Clonal integration increases tolerance of a phalanx clonal plant to defoliation

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HIGHLIGHTS

- *Iris delavayi* is a phalanx clonal plant growing in subalpine grassland.
- We tested how clonal integration affects tolerance of *I. delavayi* to defoliation.
- Defoliation reduced growth of *I. delavayi*.
- Clonal integration increased tolerance of *I. delavayi* to heavy defoliation.

GRAPHICAL ABSTRACT
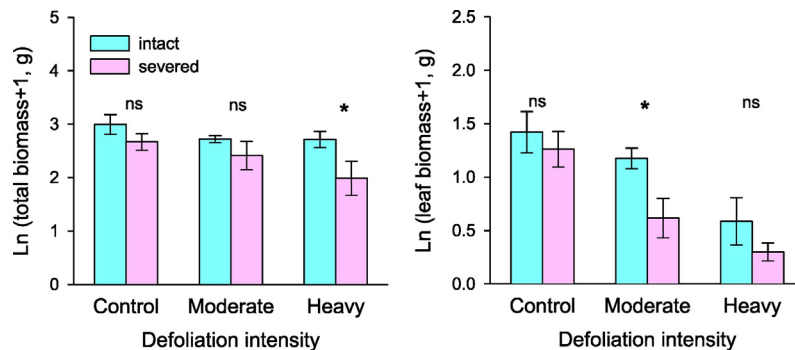
ABSTRACT

Defoliation by herbivores commonly imposes negative effects on plants, and physiological integration (resource sharing) can enhance the ability of guerilla clonal plants to tolerate stresses. Here we examined whether physiological integration can increase the ability of phalanx clonal plants to withstand defoliation. On a high mountain grassland in southwestern China, we subjected the phalanx clonal plant *Iris delavayi* within 10 cm × 10 cm plots to three levels of defoliation intensity, i.e., control (no defoliation), moderate (50% shoot removal to simulate moderate herbivory) and heavy defoliation (100% shoot removal to simulate heavy herbivory), and kept rhizomes at the plot edges connected (allowing physiological integration) or disconnected (preventing integration) with intact ramets outside the plots. Defoliation significantly reduced leaf biomass, root biomass and ramet number of *I. delavayi*. Clonal integration did not affect the growth of *I. delavayi* under control, but significantly increased total biomass, rhizome and root biomass under heavy defoliation, and leaf biomass and ramet number under moderate defoliation. We conclude that clonal integration associated with resource reallocation plays an important role in maintaining the productivity of the alpine and subalpine grassland ecosystems in SW China where clonal plants are a dominant component of the grasslands and are commonly extensively managed with moderate grazing intensity. Our results also help to better understand the adaption and tolerance of phalanx clonal plants subjected to long-term grazing in the high mountain environment.

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1. Introduction

Partial or entire defoliation by herbivores is very common in natural habitats and can greatly affect plant growth, competitive interactions, species coexistence and ecosystem functioning (Augner et al., 1997; Hartley and Amos, 1999; Hulme, 1996; Pietikäinen and Kytöviita, 2007). Many previous studies have tested the effects of different defoliation regimes on the growth of plants (Anten et al., 2003; Benot et al., 2009; Ferraro and Oesterheld, 2002; Stevens et al., 2008). At the individual species level, defoliation by herbivores has diverse consequences on plant growth and biomass allocation (Ferraro and Oesterheld, 2002; Zhao et al., 2008). Many plant species experience decreased growth after defoliation due to the loss of photosynthetic or other functional tissues (Esmaeili et al., 2009; Ferraro and Oesterheld, 2002; Li et al., 2002; Van Staalduinen and Anten, 2005).

