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Quantifying resource use complementarity in grassland species: A comparison of different nutrient tracers

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ABSTRACT

Stable isotopes (e.g. ^{15}N) and rare elements (e.g. Li^+, Rb^+, Sr^{2+}) have been applied to trace nutrient uptake in plants. Tracer methods are increasingly used to quantify soil resource niche partitioning in multi-species communities. Niche partitioning allows for complementarity in nutrient uptake. Spatial complementarity is most frequently measured on separate plots, which bears a risk of between plot variations. This could be avoided with a method that allows for quantification of nutrient partitioning within the same plot. However, there is uncertainty whether uptake is sufficiently similar among different tracers to allow for direct comparison. Therefore we tested uptake similarity between Li^+ and Rb^+ to determine if they can serve as analogues to quantify nutrient uptake from different soil depths. We found a strong overall correlation between Li^+ and Rb^+ accumulation, irrespective of the duration of tracer exposition and plant species identity. However, the slope of the regression between both elements was different in roots and shoots and between different functional groups, pointing to the need of correction factors. Comparisons with other tracers showed that Li^+ and Rb^+ accumulation is clearly more similar to each other than to Sr^{2+} and ^{15}N accumulation. We therefore conclude: Li^+ and Rb^+ have a strong potential to be used as tracers for quantifying spatial complementarity within one given plot under field conditions.

Introduction

Mineral nutrients are essential for plant growth and development. Nutrient concentrations in soil can vary considerably in space and time and, therefore, plants had to develop adaptive and flexible strategies for nutrient acquisition (Maathuis, 2009). Morphological and physiological adaptions help plants to survive less favourable conditions, e.g. drought or nutrient deficiency (Orcutt and Nilsen, 2000). Plants have also developed various strategies to avoid competition for nutrients, such as spatial segregation of the root system within soil, or temporal segregation of nutrient uptake activity (Schenk et al., 1999; McKane et al., 2002). However, we still lack reliable information on temporal and spatial dynamics of belowground resource uptake in ecosystems, processes that are considered to affect species co-existence (Casper and Jackson, 1997). Niche differentiation and resource partitioning among coexisting species potentially allows diverse communities to exploit available resource pools more fully. Such resource complementarity is thus considered to be responsible for the observed positive effects of species richness on plant community productivity (Van Ruijven and Berendse, 2005; Cardinale et al., 2007), but there is a knowledge gap about the mechanistic link between belowground resource uptake and the effects of biodiversity. To date, mathematical approaches have been applied to detect complementarity effects based on plant performance in monoculture and in mixtures ("additive partitioning" by Loreau and Hector, 2001), but they do not provide a direct link to physiological mechanisms. Alternatively, the determination of root distribution might give information on vertical niche differentiation, but does not necessarily provide evidence for root activity, i.e. nutrient uptake by roots. A functional explanation for the observed biodiversity effects must rely on approaches that directly identify and quantify nutrient uptake by plant roots in an ecosystem.

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Tracer techniques have been used in various grassland experiments to study nutrient uptake patterns. Tracers applied at different depths in soil (e.g. Fitter, 1986; Mamolos et al., 1995), in different chemical forms (e.g. Weigelt et al., 2005; Kahmen et al., 2006; Von Felten et al., 2009) or plant material harvested after different incubation times past application (e.g. Ho et al., 1996; da Silva et al., 2011) can help identify and quantify spatial, chemical and temporal patterns of nutrient uptake in plants. However, to address spatial resource complementarity, i.e. the uptake of a tracer from different soil depths, different subplots need to be used. This inevitably includes a large source of variation under field conditions, e.g. small-scale variability in soil conditions, particular plant community composition and their rooting patterns. There is thus the need for methods allowing quantification of root activity from different soil layers within one plot, which requires distinguishable tracers taken up by plants with similar rates.

Moreover, tracer studies need to reflect uptake processes of relevant nutrients, and tracers should be taken up in detectable amounts on a rather short time scale. Tracers enriched in naturally low abundant stable isotopes of an element (e.g. ^{15}N, ^{41}K, ^{42}Ca, ^{43}Ca, ^{44}Ca) have the same chemical properties as the non-enriched nutrients. Discrimination of the heavier isotope can be neglected when a strong enrichment above the natural abundance level is applied (Fry, 2006). Mass spectrometric techniques are now advanced and thus allow very precise detection of isotopes in plant tissues (Stürup et al., 2008). However, equipment and isotopically labelled compounds are costly, especially when applied under field conditions. Rare elements (Li^+, Rb^+, Cs^+, Sr^{2+}, Ba^{2+}) might serve partially as alternatives to study nutrient uptake in ecological studies. These tracers are generally cheaper, naturally present in low concentrations in soil, absorbed freely by plants, toxic only at high concentrations and can be detected at low concentrations (Martin et al., 1982).

