Flora 205 (2010) 399–403

Contents lists available at ScienceDirect

Flora

journal homepage: www.elsevier.de/flora

Clonal integration increases performance of ramets of the fern *Diplopterygium glaucum* in an evergreen forest in southeastern China

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ARTICLE INFO

Article history:
Received 24 February 2009
Accepted 8 May 2009

Keywords:
Clonal integration
Pteridophyte
Resource sharing
Rhizome severing
Subtropical forest
Survivorship

ABSTRACT

Physiological integration is a major ecological advantage of clonal growth in angiosperms. Clonal growth is also common in pteridophytes, but almost no study has tested whether clonal integration increases performance in ramets of pteridophytes in natural populations. To test this hypothesis and also whether the positive effect of integration is greater on smaller ramets, we severed the connecting rhizomes of individual ramets of the common, understory fern *Diplopterygium glaucum* in an evergreen, broadleaf forest in southeastern China. In another experiment, we severed rhizomes around the edges of small plots each containing several ramets. After 19.5 weeks, survival was 100% in intact individual ramets but only 27% in severed ones. Among surviving ramets, final dry mass and lamina mass were also less in severed than in intact ramets, though stalk, rhizome, and root mass and maximum quantum yield of PSII (F_v/F_m) were not reduced. Individual ramets with fewer stalk nodes had lower dry mass but were not more affected by severing than ramets with more stalk nodes. Severance around the edge of plots did not significantly affect the combined final mass of the ramets within a plot. We conclude that clonal integration can have significant positive effects on both survival and growth of individual ramets of ferns in natural populations.

Introduction

Many angiosperms have the capacity for clonal growth, in which a plant and its vegetative offspring remain connected by stems or roots at least until the offspring establish (de Kroon and van Groenendael, 1997). A major ecological advantage of clonal growth is physiological integration between connected ramets, including translocation of resources such as carbohydrates, water, and nutrients (Alpert et al., 2003; Gómez et al., 2007; Jónsdóttir and Watson, 1997; Nilsson and D'Hertefeldt, 2008; Zhang and He, 2009). Evidence that clonal integration can increase the performance of clonal angiosperms comes from numerous studies in which the prevention of integration by severing connections between ramets decreases survival, growth, or further vegetative reproduction (Roiloa et al., 2007; Yu et al., 2008). A few studies have also shown effects of connection on physiological parameters such as capacity for resource uptake or photosynthesis (de Kroon et al., 1996; Nielsen and Pedersen, 2000; Roiloa et al., 2007; Wang et al., 2008).

Although many pteridophytes also show clonal growth, often via rhizomes (Carlquist and Schneider, 2001; Klimeš et al., 1997; Lu, 2007), much less is known about the effects of clonal integration on their performance, especially in pteridophytes other than lycopods. A number of studies have demonstrated extensive sharing of resources between ramets in lycopods (Callaghan, 1980; Carlsson et al., 1990; Headley et al., 1985, 1988a, b). Two papers have reported that severing connections in natural populations of lycopods in deciduous forests in the eastern US increased the mortality of ramets (Lau and Young, 1988; Railing and McCarthy, 2000).

Another open question in clonal plant biology is the degree to which clonal integration is mutualistic in connected ramets in natural populations. Greenhouse and garden experiments show that connection between ramets given different levels of a resource generally increases the performance of the ramets given the lower level but not of the ramets given the higher level (Alpert, 1999; Chen et al., 2006; D'Hertefeldt and Falkengren-Grerup, 2002). This suggests that integration may benefit only certain ramets in a clone in habitats where a single resource is patchy. Similarly, ramets whose size or rooting depth

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doi:10.1016/j.flora.2009.12.018

gives them greater access to resources may subsidize connected, smaller or more shallowly rooted ramets in natural populations (Alpert, 1990, 1996; Marshall and Anderson-Taylor, 1992; Zhang and He, 2009).

We therefore hypothesized that (1) clonal integration increases performance of ramets in natural populations of pteridophytes, as measured both by growth and physiology, and that (2) this positive effect of integration is greater in smaller ramets. To test these hypotheses, we conducted two experiments on a common fern, one at the level of individual ramets and one at the level of small groups of neighboring ramets. We predicted that (1) severing the connecting rhizomes to a ramet would decrease its survivorship, accumulation of dry mass, and photosynthetic capacity, and that (2) these effects of severing would be greater in ramets with fewer stalk nodes.

Material and methods

The species

Diplopterygium glaucum (Thunb. ex Houtt.) Nakai (Gleicheniaceae), formerly called *Gleichenia glauca* Hook or *Hicriopteris glauca* (Thunb.) Ching, is a perennial, terrestrial fern that grows clonally via rhizomes that bear vertical, perennial fronds (i.e., ramets) with adventitious roots (Lu, 2007). The rhizomes are about 3 mm in diameter (Qian and Chen, 1959), and the inter-ramet distance is on average 8.2 cm (n=507, S.E.=0.199; G.-L. Yu, Y.-B. Song, and F.-H. Yu unpublished data). The stalk of the frond is pseudodichotomous at the first node, producing a pair of opposite rachises and a bud between them. After the rachises grow into pinnae, the bud produces another internode and node with a new pair of rachises and a bud, and the process repeats. *D. glaucum* mainly inhabits the understories of evergreen forests in mountain ravines at elevations below 1500 m in much of southeast China (Qian and Chen, 1959).

