



Plant and microbial uptake of nitrogen and phosphorus affected by drought using ^{15}N and ^{32}P tracers



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ABSTRACT

Competition for nutrients between plants and microbes is an important determinant for plant growth, biodiversity and carbon cycling. Perturbations such as drought affect the availability of nitrogen (N) and phosphorus (P), and may cause shifts in uptake of N and P between plants and microbes. Competitiveness for these nutrients may depend on how flexible plants and microbes are in taking up N and P. We used a novel dual isotope labelling technique (^{15}N and ^{32}P) to assess short-term uptake of N and P by plants and microbes affected by drought in two different plant–soil systems. Mesocosms were extracted from two grassland sites differing in soil nutrient availability and plant species. Half of the mesocosms were subjected to drought one week prior to injection of ^{15}N (as KNO_3) and ^{32}P (as H_3PO_4) tracers. Uptake rates of NO_3^- and P in plants and microbes were estimated based on average source pool enrichment during the labelling period and on plant and microbial recovery of ^{15}N and ^{32}P measured after 4 days of labelling. Overall competition for N and P was reduced with drought as less NO_3^- and P was taken up in plants and microbes. However, plant uptake of NO_3^- was more sensitive to drought than microbial NO_3^- uptake, while microbial P uptake was more sensitive than plant P uptake. These different sensitivities to drought by plants and microbes may decouple the N and P cycle with increased drought conditions.

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1. Introduction

In most terrestrial ecosystems plants and soil microbes strongly compete for nutrients that are in limited supply (Schimel et al., 1989; Zak et al., 1990; Kaye and Hart, 1997). Nitrogen (N) is often the most limiting nutrient for plant growth in many ecosystems (Vitousek and Howarth, 1991). Nitrogen is made available to plants through decomposition of soil organic matter (SOM), but microbes also require N for growth. Plant–microbe competition for N can be intense when both the demand for N by plants and microbes to grow is high (Dunn et al., 2006; Månsson et al., 2009; Inselsbacher et al., 2010; Xu et al., 2011) affecting plant community composition, ecosystem N retention and carbon (C) sequestration (Zak et al.,

1990; van der Heijden et al., 2008; Bloor et al., 2009; Averill et al., 2014).

Plant growth in many terrestrial ecosystems is also limited by phosphorus (P, Elser et al., 2007; Harpole et al., 2011), but plant–microbe competition for P is much less understood. In general, N/P ratios in microbial biomass are lower than in plants or SOM (Cleveland and Liptzin, 2007) suggesting a higher microbial P requirement relative to N. Microbial P limitation was shown in a tropical rainforest where soil microbial activity was stimulated by P additions while plant growth was enhanced by N additions (Cleveland and Townsend, 2006). Furthermore, microbes showed a large capacity to immobilise ^{33}P added to a P-poor grassland soil (Bünemann et al., 2012) and a sandy forest soil (Achat et al., 2010), indicating a large microbial demand for P that could negatively affect plant growth. However, microbes could also facilitate plant P uptake in P-limited systems by extending plant roots through mycorrhizal hyphae and by enhancing P solubilisation and mineralisation in the rhizosphere (Marschner et al., 2011). The

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Table 1
Soil properties of the two mesocosm types.

	N-limiting system (Tenosol)	P-adsorbing system (Kurosol)
Clay (%)	4	18
Silt (%)	8	19
Sand (%)	88	63
pH (H ₂ O)	6.4	5.1
Total organic C (g kg ⁻¹)	5.6	39
Total N (g kg ⁻¹)	0.40	4.0
Total P (g kg ⁻¹)	0.41	1.38
C:N:P	14:1:1	28:3:1

importance of microbial P for plant P uptake was also illustrated by observations of P pools in microbial biomass being larger than in plant biomass in a temperate rainforest (Turner et al., 2013) and in an arctic ecosystem (Jonasson et al., 1999), suggesting that even small changes in size or turnover time of the microbial P pool could have large effects on P availability to plants (Jonasson et al., 1999). Therefore, short-term plant-microbial competition for P in P-limited systems may be as intense as for N in N-limited systems.

Large parts of the world are increasingly affected by drought (Handmer et al., 2012), with potentially important consequences for plant-microbe competition for N and P. A reduction in soil moisture can directly alter the availability of N and P by reducing their mobility in soil where the mobility of P may show greater sensitivity to soil moisture than N, particularly when N is in the nitrate (NO₃⁻) form. For instance, a reduction in soil moisture reduces the diffusivity of N and P, but this effect is greater for P than for N (Lambers et al., 2008). A reduction in soil moisture may also reduce the dissolution and desorption of inorganic P in the soil (Belnap, 2011). Therefore, drought may reduce soil P availability more than N, at least in the short-term. In contrast, long-term effects of drought may enhance physical weathering of P and reduce biological cycling of N thereby increasing the availability of P relative to N in the soil (Delgado-Baquerizo et al., 2013).