However, plants may respond to defoliation by compensatory growth, which can alleviate the potential negative effects of defoliation (McNaughton, 1983; Van Staalduinen and Anten, 2005). The mechanisms of compensatory growth involve changes in physiology and development, as well as the modification of the environment (McNaughton, 1983). Compensatory growth following defoliation may result from the stimulation of photosynthesis of remaining green tissues (Anten and Ackerly, 2001; Detling et al., 1979), reallocation of resources (i.e. carbohydrates, water and nutrients; Briske et al., 1996; Zhao et al., 2008), and/or activation of additional meristems because of release of apical dominance (Hay and Newton, 1996; Liu et al., 2009). When compensatory growth is limited (i.e. under-compensatory growth), defoliation will decrease the growth of the plant (Li et al., 2004). Many plant species can exhibit marginal (Moser and Schütz, 2006) or even over-compensatory response to defoliation (Zhao et al., 2008). However, the magnitude of compensatory growth after defoliation strongly depends on the availability of resources such as nutrients, light and water (Anten et al., 2003; Coughenour et al., 1990), as well as the time of recovery (Oesterheld and McNaughton, 1988, 1991).

Clonal plants can produce new, genetically identical individuals (ramets) (Klimeš et al., 1997). Within a clonal network, ramets can translocate and share resources through the physical connections of stolons, rhizomes or roots (Alpert, 1991, 1996; Xu et al., 2012). Such clonal integration can increase the performance of ramets subjected to various stresses as well as the performance of the whole clone (Roiloa and Retuerto, 2007; Roiloa et al., 2010; Song et al., 2013; Wang et al., 2008). Clonal integration is also proved to be adaptive (van Kleunen, 2000). A few studies have examined the effects of clonal integration on compensatory growth of clonal plants after clipping (Liu et al., 2009; You et al., 2014). Schmid et al. (1988) showed that intact ramets can translocate assimilates, water and nutrients to support the defoliated ramets within a clone. Disconnecting rhizome between intact (undefoliated) and defoliated ramets may strongly retard the recovery or decrease the compensatory growth (Schmid et al., 1988; Wang et al., 2004).

Clonal plants can be classified into two different clonal growth forms based on inter-ramet spacing: phalanx and guerrilla (Chen et al., 2011; Humphrey and Pyke, 1998; Lovett-Doust, 1981; Ye et al., 2006). Phalanx clonal plants produce short stolon or rhizome internodes and thus closely packed ramets, while guerrilla clonal plants form long internodes and thus widely spaced ramets (Bernard, 1990; Lovett-Doust, 1981). In general, guerrilla clonal plants are advantageous over phalanx ones in exploiting open space (Humphrey and Pyke, 1998; Lovett-Doust, 1981). Guerrilla species can spread quickly and escape from less favorable patches where resources are deficient or stress is high, so that it is common in early successional stages (Bernard, 1990; Chen et al., 2011; Humphrey and Pyke, 1998; Ye et al., 2006). In contrast, phalanx species benefit from local abundant resources and tolerate more stressful conditions, so that it is more common in late successional stages (Bernard, 1990; Chen et al., 2011; Humphrey and Pyke, 1998; Ye et al., 2006). Many studies have examined effects of clonal integration

on the performance of guerilla clonal plants, but very few have examined those in phalanx clonal plants (Liu et al., 2007). Furthermore, no study has tested effects of clonal integration on compensatory growth of phalanx clonal plants subjected to grazing. Liu et al. (2007) conducted a greenhouse experiment with a phalanx clonal grass *Cleistogenes squarrosa*, and clearly showed that clonal integration can significantly benefit the growth of its ramets growing in the stressful, low nutrient conditions. We thus expect that clonal integration can also help phalanx clonal plants to tolerate heavy grazing.

Field experiments provide a more realistic test, but are more difficult to conduct and thus are usually fewer compared to greenhouse experiments. Still a number of experiments have been conducted in the field to test the effect of clonal integration (e.g. Roiloa et al., 2010; Lu et al., 2015, 2016; Yuan et al., 2017). However, no field experiment has assessed the roles of clonal integration in growth of alpine and subalpine clonal plants, which are a dominant component of the ecosystems (Körner, 1997; Yu et al., 2006). *Iris delavayi* is a phalanx clonal plant widely distributed in the area at 3000–4000 m asl. in southwestern China. In a field study, we subjected *I. delavayi* ramets within plots to three levels of defoliation intensity and kept rhizomes at the plot edges connected (i.e. to allow clonal integration) or disconnected (to prevent integration) with intact ramets outside plots. Specifically, we tested the hypothesis that clonal integration will improve the performance of *I. delavayi* in response to defoliation, especially when the defoliation intensity is heavy.

