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Root responses to legume plants integrate information on nitrogen availability and neighbour identity

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Abstract

Rhizobial symbiosis is known to increase the nitrogen availability in the rhizosphere of legumes. Therefore, it has been hypothesized that other plants' roots should forage towards legume neighbours, but avoid non-legume neighbours. Yet, root distribution responding to legume plants as opposed to non-legumes has not yet been rigorously tested and might well be subject to integration of multiple environmental cues.

In this study, wedevised an outdoor mesocosm experiment to examine root distributions of the two plant species *Pilosella officinarum* and *Arenaria serpyllifolia* in a two-factorial design. While one factor was 'neighbour identity', where plants were exposed to different legume or non-legume neighbours, the other factor was 'nitrogen supply'. In the latter the nutrient-poor soil was supplemented with either nitrogen-free or with nitrogen-containing fertilizer.

Unexpectedly, of all treatments that included a legume neighbour (eight different species or factor combinations), we found merely one case of root aggregation towards a legume neighbour (*P. officinarum* towards *Medicago minima* under nitrogen-fertilized conditions). In this very treatment, also *P. officinarum* root–shoot allocation was strongly increased, indicating that neighbour recognition is coupled with a contesting strategy.

Considering the various response modes of the tested species towards the different legume and non-legume neighbours, we can conclude that roots integrate information on neighbour identity and resource availability in a complex manner. Especially the integration of neighbour identity in root decisions must be a vital aptitude for plants to cope with their complex biotic and abiotic environment in the field.

Keywords: Facilitation; Information integration; Intercropping; Legume; Mesocosm experiment; Neighbour recognition; Plant–plant interactions; Root aggregation; Root distribution; Root foraging

Introduction

Root responses to neighbours can be direct outcomes of competitive or facilitative interactions (Schmid, Bauer, & Bartelheimer 2015). Likewise they may be a result of neighbour recognition, and these processes are not mutually

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exclusive. Neighbour recognition distinguishes between kin and species recognition. While the formerrefers to within-species perception of genetic relatedness (e.g. Dudley & File 2007), the latter refers to the perception of neighbour species identity (e.g. Semchenko, Saar, & Lepik 2014; Mommer et al. 2010; Padilla et al. 2013; see Chen, During, & Anten 2012 for an overview).

Faget et al. (2013) suggested a conceptual framework for root distribution responses to neighbouring plants. This framework proposes that in certain contexts, roots of neighbouring plants will spatially avoid each other (segregation), while in other contexts, they will forage near each other. Segregation would be associated especially with competition for and depletion of soil resources (Faget et al. 2013). It should therefore minimize unprofitable investment of root growth into soil space where resources are scarce and contested (Schenk, Callaway, & Mahall 1999). Conversely, the proposed framework expects roots to forage towards those neighbours that can build up an increased resource availability. This should be the case especially in legumes, considering their capacity of increasing nitrogen (N) availability (Faget et al. 2013). Indeed, N has been found to be significantly increased in the rhizosphere of legumes (Amossé, Jeuffroy, Mary, & David 2014; Ramirez-Garcia, Martens, Quemada, & Thorup-Kristensen 2014). Additionally, increased available N was found in the rhizosphere of rhizobial roots (Fustec, Lesuffleur, Mahieu, & Cliquet 2010; Amossé et al. 2014), making even young legume roots potentially highly attractive for foraging neighbour roots. Up to 30% of rhizobia-fixed N has been shown to be released (Ofosu-Budu, Fujita, & Ogata 1990). Hence, in legumes the amount of N-containing root exudates reaches much higher values than in non-legume plants (compare Lesuffleur, Paynel, Bataillé, Le Deunff, & Cliquet 2007). Furthermore, root systems respond to a moderate increase in N with a stronger elongation of lateral roots (Gruber, Giehl, Friedel, & von Wirén 2013). In soils with heterogeneous nitrogen distribution roots show an increased proliferation in patches with high N availability (Hodge 2004; Mommer, van Ruijven, Jansen, van de Steeg, & De Kroon 2012). Such proliferation can secure high N-uptake, especially during competition with other roots (Robinson, Hodge, Griffiths, & Fitter 1999).

Next to resources attracting foraging roots, it is also increasingly acknowledged that roots can identify their neighbours (Dudley & File 2007; Badri et al. 2012; Chen, During, & Anten 2012). Here, among other possible mechanisms, root exudates are likely among the agents of identification mechanisms (Bais, Weir, Perry, Gilroy, & Vivanco 2006; Semchenko et al. 2014). Different plant species exude characteristic compounds, which for example also promote the association with rhizobia in legumes (Peters, Frost, & Long 1986; Zhang, Subramanian, Stacey, & Yu 2009). Hence, it might even be possible that roots perceive a legume neighbour and prospective facilitative partner by its exuded chemicals.

A conceptual framework like the one presented by Faget et al. (2013) is a useful tool to integrate different theories on root–root interactions. These are naturally very complex, since, even when facilitation occurs, there may be simultaneous competition for different resources. Root interactions are also influenced by identity recognition and strongly dependent on different environmental factors (Mommer, Kirkegaard, & van Ruijven 2016). Hence, root foraging behaviour is known to integrate many different cues (Cahill & McNickle 2011).

In the case of neighbour interactions, the possible integration of neighbour identity into rooting decisions (sensu Hodge 2009) is largely unexplored. In the specific case of interactions between non-legume plants and legumes, the notion that non-legume roots forage towards legumes is often assumed, but scarcely examined. In this study, we therefore examined how far these assumptions can hold. Specifically, based on Faget et al. (2013), we hypothesize that roots of non-legume species are attracted to legume neighbours (‘aggregation’ sensu Bartelheimer, Steinlein, & Beyschlag 2006 with the horizontal distribution of the root system being skewed towards the neighbour), while they are irresponsive to or segregate spatially from non-legume neighbours. We further hypothesize that the named attraction should be especially pronounced, when N availability is low, and less pronounced, when N is in higher supply. As an alternative scenario, we propose that non-additive responses to the factors ‘neighbour identity’ and ‘nitrogen addition’ could play a role. This would indicate that in root interactions, information from neighbour recognition is integrated with other cues.

To investigate these hypotheses, we devised an outdoor mesocosm experiment to examine two plant species in a two-factorial design: (i) the first factor was ‘neighbour identity’, and plants were exposed to different legume or non-legume neighbours, (ii) the second factor was ‘nitrogen treatment’, and nutrient-poor soil was supplemented with either N-free or N-containing fertilizer.

Materials and methods

Study species

Five plant species from central Europe were chosen for the experiments for two reasons: they are all perennial species occurring in sandy grasslands and their roots can all be visually distinguished. Two part experiments were conducted with *Pilosella officinarum* Vaill. Asteraceae or *Arenaria serpyllifolia* L. Caryophyllaceae as the focal species. All used species are elements of the vegetation class Sedo-Scleranthetea (dry sandy grasslands of Central Europe) of which *A. serpyllifolia* is a character species, and in which *P. officinarum* is a widespread species (Pott 1995; Oberdorfer 2001). Hence, both *A. serpyllifolia* and *P. officinarum* co-occur naturally with all species used as neighbours in this experiment.

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