

## Commentary

# Modulating effects of ontogeny on the outcome of plant–plant interactions along stress gradients

Plant–plant interactions modulate the structure and dynamics of plant communities and are an important part of the mechanisms that govern the response of species and plant communities to global environmental changes (Brooker, 2006). An accurate understanding of the shifts in the outcome of interactions along environmental gradients is important to improve our ability to forecast future changes in the structure, function, and assembly of communities affected by global change (Callaway, 2007; Brooker *et al.*, 2008; Michalet *et al.*, 2013). During the last two decades plant ecologists have discussed how competitive and facilitative interactions among plants vary with ecosystem productivity and environmental severity. One of the first conceptual models on this topic was the stress gradient hypothesis (SGH), which predicts an increase in the frequency and importance of facilitation with increasing disturbance and environmental severity (Bertness & Callaway, 1994; Brooker & Callaghan, 1998). There is general support for the SGH across different severity gradients and ecosystems (Armas *et al.*, 2011; He *et al.*, 2013). Nevertheless, some relevant case studies showed a great deal of variation in the outcomes of interactions along gradients; this fostered proposals for refinement of the SGH taking into account that the outcome of interactions may also vary depending on intrinsic characteristics of the species involved and the environmental stress they experience (Maestre *et al.*, 2009; Malkinson & Tielbörger, 2010; Soliveres *et al.*, 2011; Schöb *et al.*, 2013). In this issue of *New Phytologist*, le Roux *et al.* (pp. 241–250) extend this set of modulating forces analyzing the combined impact of ontogeny and environmental severity gradients on the prevailing type of plant interactions. They showed that individuals of intermediate size were most strongly facilitated, which had significant consequences on the plant population structure (such as life stage-abundance and survival relations or initial age for reproduction).

Performing an observational study in a subantarctic island ecosystem, le Roux *et al.* examined the effects of the interaction between two dominant species in the area, a cushion benefactor plant, *Azorella selago*, and a beneficiary grass, *Agrostis magellanica*. They measured the performance of *Agrostis* (abundance, size, mass and reproductive effort) in > 12 000 individual grasses collected on and off cushions from adjacent bare soils along both an altitudinal and a wind-exposure gradient. The outcome of the interaction was calculated by comparing grass performance in the presence and absence of the cushion. Results showed that *Agrostis* was generally more abundant and showed higher reproductive output when associated with the cushion compared with its performance on

adjacent bare soil, which was interpreted as a significant facilitation effect by the cushion on the grass. Furthermore, the frequency of facilitation increased with increasing environmental severity, overall supporting predictions of the SGH.

In order to analyze the effects of plants' ontogeny on interactions, the authors combined aboveground and belowground biomass as a surrogate of age, and then related the cushion effects on *Agrostis* to the estimated age of the grass species. Long ago it was proposed that the outcome of plant–plant interactions would change with ontogeny, that is, across the life stages of the interacting plants (Callaway & Walker, 1997), so that net facilitative effects may prevail for longer in the life of a species under increasingly severe conditions (Schiffers & Tielbörger, 2006). However, the consequences of such ontogenetic shifts in plant–plant interactions as related to the SGH have been largely ignored so far. In a sophisticated way, le Roux *et al.* now empirically show such a delay in the shift from positive to neutral or negative outcomes between *Azorella* and *Agrostis* under increasing environmental severity. These trends were observed for *Agrostis* abundance but not for biomass or reproduction. This finding does therefore show the potential modulating effect of ontogeny on the outcome of plant–plant interactions along stress gradients and its relevance for the SGH.