2. Materials and methods

2.1. The study site

The experiment was carried out in a subalpine grassland on the east-facing slope of Balang Mountain (30°53′4.164″ E, 102°58′19.992″ N, 3481.8 m asl.) in Wolong Nature Reserve in Wenchuan county, Sichuan Province, Southwestern China. This area belongs to subtropical monsoon moist climate. Mean annual temperature is 8.5 ± 0.5 and mean annual precipitation is 862–962 mm (Cai et al., 2011; Song et al., 2006).

The subalpine grassland is dominated by *Euphorbia micractina* Boiss., *Caltha fistulosa* Schipcz. and *Geranium strictipes* R. Knuth. The common species include *Iris delavayi* Mich., *Polygonum viviparum* Linn., *Fragaria vesca* Linn., *Trollius buddae* Schipcz., *Anaphalis nepalensis* (Spreng.) Hand.-Mazz., *Epilobium brevifolium* subsp. *trichoneurum* (Hausskn.) Raven, *Polygonatum curvistylum* Hua, *Anemone rivularis* Buch.-Ham. and *Angelica nitida* Wolff.

2.2. The species

Iris delavayi Mich. is a rhizomatous perennial herb of the Iridaceae family and native to southwestern China (Wu and Raven, 2003). It is widely distributed at 3000–4000 m asl. in Sichuan, Yunnan and Tibet (Zhao et al., 2000). *Iris delavayi* is capable of clonal growth by forming very short and non-directional rhizomes (Song et al., 2002), and off-spring ramets are developed very close to the mother ramets. Under common conditions (without strong disturbance), each clone of *I. delavayi* will develop into a roughly circular clump consisting of many ramets so that this species shows a typical phalanx growth form (Lovett-Doust, 1981; Song et al., 2002). The diameter of the clones can reach up to 3 m (personal observation). *Iris delavayi* blooms in summer and produces variable seeds in autumn, and it is a species of cold-resistance and light-demanding (Wu and Raven, 2003).

2.3. Experimental design

The experiment took a randomized block design with three levels of defoliation intensity crossed with two levels of clonal integration (without vs. with integration by severing rhizomes or not). The treatments were performed on six plots of 10 cm × 10 cm located at the inner
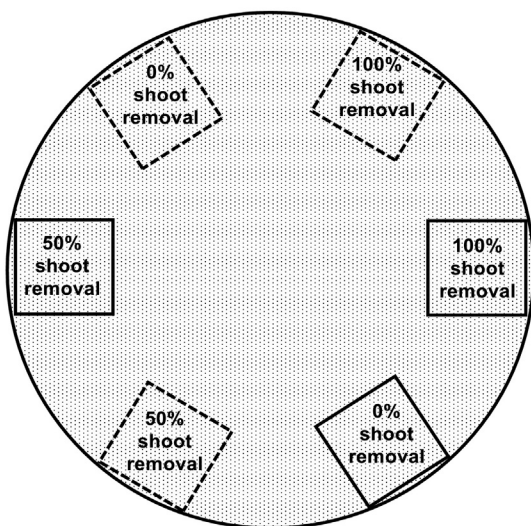
edge of each of eight clones of *I. delavayi*, with each clone being treated as a block (Fig. 1). Within each clone, the six treatments were randomly assigned to the six plots (Fig. 1). The eight clones differed in diameter, but each clone had a diameter of >1.5 m. Adjacent clones were at least 20 m apart, and adjacent plots within each clone were at least 15 cm apart. As the diameters of the clones were much larger than the size of the treatment plots, resource translocation between plots was expected to be little.