A reduction in soil moisture will also reduce plant growth and microbial activity (Huxman et al., 2004; Carbone et al., 2011). Compared to plants, microbes have shown lower soil moisture threshold values below which growth shuts down (Schwinning and Sala, 2004; Collins et al., 2008). This suggests that when soil moisture is reduced below a certain level, microbes may still take up N and P when plants no longer do. Plant-microbe competition for N and P with drought may further depend on how flexible plants and microbes are when taking up N and P from the soil in response to drought. Flexible allocation of N and P can be advantageous for plant growth when the relative supply of N and P is suboptimal (Ågren et al., 2012), while microbes may adapt to changes in the relative availability of N and P through changes in the microbial community thereby causing changes in microbial N/P (Tischer et al., 2014). It is unclear how flexible plants and microbes are in taking up N and P with drought.

We conducted a unique study examining short-term plant-microbe competition for N and P in response to drought using ¹⁵N and ³²P tracers in mesocosms where plants showed low tissue N concentration compared to P, suggesting N limitation (N-limiting system) and in mesocosms where soils showed a high capacity for P sorption (P-adsorbing system). We compared N (as NO₃⁻) and P uptake rates in plant and microbial biomass between mesocosms kept under constant moisture and mesocosms exposed to a 9-day drought. We hypothesised that plant N and P uptake rates would be more negatively affected by drought than microbial N and P uptake rates, and that the negative effect of drought on recovery and uptake in plants would be relatively larger for P than for N. We further hypothesised that the proportional uptake of N relative to P in response to drought would show less variation (or less flexibility) in plants than in microbes.

2. Materials and methods

2.1. Experimental design

We extracted 20 mesocosms from grasslands on 21 November, 2013, 10 at Lansdowne farm (34° 1'16''S, 150°39'56''E) and 10 from Westwood farm (33°59'46''S, 150°39'16''E) near Camden, NSW, Australia. The mesocosms from the Lansdowne farm came from an area sown in 2008 with the tussock grass *Poa labillardieri* that was not fertilised. For our mesocosms whole tussock plants were dug up. The soil at this site is a well-drained sandy Tenosol with very low total organic C and N content (Table 1) and low extractable inorganic N concentrations (Table 2), and we will refer to these mesocosms as the “N-limiting” system. The pasture at the Westwood farm was dominated by *Paspalum dilatatum* Poir. This pasture was grazed by cattle at moderate stocking rates and was not fertilised. The soil is a well-drained sandy loam red Kurosol, acidic with a high P adsorption capacity and low extractable inorganic P concentrations (Table 2). Mesocosms from this site will be referred to as the “P-adsorbing system”. Annual precipitation at both sites is 790 mm with mean air temperature of 10.4 and 23.0 °C in July and January respectively.

Mesocosms were extracted by digging up columns (15 cm in diameter, 20 cm in height) and placing them in plastic buckets. We estimated the dry soil weight of each mesocosm by subtracting the weight of plant biomass measured in extra mesocosms from the total weight (fresh plant biomass weight was less than 3% of the total weight), and by measuring soil moisture content at the time of extraction. These mesocosms were also used for measurement of background ¹⁵N pools in plant, soil and microbes (see below). Mesocosms were transported to the Controlled Environment Facility at the Centre for Carbon, Water and Food in Camden, NSW. Plants were kept in a growth chamber (30/20 °C during the day/night, 60% relative humidity, 12 h of light of ~500 μmol m⁻² s⁻¹ using 1000 W metal halide lamps). Because mesocosms were

Table 2
Effects of drought on soil extractable organic C, NH₄⁺, NO₃⁻, and P (mean ± standard error) at the time of harvest in N-limiting and P-adsorbing mesocosms. ANOVA P values are in bold when P < 0.05.

System	Watering treatment	Extractable org C (mg kg ⁻¹) ^a	NH ₄ ⁺ (mg kg ⁻¹) ^a	NO ₃ ⁻ (mg kg ⁻¹) ^a	Extractable P (mg kg ⁻¹) ^a
N-limiting	Constant	7.4 ± 1.0	0.6 ± 0.3	1.3 ± 0.5	53.6 ± 3.0
	Drought	8.5 ± 0.2	0.7 ± 0.3	1.3 ± 0.2	49.8 ± 1.9
P-adsorbing	Constant	20.7 ± 2.2	1.7 ± 1.0	3.9 ± 0.8	5.2 ± 2.2
	Drought	28.9 ± 4.6	2.5 ± 0.9	4.3 ± 0.7	2.7 ± 0.6
ANOVA results (P-values)					
System		<0.0001	0.05	0.0003	<0.0001
Water		0.05	0.57	0.76	0.16
System × Water		0.54	0.58	0.72	0.75

^a Extractable org C, NH₄⁺ and NO₃⁻ were extracted with 0.05 M K₂SO₄, extractable P with 0.03 M NH₄F – 0.025 M HCl.

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