ramets within clones are often physiologically integrated via the translocation of signals or resources such as water, nutrients, and photosynthates through the connecting stems or roots (e.g., Roiloa et al. 2007; Yu et al. 2009; Xu et al. 2012; Luo et al. 2014; Chen et al. 2015). Physiological integration is well known to increase the growth of clonal fragments in heterogeneous environments where connected ramets experience contrasting conditions or levels of resource availability (Roiloa and Retuerto 2006; Song et al. 2013; Wang et al. 2017).

The ecological benefits of physiological integration within clones have mostly been tested within habitats where resources are patchy, such as habitats with scattered, nitrogen-fixing shrubs (e.g., Alpert and Mooney 1986; Alpert 1996; Roiloa et al. 2007) or gaps in vegetation (e.g., Alpert 1999; Wang et al. 2008), or salt marshes where elevational gradients in flooding create distinct zones (Evans and Whitney 1992; Amsberry et al. 2000). We hypothesized that integration between connected ramets within a clone can also increase their combined performance, a measure of total clonal performance, when ramets grow in different, adjacent habitats (Wang et al. 2009; Xiao et al. 2010; Luo et al. 2014).

One probable case is that of amphibious clonal species that grow between streams or ponds and their banks or shores; connected terrestrial and aquatic ramets are likely to experience different levels of availability of light, carbon dioxide, oxygen, and nutrients, such that translocation of resources between ramets could increase the overall performance of clones. Previous work on integration within clones of amphibious plant species spanning terrestrial and aquatic environments appears limited. Connection to unflooded ramets increased performance of flooded ramets in *Spartina alterniflora* (Xiao et al. 2010) and *Cynodon dactylon* (Li et al. 2015). Wang et al. (2009) found that ramets of the invasive, perennial, creeping herb *Alternanthera philoxeroides* submerged in water achieved greater final mass and size if connected to older ramets on open soil than if disconnected, although connection did not increase overall growth of clonal fragments. Guo and Hu (2012) and Luo et al. (2017) found that connection increased final mass in both aquatic and terrestrial ramets of *A. philoxeroides* and a creeping grass *Paspalum paspaloides*, respectively.

This study extends the realism and relevance of previous work by considering growth from a vegetated terrestrial habitat rather than a bare one into an aquatic habitat and by testing the effects of adding nitrogen (N) to the aquatic habitat. Many riparian habitats are densely vegetated, and many wetlands have been subject to eutrophication (Cronk and Fennessy 2001). Since the benefit of physiological integration tends to go up with difference between resource availability to connected ramets within a habitat (Friedman and Alpert 1991), we used the manipulation of N to test the hypothesis that the positive effect of integration between ramets in different habitats on clonal performance will be greater when resource availability differs more between habitats. Based on our two hypotheses, our main predictions were that: (1) severing the connection between terrestrial and aquatic ramets within a clonal fragment would decrease its dry mass accumulation and ramet production; and (2) the effect of severance would be greater when the level of N in the aquatic habitat was greater.

2. Materials and methods

2.1. Species and propagation

Ipomoea aquatica Forsk (Convolvulaceae, water spinach or water morning glory), is an amphibious, clonal, perennial herb native to southeastern Asia (Cook 1990). The species produces long, branching, creeping or twining and climbing, hollow stems that bear simple, alternate leaves 3–14 cm long (Wu 1979; Langeland and Craddock Burks 1998). A leaf axil can produce a new stem or a flower. *I. aquatica* reproduces sexually by seeds and asexually by rooting of stem nodes, which can then function as ramets (Harwood and Sytsma 2003). The species is cultivated as a vegetable in Asia but considered invasive in the U.S., where it has been introduced and spread into canals, lakes, and riparian areas (Langeland and Craddock Burks 1998; Harwood and Sytsma 2003; Austin 2007).