Study area

The study site was located in an evergreen, broadleaf forest (29°14′29.5″N–29°14′55.8″N, 118°06′31.4″E–118°08′06.8″E, 351–633 m a.s.l.) in the Gutian Mountain National Nature Reserve in Zhejiang Province, China. The study site has a subtropical, moist, monsoon climate, with mean annual precipitation of 1964 mm, temperature of 15.3 °C, 1334 h of sunlight, and frost-free period of 250 days (Ding et al., 2001). *D. glaucum* is one of the dominant understory herbs in the forest.

Individual ramet experiment

For the experiment on individual ramets, we haphazardly selected 70 ramets of *D. glaucum* with 1 stalk node and 64 with > 1 stalk node shortly after the start of the growing season, on 17–18 May 2008. Ramets were at least 1 m apart, and it was assumed that each ramet came from a different rhizome. Half of the ramets in each size class were randomly assigned to each of the two treatments, severed or intact. For the severed treatment, the rhizome at the base of each ramet was carefully excavated and cut 4 cm away from the base in both the distal and proximal directions, after which the soil was replaced. Consider the average distance (8.2 cm) between adjacent ramets and the thin rhizome diameter (about 3 mm), it is unlikely that a cut 4 cm away from the ramet base would bring much reserve loss to the target ramets. This means that the severance treatment mainly functioned to prevent resource sharing (i.e., physiological integration) between the target ramets and the others. For the intact treatment, rhizomes were exposed and reburied without being cut.

After 137 days on 1–2 October, near the end of the growing season, we measured the maximum quantum yield (F_v/F_m) of photosystem II (PSII) on a fully developed, healthy pinna at the upper node of each of the ramets, using a portable chlorophyll fluorometer (Fluorescence Monitoring System 2, Hansatech, UK; saturation pulse method). Measurements were made at 0800–1000 h, after a preliminary, dark adaptation period of at least 30 min (Maxwell and Johnson, 2000). We then harvested each ramet, including the portions of the rhizome within 4 cm of the base of the frond of each intact ramet. Laminas, stalks, rhizomes, and roots were dried separately at 70 °C for 48 h, and weighed. Final sample sizes were 57 intact and 56 severed ramets, because 10 intact and 6 severed ramets could not be relocated at the end of the treatments and 5 additional severed ramets were discovered to have an uncut connection.

Effects of severance (intact or severed) and size (1 or > 1 node) on survivorship were tested using logistic regression (GENMOD procedure with a logit link function; SAS Institute Inc., 1999). Differences in F_v/F_m and final dry mass were tested in separate ANOVAs with severance and size as fixed effects.

Plot experiment

For the experiment in plots, we randomly located 7 pairs of 50 cm × 50 cm plots with 5–7 ramets of *D. glaucum* each; plots within pairs were 2–4 m apart. On 16 May 2008, the soil was cut down to a depth of 30 cm with a sharp blade around the perimeter of one plot in each pair, chosen at random, a depth sufficient to sever all rhizomes of *D. glaucum* crossing into or out of the plot. On 1–2 Oct 2008, we harvested all the ramets in each plot as described above. We used paired t-tests to compare the combined dry mass of the ramets in each plot between the severed and intact treatments.

Results

In the experiment on individual ramets, severing rhizomes decreased the survivorship of ramets by 73% (Fig. 1; χ^2=82.91,

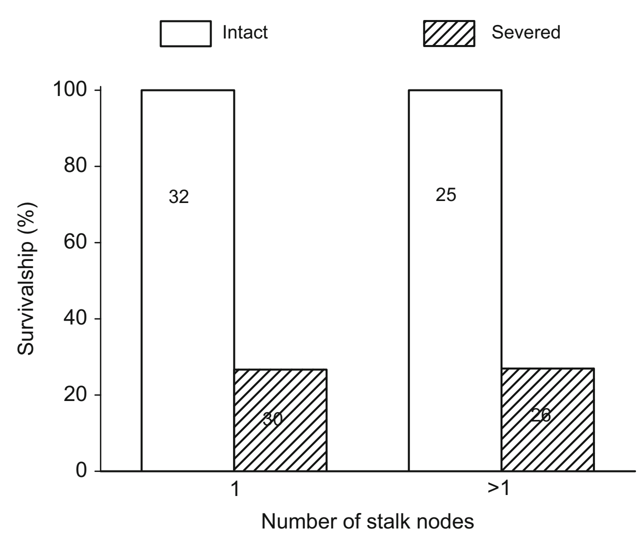

Fig. 1. Survivorship of the intact and severed *D. glaucum* ramets of different sizes (1 or > 1 stalk node). Numbers within the bars are the final number of replicates in the analysis.