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Consequences of ramets helping ramets: No damage and increased nutrient use efficiency in nurse ramets of *Glechoma longituba*

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Abstract

Source–sink relationships determine the transfer of resources among interconnected ramets of clonal plants and these relationships depend on resource regimes experienced by ramets. We hypothesized that if ramets growing in nutrient-richer patches support ramets in nutrient-poorer patches, then this support would weaken the performance of supporters themselves. This hypothesis was tested in an experiment, in which two interconnected ramet-groups of *Glechoma longituba* were subjected to four levels of nutrient-patch contrast. For nurse ramets, midday leaf water potential, net photosynthetic rate, fluorescence yield, specific root length, biomass, and root weight ratio remained unchanged along the gradient of patch contrast, indicating that no damage occurs to these ramets. Nitrogen use efficiency and phosphorus use efficiency of nurse ramets significantly increased with increasing patch contrast, suggesting that these increases may allow nurse ramets from habitats higher in patch contrast to have a greater capacity for export of nutrients than those ramets from habitats lower in patch contrast. In addition, we discuss the likely implications of these findings.

Keywords: Chlorophyll fluorescence; Growth and allocation; Midday leaf water potential; Nutrient use efficiency; Patch contrast; Photosynthesis

Introduction

In natural habitats, soil nutrients essential for plants (e.g. nitrogen (N), phosphorus (P), and potassium (K)) are heterogeneously distributed, thereby resulting in resource patchiness with favorable and unfavorable microhabitats (Hodge, 2004; Huber-Sannwald and Jackson, 2001; Hutchings and de Kroon, 1994; Hutchings and Wijesinghe, 1997; Kolasa and Pickett, 1991; Stuefer, 1996). Patch contrast refers to the degree of difference between patches, and is among the basic traits of heterogeneity (He et al., 2004; Jackson and Caldwell, 1993; Kotliar and Wiens, 1990; Stuefer, 1996; Wijesinghe and Hutchings, 1999). Since clonal plants usually have ramets in different resource patches, it is necessary for them to effectively cope with patchy resources (Alpert, 1999; de Kroon et al., 2005; Stuefer, 1996).

Resource sharing (i.e. the translocation of resources among interconnected ramets) has long been recognized as an adaptive strategy through which clonal plants can deal with resource patchiness and benefit from such habitats (Alpert, 1991, 1996; Alpert and Mooney, 1986;

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de Kroon et al., 2005; Evans, 1991; Friedman and Alpert, 1991; Liu et al., 2007). Habitat patchiness can induce such resources as nutrients and photosynthate to be transported from the sources to sinks within a clone, enabling it to maximize resource uptake (Farley and Fitter, 1999; Huber-Sannwald and Jackson, 2001; Hutchings and Wijesinghe, 1997; Stuefer, 1996).

The aim of this paper is to investigate how soil nutrient patches affect the growth and physiology of clonal fragments of *Glechoma longituba* L., which has a high capacity for resource sharing (Liao et al., 2003) and is distributed in a wide range of habitats (e.g. forests, roadsides or creeks) in tropical, subtropical, and temperate areas in China (Wu and Chen, 1974). It is most likely that some *G. longituba* ramets grow in habitats higher in patch contrast and others grow in habitats lower in patch contrast. Source–sink relationships, determining resource sharing, are associated to patch contrast (Marshall, 1990; Pitelka and Ashmun, 1985). Here, we hypothesized that if ramets growing in nutrient-richer patches help those ramets in nutrient-poorer patches, then this help would weaken the performance of supporters themselves.

To test this, we conducted an experiment in which two interconnected ramet-groups of *G. longituba* were subjected to four levels of nutrient-patch contrast, and analyzed midday leaf water potential, net photosynthetic rate, fluorescence yield, specific root length, biomass, root weight ratio (RWR), and N and P use efficiency (PUE) of nurse ramets. This hypothesis predicts (i) that the overall performance of nurse ramets may decrease with increasing patch contrast and (ii) that increased patch contrast may induce compensatory responses, thereby mitigating the risk of nutrient sharing.

Methods

G. longituba plants were subjected to four levels of nutrient-patch contrast (Fig. 1). The experiment was started with size-similar clonal fragments consisting of two interconnected ramets, which were derived from the clones of *G. longituba*. Although it is most likely that there exist ecotypic differences between populations of *G. longituba* due to wide distribution, here we chose only one population because of limitation of greenhouse space. Size-similar ramet pairs, each ramet with two leaves (about 3–4 cm height), were grown in a pair of 60 cm length × 20 cm width × 25 cm height plastic trays filled with pure river sand. This sand was chosen because its texture (e.g. grain size) is homogeneous and its contents of N and P were <0.003%, thereby minimizing the effects of substrate per se. The experiment was

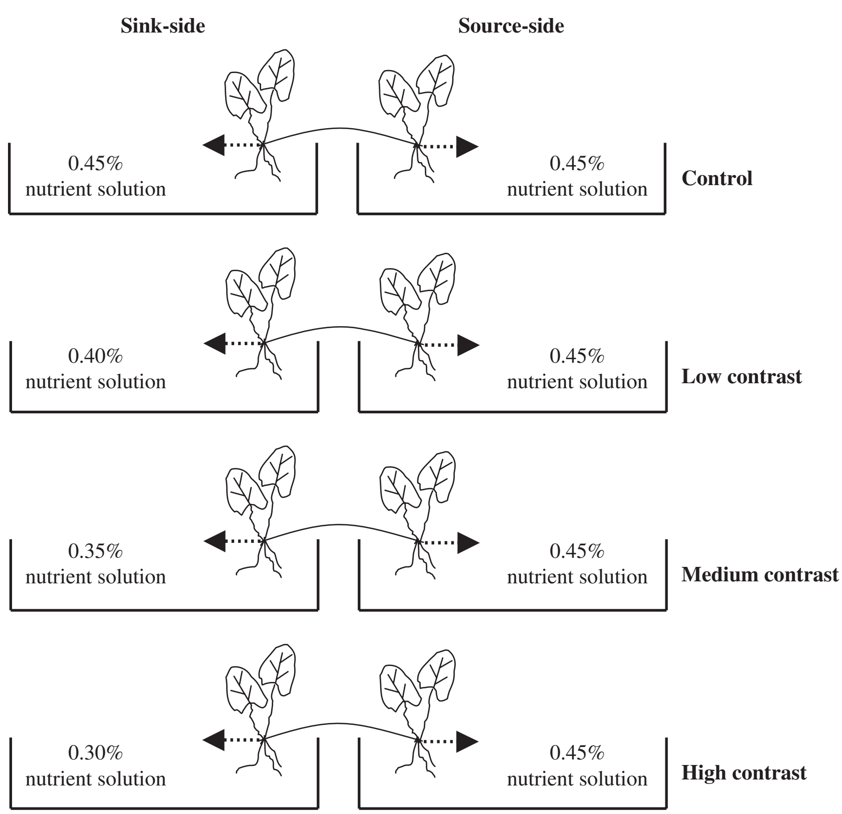

Fig. 1. Scheme of the experiment, showing the four levels of nutrient-patch contrast and source- and sink-side ramet-groups. The arrows indicate the growth direction of young ramets. For more details see text.