In July 2011, four to five plants of *I. aquatica* were collected from riparian zones in each of five sites in Xishuangbanna, Yunnan Province, China. Plants were collected at least 20 m apart to increase the probability that they belonged to different clones, or genets. The sites were selected for high abundance of *I. aquatica* and for growth of *I. aquatica* between terrestrial and aquatic habitats. Because *I. aquatica* is cultivated in China, sites were also chosen for low apparent human accessibility and disturbance to increase the possibility that populations were natural. Plants were propagated vegetatively in a greenhouse at the Forest Science Company, Ltd., of Beijing Forestry University.

To simulate a terrestrial, riparian environment in the experiment, four common, herbaceous species often associated with *I. aquatica* in riparian habitats were selected for planting as riparian species: *Polygonum lapathifolium* and *Commelina communis*, both annual forbs; *Echinochloa crus-galli*, an annual grass; and *Cynodon dactylon*, a perennial grass with both stolons and rhizomes. Seedlings of *P. lapathifolium* and *C. communis* were collected from riparian habitats along Baisha River in Beijing; seedlings of *E. crus-galli* were collected from Cuihu National Urban Wetland Park in Beijing, and ramets of *C. dactylon* were taken from a stock population propagated in the greenhouse. Within each species, plants of similar size were used in the experiment.

2.2. Experimental design

In June 2012, six clonal fragments each consisting of two newly produced adjacent ramets and a stem connecting them were obtained from each of seven randomly selected clones of the *I. aquatica* propagated in the greenhouse, giving a total of 42 experimental fragments. To prepare them for use, the fragments were grown in plastic boxes filled with a 1:1 mixture of river sand and peat for approximately 20 days, until each fragment had at least three expanded leaves and some elongated roots, indicating that they were fully established.

Each fragment was then transplanted into a plastic container that was 61 cm long by 41.5 cm wide by 35 cm deep, and divided crosswise with a plastic partition into two equal sections (Fig. 1). To simulate a terrestrial habitat, one section in each container was filled to a depth of 25 cm with riparian soil (1.35 ± 0.02 [mean ± SE] mg g^{-1} total N, 0.77 ± 0.03 mg g^{-1} total P, and 19.30 ± 0.43 mg g^{-1} total K, $N = 3$) taken from the upper part of a riverbank at Yanqing, Beijing, and planted with four individuals of each of the riparian species noted above. To simulate an adjacent, aquatic habitat, the other section of the container was filled to a depth of 5 cm with an equal mixture (0.82 ± 0.02 [mean ± SE] mg g^{-1} total N, 0.82 ± 0.05 mg g^{-1} total P, 19.55 ± 0.44 mg g^{-1} total K, $N = 3$) of riparian soil taken from the lower part of the same riverbank and com6(d)-218(c)16(h0(e)-2w30(s)12(o)1w)15(y2(m)07(ia)277((0)-8o)1