The three treatments of defoliation intensity were control (no shoot removal), moderate (removing 50% leaves of each ramet) and heavy (removing 100% leaves of each ramet). The defoliation treatments were to simulate different levels of grazing intensity by domestic livestock (mainly yaks) as they commonly eat *I. delavayi* when palatable forage is insufficient. Defoliation was carried out only once at the beginning of the experiment. For treatments without clonal integration, we severed rhizome connections along the four edges of the plots to prevent integration between ramets inside and outside the plots. We inserted a sharp blade along the edges of the plots to a depth of 20 cm, which was deep enough to sever most of the rhizomes based on pilot digging. For treatments with clonal integration, we disturbed the edges of the plots in the same way but left the rhizomes intact. The experiment lasted four months from 9 June to 9 October 2015. According to the meteorological data from the ecological station in Wolong Nature Reserve, mean temperature was 8.8 °C, mean humidity was 84.8% and mean precipitation was 1022.8 mm from April to October in 2015.

2.4. Measurements and data analysis

Before harvest, we measured the height of each ramet and counted the number of ramets in each plot. Then we harvested all plants of *I. delavayi* in each plot, divided them into leaves, roots and rhizomes, oven-dried at 70 °C for 48 h and weighed. We calculated mean ramet height, biomass per ramet and root to shoot ratio in each plot.

We used two-way ANOVA with a randomized block design to test the effects of clonal integration and defoliation on the growth (total biomass, leaf biomass, rhizome biomass, root biomass and number of ramets) and morphology (ramet height and biomass per ramet) of *I. delavayi* in the plots. We further conducted linear contrasts to test

Fig. 1. Experimental design. Six plots (squares) of 10 cm × 10 cm were established at the inner edge of each of the eight clones (circle) of *Iris delavayi* (diameter > 1.5 m). Three plots (squares with dotted lines) were randomly selected and rhizomes connections along the edges of the plots were severed; in the other three plots (squares with solid lines), rhizome connections were remained intact. The three plots of both the severed and intact rhizome treatments were randomly assigned to three clipping treatments, i.e., 0 (control), 50% (moderate) or 100% (heavy) shoot removal.

the effect of clonal integration at each level of defoliation (Sokal and Rohlf, 1981), and used Duncan methods to compare grand means among the three defoliation treatments. Before analysis, all data except biomass per ramet and root to shoot ratio were log-transformed to meet the assumptions of normality and homoscedasticity. All data were analyzed using SPSS 16.0 (SPSS, Chicago, IL, USA).

3. Results

3.1. Effects of clonal integration and defoliation on growth measures

Clonal integration (rhizome connection) significantly affected the growth measures of *I. delavayi* (Table 1). Clonal integration significantly increased total biomass, rhizome biomass and root biomass under heavy defoliation (Fig. 2A, C and D) and leaf biomass and number of ramets under moderate defoliation (Fig. 2B and E). Defoliation significantly affected leaf biomass, root biomass and number of ramets, but not total biomass or rhizome biomass (Table 1). Leaf biomass of *I. delavayi* decreased markedly with increasing defoliation intensity (Fig. 2B). Compared to the control (no defoliation), root biomass of *I. delavayi* was significantly smaller under heavy defoliation, but not under moderate defoliation (Fig. 2D). Number of ramets of *I. delavayi* was significantly smaller under both moderate and heavy defoliation than under the control, but it did not differ between moderate and heavy defoliation (Fig. 2E).

3.2. Effects of clonal integration and defoliation on morphological measures

Clonal integration significantly increased mean ramet height of *I. delavayi*, but only under moderate defoliation (Fig. 3A, Table 2). Ramet height decreased markedly with increasing defoliation (Table 2, Fig. 3A). Biomass per ramet was influenced by neither clonal integration nor defoliation (Table 2). Root/shoot ratio was greatly increased by defoliation, but was not influenced by clonal integration (Table 2, Fig. 3C).

4. Discussion

While benefits of clonal integration have been repeatedly shown in guerilla clonal plants (e.g. Song et al., 2013; You et al., 2013), its effects in phalanx clonal plants have been understudied (Liu et al., 2007). We found that clonal integration significantly improved total biomass of *I. delavayi* suffered from heavy defoliation, but had no significant effect under moderate or no defoliation. These results support our hypothesis and suggest that clonal integration can help phalanx clonal plants to tolerate heavy grazing.