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In contrast to most empirical evidence showing that seedlings are generally facilitated more frequently or strongly than larger, older plants (Callaway, 2007), in the study system of le Roux *et al.* intermediate-sized *Agrostis* were most strongly facilitated by the cushion, whereas seedlings and large individuals were less or not facilitated at all, displaying a unimodal relationship between plant interactions and ontogeny. However, the underlying mechanisms are unclear and will need further exploration. Changes in the balance between competition and facilitation can occur either due to changes in beneficiary plant performance without a benefactor due to environmental constraints, to changes of the plant with benefactor due to benefactor trait effects, or both changes combined (Michalet *et al.*, 2013). In order to narrow down the

underlying mechanism of ontogenetic shifts in plant–plant interactions, future experiments should focus on the relative change of performance of beneficiary species over time when growing both with and without the benefactor (e.g. experimental transplants of grass seedlings on both *Azorella* and soil microsites). If reduced facilitation of seedlings and large individuals is due to interference or competition with the cushion, as suggested by le Roux *et al.*, then this would be observed by a change in *Agrostis* performance with *Azorella*, as it is indicated by the sharp decline of *Agrostis* abundance from intermediate-sized to large grasses growing within *Azorella* (fig. 2 in le Roux *et al.*). Therefore, the ontogenetic shift in plant interactions at the late life history stage could indeed be due to increasing interference or competition with the benefactor. By contrast, a similarly sharp decline in the performance in bare soil of *Agrostis* from seedlings to intermediate-sized grasses (fig. 2 in le Roux *et al.*) seems to indicate high mortality soon after germination, probably due to environmental severity, whereas seedling and intermediate-sized grasses on the cushion may experience lower mortality thanks to the ameliorated environmental conditions provided by cushions. Overall, the unimodal relationship between the prevailing type of plant interactions and ontogeny could, therefore, be the result of different mechanisms, which can be only disentangled with appropriate experiments.

Finally, le Roux *et al.* found that interactions led to great changes in the population structure of the grass species by increasing the absolute and relative abundance of medium-sized *Agrostis*, which also flowered at smaller sizes than those growing on bare soil. Therefore, positive biotic effects by the cushion significantly increased both the population size and fitness of *Agrostis*. Consequently, the facilitation effect of *Azorella* could strongly promote the genetic diversity of the *Agrostis* population and increase the species' ability to adapt to changing environmental conditions (Leimu *et al.*, 2006). Interestingly, biotic interaction effects on population structure were more important than environmental gradients in this study. This outcome challenges the general perspective that in extreme environments biodiversity is predominantly controlled by abiotic conditions that determine which species have appropriate adaptations to survive and much less by interactions among the tough organisms that can establish there (Callaway, 2013).

This observational study has, thus, several novel approximations and results that overall highlight the relevant impact of interactions on plant population structure, dynamics and fitness in subantarctic ecosystems. Future work might now focus on designing experimental studies that disentangle the mechanisms behind observed patterns and that assess the relevance of facilitation for community stability in a changing environment. Observational studies, as this one, are undoubtedly valuable and reveal unforeseen community patterns. But without controlled experiments, studies may include some potentially confounding effects, as outlined earlier, or suffer from lack of independence among variables that might hinder the capacity to unambiguously reveal mechanisms operating in the community. For example, future experimental studies should avoid the potential confounding effects when using biomass as proxy of plant size (response variable) and life history stage (predictor

variable). Only by experimentally controlling plant age changes in biomass would allow to unambiguously interpret biomass changes as the response of the grass to plant interactions or to time.

The study by le Roux *et al.* significantly improves our understanding of the context dependence of plant–plant interactions and their relevance for population dynamics. Furthermore, it has opened up a range of questions that may stimulate future experimental studies to improve our ability to predict when and how biotic interactions might modulate responses of plant communities from extreme environments to climate change.

**Cristina Armas<sup>1,2\*</sup>, Christian Schöb<sup>3</sup> and Julio R. Gutiérrez<sup>1,2</sup>**

<sup>1</sup>Institute of Ecology and Biodiversity (IEB), Casilla 653, Santiago, Chile;

<sup>2</sup>Facultad de Ciencias, Universidad de La Serena, Casilla 554, La Serena, Chile;

<sup>3</sup>The James Hutton Institute, Craigiebuckler, Aberdeen, AB15 8QH, UK

(\*Author for correspondence: tel +56 51 204414; email carmas@userena.cl)

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