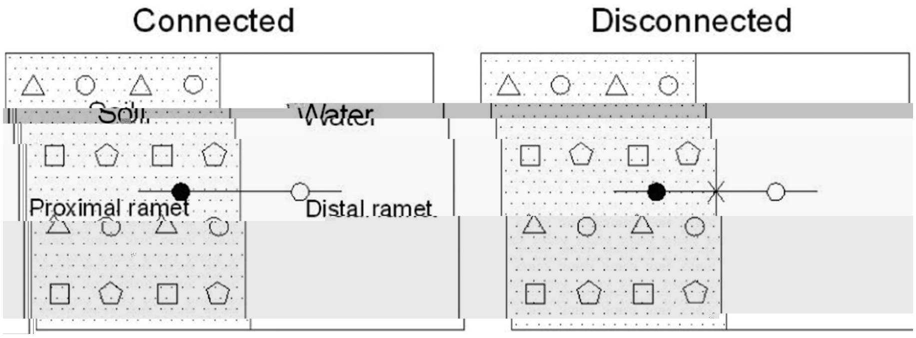

Fig. 1. Experimental design. Two-ramet clonal fragments of *Ipomoea aquatica* were planted into two-compartment containers, with the proximal, older ramet (terrestrial ramet) in a terrestrial environment and the distal, younger ramet (aquatic ramet) in an aquatic environment. The terrestrial compartment was also planted with four individuals of each of four riparian species: triangles – *Polygonum lapathifolium*, circles – *Commelina communis*, pentagons – *Echinochloa crus-galli*, and rectangles – *Cynodon dactylon*. Treatments in which the stem connecting the proximal and distal ramets was left intact or cut off were crossed with three levels of addition of N to the aquatic environment: 0, 5 or 25 mg L^{-1}.

connecting the terrestrial and the aquatic ramet of *I. aquatica* disconnected or left connected) crossed with three N addition treatments (0, 5, and 25 mg N L^{-1} added to the aquatic section of the container). Since there were seven clones, there were seven replicates for each treatment and a total of 42 containers. For the disconnected treatment, the stem internode connecting ramets was severed halfway between the ramets to prevent physiological integration. For the 5 and 25 mg N L^{-1} treatments, N was supplied as NH_4NO_3 to the aquatic section of a container only. Levels of N were intended to represent different degrees of eutrophication in Chinese wetlands (Li et al. 2010).

The four riparian species were planted into the containers on 5 July 2012. After 10 days, any plants that had not survived were replaced. Fragments of *I. aquatica* were planted into the containers on 16 July; all survived. Treatments began on 27 July. During the experiment, which lasted two months, the mean temperature in the greenhouse was 25.1 °C (range: 13.1 to 39.6 °C); light intensity at noon on sunny days varied from 350 to 560 μmol m^{-2} s^{-1}. Distilled water was added to the aquatic section of each container every 2–3 days to maintain a constant water depth; the terrestrial section was watered at the same time. This provided enough water to keep the soil in the terrestrial section moist at the surface. Twice during the experiment, the water in the aquatic section was replaced with fresh water and the N additions were repeated. The original ramets of *I. aquatica* produced new stems and ramets, which were kept within the same section of the container. In the terrestrial section, stems of *I. aquatica* twined around and climbed up stems of the other species. Five of the 42 containers or fragments were damaged during the experiment and had to be excluded from analysis: one from the 0 N, disconnected treatment, one from the 0 N, connected treatment, two from the 5 N, connected treatment, and one from the 25 N, connected treatment. In addition, the aquatic portion of a second fragment in the 0 N, disconnected treatment was damaged and excluded. The final number of replicates thus varied from five to seven for the different treatments.

2.3. Measurements and data analysis

Plants of *I. aquatica* were harvested on 28 September 2012. The clonal fragment in each container was separated into two portions, a terrestrial portion consisting of the original terrestrial ramet and any new stems and ramets it had produced, and an aquatic portion consisting of the original aquatic ramet and any new stems and ramets it had produced. Within each portion, numbers of leaves and new ramets and stem branches were counted, and total length of stems was measured. In addition, total leaf area was measured with a WinFOLIA Pro 2004a (Regent Instruments, Inc., Canada). To calculate mean petiole length and specific petiole length (cm length g^{-1} dry mass of petiole), the petioles of 10 to 20 randomly selected mature leaves from each portion were measured, dried to constant mass at 70 °C, and weighed. The rest of the portion was separated into roots, stems, leaf petioles, and leaf blades; similarly dried; and weighed. To test that simulated plant communities did not differ between connection or N treatments by the end of the experiment and potentially confound effects of treatments, plants of each of the four riparian species in the section of each container with the terrestrial portion of a fragment of *I. aquatica* were also harvested on 28 September, dried as above, and weighed.