Compensatory growth can help plants to mitigate negative effects of defoliation on plants (Ferraro and Oesterheld, 2002; Xu et al., 2012). In addition to the function as the physical connection and thus the channel of resource translocation between ramets, rhizomes also function as a storage tissue for carbohydrates and meristems (Wang et al., 2004). Thus, they are important for compensatory growth and may potentially promote growth of plants after defoliation (Wan and Sosebee, 2002). In the present study, defoliation only marginally significantly ($P = 0.07$) decreased total biomass of *I. delavayi*. This result may be mainly because

Table 1
Two-way ANOVA for the effects of clonal integration, defoliation and their interaction on the growth measures of *Iris delavayi*. Values are in bold where $P < 0.05$.

| Variable	Integration (I)		Defoliation (D)		I × D		Block	
	$F_{1,34}$	P	$F_{2,34}$	P	$F_{2,34}$	P	$F_{7,34}$	P
Total biomass	**8.0**	**0.008**	2.9	0.070	0.6	0.554	1.0	0.438
Leaf biomass	**7.2**	**0.011**	**16.0**	**<0.001**	1.0	0.373	1.3	0.264
Rhizome biomass	**7.0**	**0.012**	1.1	0.344	0.6	0.555	0.9	0.551
Root biomass	**6.7**	**0.014**	**4.4**	**0.020**	1.0	0.393	**3.0**	**0.015**
No. of ramets	**7.6**	**0.009**	**8.2**	**0.001**	2.7	0.083	1.4	0.235
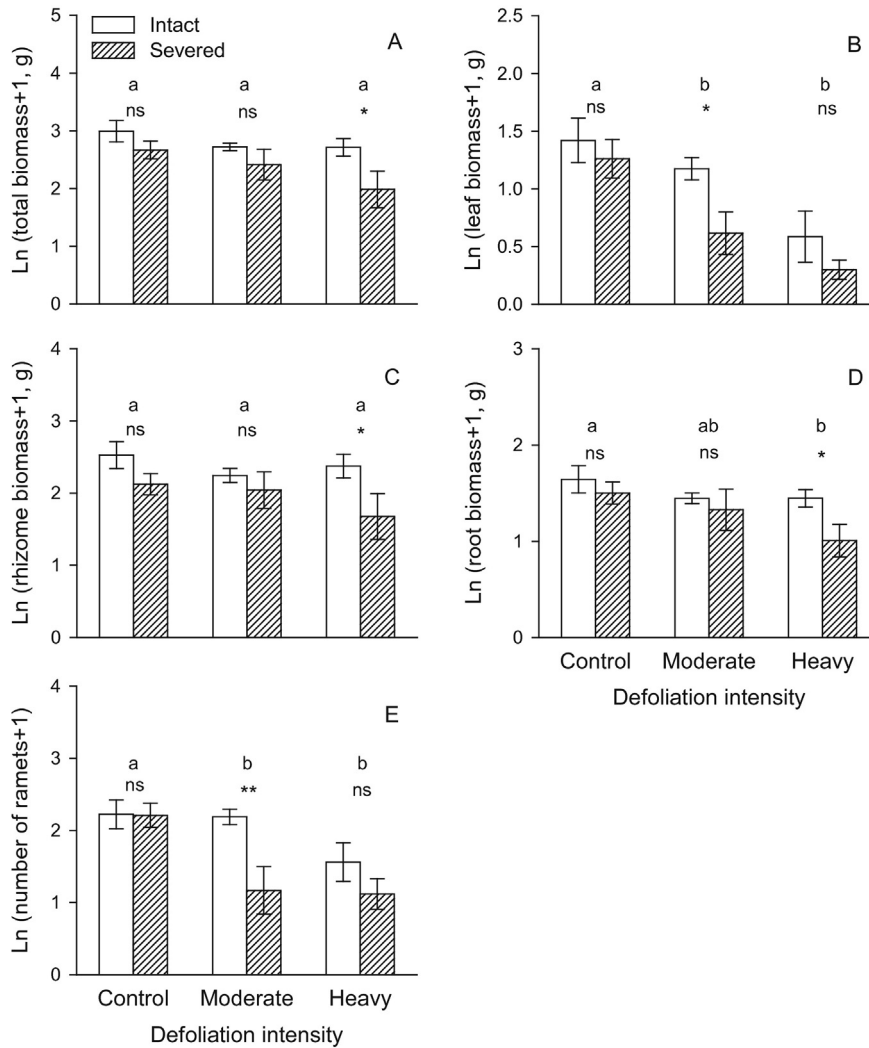
Fig. 2. Effects of clonal integration and defoliation on the growth measures of *Iris delavayi* in the plots. Mean values ($\pm$SE; $n = 8$) of (A) total biomass, (B) leaf biomass, (C) rhizome biomass, (D) root biomass and (E) number of ramets are given. *Symbols* show which means differed between integration treatments on each of the three defoliation intensities: ns means $P > 0.05$, *$P = 0.01$–0.05, **$P = 0.001$–0.01. Different *small letters* indicate that grand means differ significantly between the defoliation treatments.

