



Clonal integration increases tolerance of a phalanx clonal plant to defoliation



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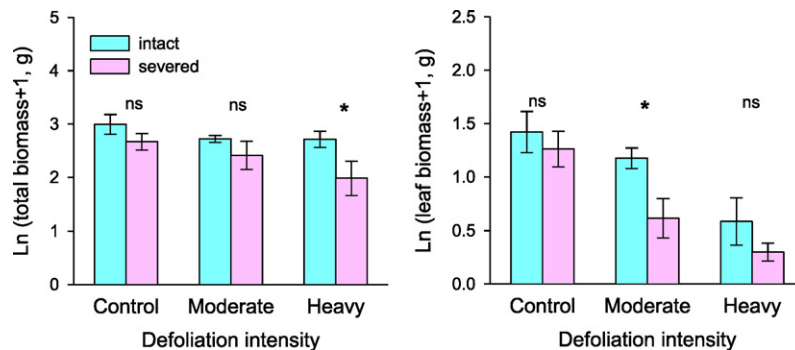
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HIGHLIGHTS

- *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



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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 adaptation 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 Oosterheld, 2002; Stevens et al., 2008). At the individual species level, defoliation by herbivores has diverse consequences on plant growth and biomass allocation (Ferraro and Oosterheld, 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 Oosterheld, 2002; Li et al., 2002; Van Staaldunin and Anten, 2005).

However, plants may respond to defoliation by compensatory growth, which can alleviate the potential negative effects of defoliation (McNaughton, 1983; Van Staaldunin 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 (Oosterheld and McNaughton, 1988, 1991).

Clonal plants can produce new, genetically identical individuals (ramets) (Klimesš 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 guerrilla 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 offspring 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

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