Separate, two-way ANOVAs were used to test effects of connection and N (both treated as fixed, categorical factors) on each measure of size, mass, or morphology of the terrestrial portion, the aquatic portion, and the whole clonal fragment (i.e. two portions combined) of *I. aquatica*, and on the final total dry mass of each of the riparian species and of the riparian species combined. Degrees of freedom for different measures were 1,29, 1,30, or 1,31 for effects of connection, and 2,29, 2,30, or 2,31 for effects of N and the interaction between connection and N. Variation in the denominational degrees of freedom was due to missing data. Data were transformed to the natural logarithm or the square root before analysis as needed to improve homoscedasticity. All analyses were conducted in SPSS 17.0 (SPSS, Chicago, Illinois, USA).

3. Results

3.1. Whole fragments

All measures of final size or mass of whole fragments of *I. aquatica*, including both the terrestrial and aquatic portions, showed the same main patterns (Fig. 2). First, net cumulative growth was significantly greater when portions of a fragment were left connected than when they were disconnected (Table 1: effect of connection). In most cases, values were at least twice as high in the connected as in the disconnected treatment. Second, fragments with connected portions had much greater final size and mass in treatments with higher N, whereas fragments with disconnected portions showed relatively little effect of N (Table 1: effect of connection × N). Values in the connected treatment were 76–187% higher in the 25 than in the 0 mg N L^{-1} treatment, while values in the disconnected treatment were only 3–67% higher in the 25 than in the 0 mg N L^{-1} treatment (Fig. 2). Fragments with connected portions accumulated more than three times as much mass as fragments with disconnected portions in the highest N treatment, compared to about two times as much mass in the lowest N treatment (Fig. 2).

3.2. Terrestrial and aquatic portions within fragments

The terrestrial and aquatic portions of the *I. aquatica* fragments likewise accumulated more dry mass and had larger final size by all measures when connected than when disconnected (Fig. 3, Table 2: effect of connection). Individual portions of fragments also had larger final size by most measures at higher N. The interactive effects of connection and N on mass or measures of size were not significant (Table 2: effect of