defoliation had no significant effect on rhizome biomass, which had a much greater biomass proportion than leaves. However, leaf biomass reduced by about 50% under moderate defoliation and about 70% under heavy defoliation (Fig. 2B). The reduction was likely to be caused directly by aboveground removal as the regrowth of this forb was not so rapidly as many grasses. It was also likely to be caused indirectly by reduced leaf regrowth due to decreased availability of resources, especially photosynthates, because defoliation reduced photosynthetically active organs and thus decreased photosynthesis and photosynthate production (Ferraro and Oesterheld, 2002; Li et al., 2002; Van Staalduinen and Anten, 2005). However, the design of this experiment does not allow us to separate these two possible effects.

More interestingly, we found that clonal integration improved the growth of *I. delavayi* subjected to heavy defoliation. This was likely because the ramets of *I. delavayi* outside the plots translocated photosynthates to the ramets inside the plots and thus supported their growth. The connections between ramets inside and outside the plots also increased the production of new ramets, but the effects were only significant under moderate defoliation (Fig. 2E). Benefits of clonal integration on the growth of ramets growing in stressful conditions have also been shown in a number of guerilla clonal plant species from various habitats (e.g. Alpert, 1991; Roiloa et al., 2014; Stuefer et al., 1994; You et al., 2014). Our results suggest that clonal integration can also increase the capacity of phalanx clonal plants to tolerate environmental stress.

Clonal integration significantly increased total biomass, rhizome and root biomass of *I. delavayi* subjected to heavy defoliation, but had no significant effect on those variables under moderate defoliation. These results suggest that the positive effect of clonal integration on plant growth increased when the level of stress and thus the unbalance of the source-sink relationship increased (Friedman and Alpert, 1991; Gruntman et al., 2016). Similarly, Liu et al. (2009) showed that clonal integration only increased the growth of heavily defoliated ramets of the clonal plant *Bromus ircutensis*, but not that of the moderately defoliated ramets. On the other hand, clonal integration significantly increased the growth of both moderately and heavily defoliated ramets of *Psammochloa villosa* (Liu et al., 2009). Thus, the effect of clonal integration on plant growth depends on both the defoliation level and the identity of plant species.