Rare elements have been used by several authors to determine root activity, e.g. the bivalent cation Sr^{2+} (e.g. Veresoglou and Fitter, 1984; Fransen et al., 2001; Tsialtas et al., 2001) and the monovalent cations Rb^+ (e.g. Fitter, 1986; Mamolos et al., 1995; da Silva et al., 2011) and Li^+ (Fitter, 1986; Tofinga and Snaydon, 1992; Rodríguez et al., 2007), in combination or alone. Rb^+ is considered an analogue of K^+ (Läuchli and Epstein, 1970; Fitter, 1986; Doyle et al., 1998) and Sr^{2+} an analogue of Ca^{2+} (Fitter, 1986; Nelson et al., 1990; Veresoglou et al., 1995) because a correlation in the uptake of these elements was reported (Collander, 1941). In addition, absorption of Rb^+ and K^+ as well as of Sr^{2+} and Ca^{2+}, were found to interfere with each other (Epstein and Hagen, 1952; Epstein and Leggett, 1954). Different nutrients show distinct chemical behaviour within soil and plants. Resource partitioning and complementarity is a complex equation of various nutrient elements. Using dissimilar nutrient tracer can help to unravel the complex interactions between nutrients and the environment. Discrimination between the nutrients and nutrient tracer might occur. Läuchli and Epstein (1970) showed that absorption and translocation of Rb^+ and K^+ differed slightly. For Li^+ uptake no relationship to K^+ uptake has been shown to date, but like the other rare elements it is used in ecological tracer studies to provide an estimate of root activity in general (e.g. Rodríguez et al., 2007).

To address spatial complementarity of nutrient uptake in different soil layers with rare element tracers, at least two distinguishable elements are needed, which are taken up by the plant with comparable rates. We designed a greenhouse experiment to test the potential use of Li^+ and Rb^+ in soil resource use studies addressing spatial complementarity. Our hypothesis is that the relationship between Li^+ and Rb^+ uptake is the same for all species and is distinct from other nutrient tracers, i.e. the rare element Sr^{2+} and the stable isotope tracer ^{15}N.

Materials and methods

Experimental set-up

The experiment was conducted in spring 2011 in a growth chamber at the University of Freiburg. We used monocultures of two grasses [*Festuca rubra* (Fr), *Anthoxanthum odoratum* (Ao)], two legumes [*Onobrychis viciifolia* (Ov), *Trifolium pratense* (Tp)] and three herbs [*Centaurea jacea* (Cj), *Leucanthemum vulgare* (Lv), *Plantago lanceolata* (Pl)] in this study. Fr, Ao, Cj, Lv and Pl seeds were obtained from Rieger-Hofmann GmbH (www.rieger-hofmann.de), Tp and Ov seeds from Appels Wilde Samen GmbH (www.appelswilde.de). The plants were sown successively according to germination time after being stratified in a refrigerator (6–7 °C) for 3–5 days. Four seedlings of the same species were transplanted to tubular pots (polyvinyl chloride, height 60 cm, diameter 11 cm) filled with topsoil from a meadow adjacent to the Saale river in Jena, Thuringia, Germany. Each monoculture (4 plants/pot) was replicated seven times. The plants were grown for 64 days in a growth chamber with 16 h light/8 h dark at 23 °C in light/15 °C in dark and approximately 60% relative humidity.

Tracer application

The mixed tracer solution contained lithium (Li^+), rubidium (Rb^+) and strontium (Sr^{2+}), all in chloride form, in a concentration of 0.3 mol/L each. The ^{15}N tracer was added as $^{15}NH_4{}^{15}NO_3$ (98%+) in a concentration of 0.019 mol/L. Based on previous work (Von Felten et al., 2009), the ^{15}N tracer concentration was estimated to result in plant $\delta^{15}N$ target values of ca. 100‰. A hole was predrilled to 5 cm depth in the middle of the pot and 2 × 5 mL of the mixed tracer solution were injected through a four-sideport needle connected to a dispenser. The solution was not soaked up by the soil immediately, but remained in the predrilled hole for 2–5 min. Dye applications in control pots showed that the solution spreads a couple of centimetres from the site of injection, indicating that the upper 10 cm of the soil column were exposed to the tracer. To obtain background values for natural ^{15}N, Li^+, Rb^+ and Sr^{2+} abundance, one pot of each species did not receive the mixed tracer solution.

Harvest

Three pots per species were harvested 24 h after tracer injection and three pots after 48 h. The aboveground plant material was cut just above the soil level, dried at 70 °C for at least 48 h, and weighed. A subsample was ground with a ball mill (Retsch MM200) to fine powder to give a mixed sample per pot. All roots growing within the 0–10 cm soil layer were washed gently with tap water. Roots with a diameter >2 mm were excluded because fine roots are considered predominantly relevant for nutrient uptake, whereas coarse roots dominate root biomass. Roots were dried and ground the same way as aboveground material.

Chemical analysis

For ^{15}N analysis, ca. 1 mg of the dried and homogenised plant material was transferred into tin capsules (IVA Analysentechnik, Meerbusch, Germany). Samples were combusted in a Thermo-Finnegan Flash HT elemental analyser. The sample gas containing the analyte N_2 was flushed via a con-flow III to a Thermo-Scientific, Delta V Advantage isotope ratio mass spectrometer (IRMS). IRMS analysis was done at the Leibniz Centre for Agricultural Landscape Research (ZALF) in Müncheberg. For Li^+, Rb^+ and Sr^{2+} analysis, a microwave accelerated acid digestion (MARS 5, CEM Cooperation) with 3 mL H_2O, 5 mL 65% HNO_3 and 3 mL 30% H_2O_2 was performed with ca. 0.3 g of the dried and homogenised material. The diluted