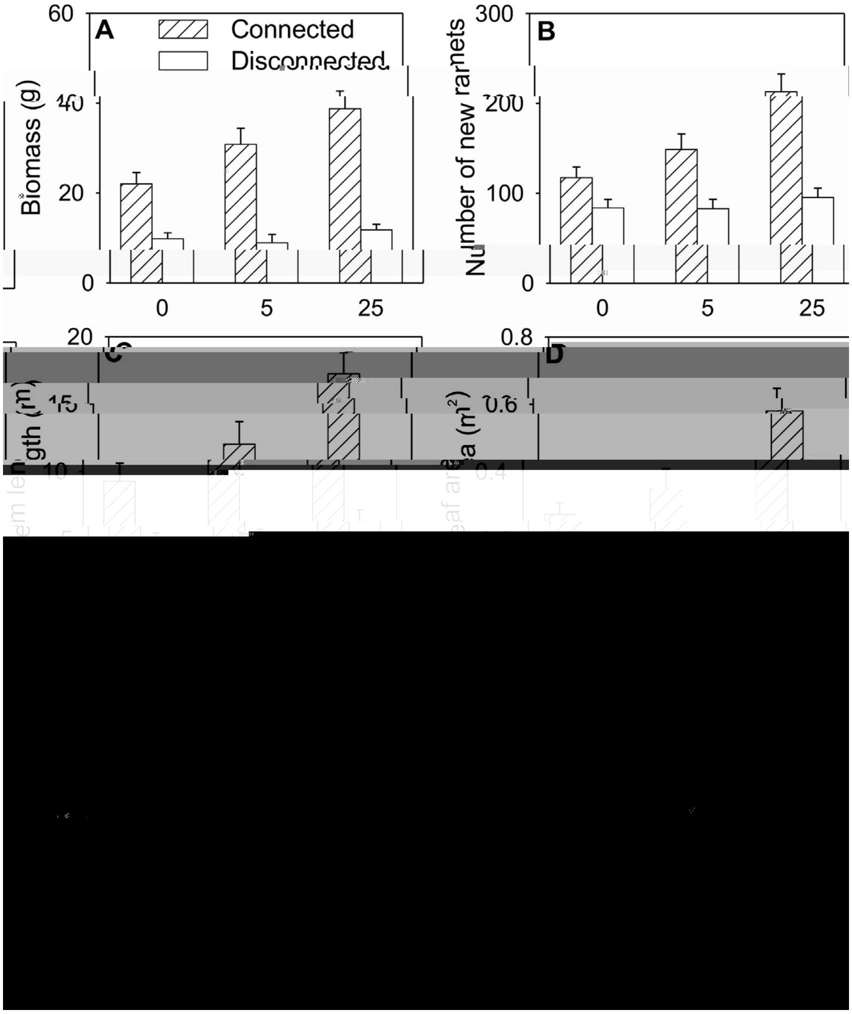

Fig. 2. Effects of connection and N on (A) final total dry mass and (B—F) measures of size of whole fragments (terrestrial and aquatic portions combined) of *Ipomoea aquatica*. Bars show mean + SE. See Table 1 for ANOVAs.

C × N, all $P > 0.05$), but response to N was nominally greater in both portions when they were connected than when they were not (Fig. 3).

Effects of connection on some measures of final morphology differed between the aquatic and the terrestrial portion of fragments (Fig. 4, Table 2). Effect of connection on root to shoot ratio was reversed in the different portions: root to shoot ratio in the terrestrial portion was higher when portions were disconnected, whereas the ratio in the aquatic portion was higher when portions were connected (Fig. 4F). Specific leaf area and specific internode length in the aquatic portion were lower when portions were connected than when they were disconnected, while connection had no effect on either measure in the terrestrial portion (Fig. 4D, E). Disconnection increased specific petiole length in both portions, but more so in the aquatic portions (Fig. 4B). These differential effects were consistent with a division of labor between connected portions of a fragment, as discussed below.

Table 1
ANOVAs for effects of connection (C), nitrogen (N), and their interaction on the final total dry mass and measures of size of the whole fragment (terrestrial and aquatic portions of a fragment combined) of *Ipomoea aquatica*. Values are F; symbols show P: *** < 0.001; ** < 0.01; * < 0.05. See text for degrees of freedom. See Fig. 2 for data.

	C	N	C × N
Total biomass	95.28^{***}	6.88^{**}	4.21^{*}
Number of new ramets	42.19^{***}	8.45^{**}	4.91^{*}
Stem length	60.16^{***}	8.60^{**}	3.60^{*}
Leaf area	71.30^{***}	9.25^{**}	6.43^{**}
Number of branches	23.15^{***}	9.28^{**}	3.96^{*}
Number of leaves	49.39^{***}	5.63^{**}	4.85^{*}

3.3. Riparian species

There was no effect of connection, N, or their interaction on the final total dry mass of any of the riparian species or of these species combined (each $P > 0.2$; Appendices S1 and S2). Final total dry mass of the riparian species was approximately 5 to 10 times greater than that of the terrestrial portions of *I. aquatica*. Approximately 59% of the final mass of the riparian species was made up by *Polygonum lapathifolium*, 22% by *Echinochloa crus-galli*, 13% by *Commelina communis*, and 6% by *Cynodon dactylon*.