Both moderate and heavy defoliation decreased ramet production of *I. delavayi*. Various responses of ramet number to clipping were reported for different species. For instance, defoliation did not affect ramet number of *Leymus chinensis* (Benot et al., 2009; Wang et al., 2004), but increased that in five caespitose grasses (Richards et al., 1988). In *Cyperus esculentus*, effects of clipping on ramet number depended on nutrient availability: clipping increased ramet number under high nutrient availability, but had little effect under low nutrient availability (Li et al., 2004). In the present study, while moderate defoliation decreased ramet production of *I. delavayi* without clonal integration, it
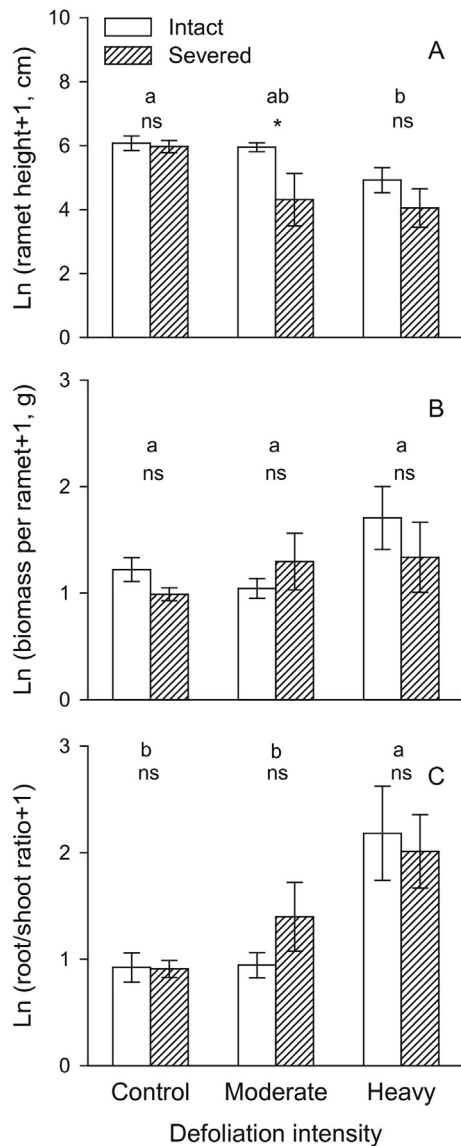
Fig. 3. Effects of clonal integration and defoliation on morphological measures of *Iris delavayi*. Mean values (±SE; n = 8) of (A) ramet height, (B) biomass per ramet and (C) root/shoot ratio are given. *Symbols* show which means differed between integration treatments on each of the three defoliation intensities: ns means *P* > 0.05, *P = 0.01– 0.05, **P = 0.001–0.01. Different *small letters* indicate that grand means differ significantly between the defoliation treatments.

had no effect with clonal integration. Consequently, clonal integration significantly increased ramet number of *I. delavayi* under moderate defoliation. This result agrees with a recent meta-analytical study showing that clonal integration generally increased asexual production of clonal plants (Song et al., 2013). However, under heavy defoliation, clonal integration did not significantly increase ramet production of *I. delavayi* although it increased its biomass. One likely explanation is that heavy

defoliation greatly restricted the production of new meristems and thus new ramets of *I. delavayi* so that resource translocated from undefoliated ramets outside the plots could only be used for the regrowth of the damaged ramets, but not for the production of new ramets.

Clonal integration significantly increased ramet height under moderate defoliation, but had little effect on biomass per ramet, implying an inconsistent effect of clonal integration on these two measures of ramet size. The unresponsiveness of biomass per ramet under moderate defoliation to clonal integration was because clonal integration increased both total biomass and ramet number (Fig. 1). Our results suggest that clonal integration can also shape individual ramet size, but such an effect may depend on what size measure is considered.

We conclude that clonal integration plays important roles in phalanx clonal plants and that it can serve as an additional mechanism of compensatory growth for defoliated phalanx clonal plants. Phalanx clonal plants are an important component of many types of grasslands subjected to heavy grazing (Humphrey and Pyke, 1998; Song et al., 2002). Our results suggest that clonal integration may help these plants to tolerate grazing and thus may confer them with competitive advantages over non-clonal plants, which may further affect competitive interactions and species coexistence in these grasslands.

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Table 2
Two-way ANOVA for the effects of clonal integration, defoliation and their interaction on the morphological measures of *Iris delavayi*. Values are in bold where *P* < 0.05.

Variable	Integration (I)		Defoliation (D)		I × D		Block	
	$F_{1,34}$	P	$F_{2,34}$	P	$F_{2,34}$	P	$F_{7,34}$	P
Ramet height	**6.0**	**0.020**	**6.2**	**0.005**	1.6	0.221	1.0	0.463
Biomass per ramet	0.4	0.521	2.2	0.129	1.1	0.333	1.1	0.359
Root/shoot ratio	0.2	0.669	**13.1**	**<0.001**	0.9	0.426	**2.5**	**0.033**

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