4. Discussion

Results strongly supported the hypothesis that physiological integration between connected ramets in different habitats can increase the performance of clonal plants. Clonal fragments of *I. aquatica* with some ramets in a terrestrial environment and some in an aquatic one accumulated much more dry mass and grew to a much larger size when the terrestrial and aquatic portions of a fragment were left connected than when they were disconnected. By some measures, performance of connected fragments was two or three times greater than performance of disconnected ones. Such effects of connection on clonal performance seem large compared to most of those found in entirely

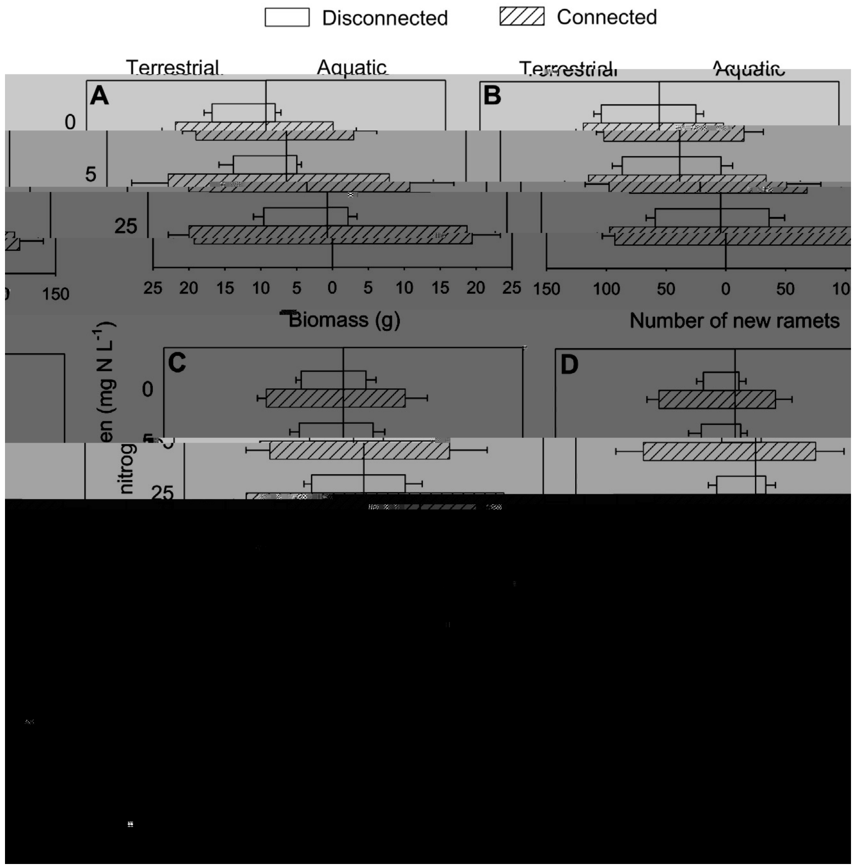

Fig. 3. Effects of connection and N on (A) final total dry mass and (B-F) measures of size of the terrestrial and aquatic portions of fragments of *Ipomoea aquatica*. Bars show mean + SE. See Table 2 for ANOVAs.

aquatic (e.g., Marba et al., 2002; Xiao et al. 2007; Schwarzschild and Zieman 2008a, 2008b; Lin et al. 2012) or entirely terrestrial environments (e.g., Peltzer 2002; Wang et al. 2008; Roiloa et al. 2014a, b). Physiological integration may thus be especially advantageous in clones that span a boundary between habitats.

Results also strongly supported the hypothesis that the positive effect of integration between ramets in different habitats on clonal performance will be greater when resource availability differs more between habitats. The effects of connection between portions of the fragments on the final total dry mass and size of fragments of *I. aquatica* were two to four times greater when the aquatic portion was given an added 25 mg N L^{-1} than when no N was added. Concentrations of N in many Chinese wetlands are in this range (Ministry of Environmental Protection of the People's Republic of China, 2015), suggesting that eutrophication of wetlands could increase the abundance of *I. aquatica*, not just in the water, but also in adjacent riparian habitats. Abundance and possibility competitive ability of amphibious clonal plants in one habitat might thus be enhanced by resource acquisition in a different habitat (Wang et al. 2009). Through eventual senescence, amphibious clones might even move resources between habitats, in similar fashion though on a very fine scale, to the ecological subsidies of nutrients or energy carried from one system to another by plants or animals (Fariña et al. 2003; Ellis et al. 2006; Kui et al. 2013; Cornelissen et al. 2014).

When two ramets of a clonal plant each experience low availability of a resource whose availability to the other ramet is high, connection between the ramets can induce a division of labor in which each ramet specializes to acquire the locally abundant resource and ramets exchange resources (Friedman and Alpert 1991; Stuefer et al. 1996; Alpert and Stuefer 1997; Hutchings and Wijesinghe 1997; Roiloa et al. 2007, 2014b). Connection between the aquatic and terrestrial portions of fragments of *I. aquatica* induced changes in root to shoot ratio indicative of a division of labor in which the aquatic ramets specialized for uptake of water or nutrients and the terrestrial ramets, able to climb on other plants, specialized for acquisition of light or CO_2. Root to shoot ratio of the aquatic portion of a fragment was about two times higher and proportion of rooted ramets was higher when the aquatic portion was connected to the terrestrial portion than when portions were disconnected (Appendix S3). Reciprocally, root to shoot ratio of the terrestrial portion was about 20–60% lower when portions were connected than when they were disconnected. Only one other study appears to have observed division of labor between large groups, rather

Table 2

ANOVAs for effects of connection (C), nitrogen (N), and their interaction on the final mass, size, and morphology of the terrestrial and the aquatic portion of the clonal fragment of *Ipomoea aquatica*. Values are F; symbols show *P*: *** < 0.001; ** < 0.01; * < 0.05; # < 0.1; ns ≥ 0.1. See text for degrees of freedom. See Figs. 3 and 4 for data.

	Terrestrial			Aquatic		
	C	N	C × N	C	N	C × N
Total biomass	17.84^{***}	1.37^{ns}	0.43^{ns}	25.67^{***}	1.90^{ns}	1.00^{ns}
Number of new ramets	11.44^{**}	1.66^{ns}	0.55^{ns}	12.18^{**}	$2.92^{\#}$	1.64^{ns}
Stem length	27.98^{***}	$2.50^{\#}$	0.89^{ns}	13.71^{**}	$2.75^{\#}$	1.07^{ns}
Leaf area	42.95^{***}	3.60^{*}	2.33^{ns}	21.72^{***}	$3.06^{\#}$	2.20^{ns}
Number of branches	9.71^{**}	4.11^{*}	0.57^{ns}	15.17^{**}	6.30^{**}	$3.24^{\#}$
Number of leaves	12.76^{**}	$2.55^{\#}$	1.72^{ns}	18.91^{***}	3.38^{*}	2.31^{ns}
Petiole length	48.40^{***}	1.88^{ns}	1.40^{ns}	16.94^{***}	1.44^{ns}	0.03^{ns}
Specific petiole length	23.50^{***}	1.04^{ns}	1.56^{ns}	19.78^{***}	1.47^{ns}	1.08^{ns}
Internode length	25.24^{***}	0.40^{ns}	0.01^{ns}	6.74^{*}	0.63^{ns}	0.05^{ns}
Specific internode length	0.19^{ns}	0.51^{ns}	0.90^{ns}	69.81^{***}	0.22^{ns}	$2.67^{\#}$
Specific leaf area	0.15^{ns}	0.47^{ns}	$2.75^{\#}$	4.57^{*}	0.67^{ns}	1.10^{ns}
Root to shoot ratio	20.01^{***}	1.79^{ns}	1.32^{ns}	12.17^{**}	4.18^{*}	0.02^{ns}

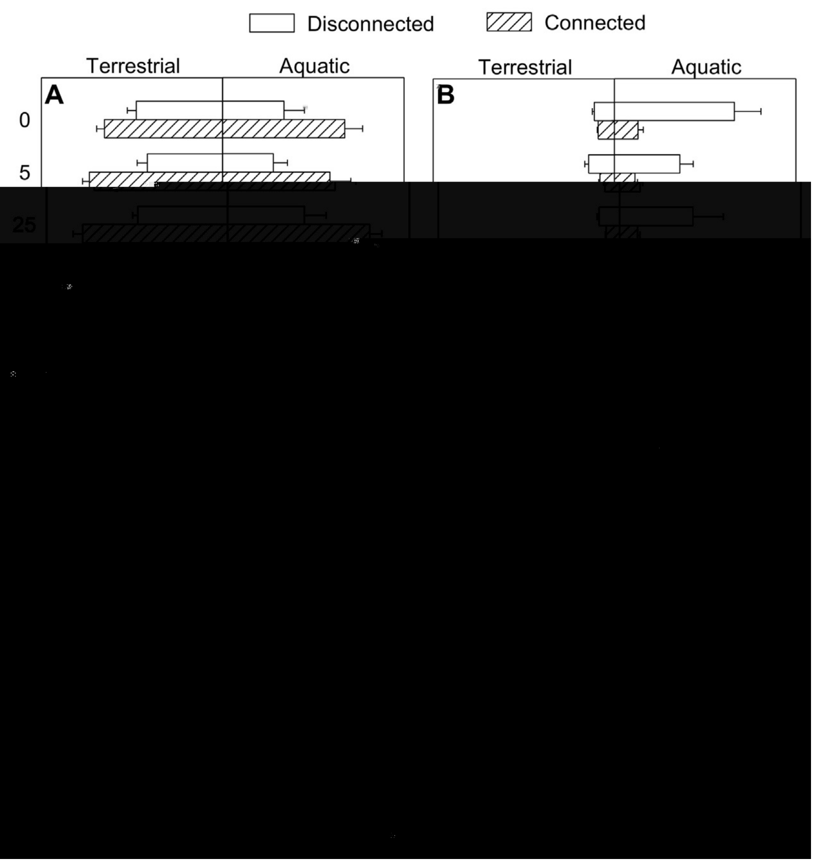

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Fig. 4. Effects of connection and N on morphological traits (mean + SE) of the terrestrial and aquatic portions of the clonal fragments of *Ipomoea aquatica*. See Table 2 for ANOVAs.

than just pairs, of established ramets (Ikegami et al. 2008). No previous study appears to have shown division of labor between connected ramets in different habitats.

A special feature of this greenhouse study was the use of relatively realistic environments that included an experimental community of potentially competing species in the terrestrial environment. The degree to which physiological integration may increase the competitive ability of clonal plants remains unclear (Wang et al. 2008; Xiao et al. 2011; Wang et al. 2016; Zhou et al. 2017). Although we did not measure competitive ability directly, connection to the aquatic portion did increase growth of the terrestrial portion of fragments, including the length of petioles and stem internodes. Elongation of petioles in other creeping, clonal plant species has been shown to confer enhanced plant performance when plants are grown together with other plants, likely due to avoidance of shade from neighbors (Huber 1996; Huber and Wiggerman 1997; Huber et al. 2008). Because stems of *I. aquatica* can also potentially avoid shade by climbing up other plants, as occurred in the terrestrial environment in this study, elongation of stem internodes may provide an additional mechanism for shade avoidance.

These strong, positive effects of connection between terrestrial and aquatic portions of fragments of *I. aquatica,* observed under relatively realistic conditions, clearly suggest that physiological integration in clonal plants can confer important ecological benefits, not just when connected ramets occur in contrasting microenvironments within a habitat, but also when they occur in contrasting, adjacent habitats. Clonal plants are particularly abundant in wetlands (Grace 1993; de Kroon and van Groenendael 1997; Song and Dong 2002; Hatton et al. 2008; Sosnova et al. 2010), and the capacity to integrate resources on land and in water could be at least partly responsible, and continued eutrophication in wetlands is expected to further increase the abundance of clonal plants in riparian habitats.

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