



# Response-based selection of barley cultivars and legume species for complementarity: Root morphology and exudation in relation to nutrient source



Courtney D. Giles<sup>a,\*</sup>, Lawrie K. Brown<sup>a</sup>, Michael O. Adu<sup>a,1</sup>, Malika M. Mezeli<sup>a</sup>, Graeme A. Sandral<sup>b</sup>, Richard J. Simpson<sup>c</sup>, Renate Wendler<sup>a</sup>, Charles A. Shand<sup>a</sup>, Daniel Menezes-Blackburn<sup>d</sup>, Tegan Darch<sup>e</sup>, Marc I. Stutter<sup>a</sup>, David G. Lumsdon<sup>a</sup>, Hao Zhang<sup>d</sup>, Martin S.A. Blackwell<sup>e</sup>, Catherine Wearing<sup>d</sup>, Patricia Cooper<sup>a</sup>, Philip M. Haygarth<sup>d</sup>, Timothy S. George<sup>a</sup>

<sup>a</sup> James Hutton Institute, The James Hutton Institute, Aberdeen, AB15 8QH and Dundee, DD2 5DA, Scotland, UK

<sup>b</sup> Wagga Wagga Agricultural Institute, Wagga Wagga NSW, Australia

<sup>c</sup> CSIRO Agriculture, Canberra ACT, Australia

<sup>d</sup> Lancaster University, Lancaster Environment Centre, Lancaster, LA1 4YQ, UK

<sup>e</sup> Rothamsted Research, North Wyke, Okehampton, Devon, EX20 2SB, UK

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## ABSTRACT

Phosphorus (P) and nitrogen (N) use efficiency may be improved through increased biodiversity in agroecosystems. Phenotypic variation in plants' response to nutrient deficiency may influence positive complementarity in intercropping systems. A multicomponent screening approach was used to assess the influence of P supply and N source on the phenotypic plasticity of nutrient foraging traits in barley (*H. vulgare* L.) and legume species. Root morphology and exudation were determined in six plant nutrient treatments. A clear divergence in the response of barley and legumes to the nutrient treatments was observed. Root morphology varied most among legumes, whereas exudate citrate and phytase activity were most variable in barley. Changes in root morphology were minimized in plants provided with ammonium in comparison to nitrate but increased under P deficiency. Exudate phytase activity and pH varied with legume species, whereas citrate efflux, specific root length, and root diameter lengths were more variable among barley cultivars. Three legume species and four barley cultivars were identified as the most responsive to P deficiency and the most contrasting of the cultivars and species tested. Phenotypic response to nutrient availability may be a promising approach for the selection of plant combinations for minimal input cropping systems.

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## 1. Introduction

There is a mounting concern for the long-term viability of conventional cropping practices, which rely on non-renewable

**Abbreviations:** A, ammonium-N; Aroot, Aitchison distance of root diameter length distribution; B, balanced nitrate-ammonium; CV, coefficient of variation; ΔpH, change in pH; H<sup>+</sup>, proton; HCO<sub>3</sub><sup>-</sup>, bicarbonate; K<sup>+</sup>, potassium ion; N, nitrogen; NH<sub>4</sub><sup>+</sup>, ammonium; NO<sub>3</sub><sup>-</sup>, nitrate; P, phosphorus; P0, no P; P1, 0.5 mM P; P2, 1.0 mM P; SRL, specific root length.

\* Corresponding author.

E-mail address: [Courtney.Giles@hutton.ac.uk](mailto:Courtney.Giles@hutton.ac.uk) (C.D. Giles).

<sup>1</sup> Present address: University of Cape Coast, College of Agriculture & Natural Sciences, School of Agriculture, Department of Crop Science, Cape Coast, Central Region, Ghana.

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mineral phosphate supplies to maintain yields and meet the dietary requirements of a growing global population [1,2]. Agricultural biotechnologies and practices which maximize the utilization of added and endogenous soil P supplies are therefore needed to reduce the dependence of agricultural production on external fertilizer inputs and minimize the loss of nutrients to surface waters [3]. Intercropping of cereals and legumes has been proposed as an approach to improve crop yields and nutrient use efficiency in agricultural systems through increased biodiversity, resource sharing, resilience to pests, and inter-species facilitation [4]. Understanding the response of barley cultivars and legume species to P supply and N source could therefore improve the selection of plants for biodiverse and nutrient efficient agroecosystems.

Complementarity between two or more plants in poly-culture is characterized by improved resource acquisition and productivity

relative to a monoculture [5]. Facilitation and reduced competition for soil resources by plants in poly-culture occur due to reduced competition for spatial (e.g., top-soil nutrient foraging) and non-spatial soil resources (e.g., chemically distinct nutrient pools), as well as enhanced productivity through N-fixation by legumes and other environmental modifications (e.g., soil moisture retention, disease suppression) [4,6]. The success of intercropping strategies is predicted to depend on architectural and anatomical properties of roots as well as the exudation of carboxylates and phosphatase enzymes, which optimize the extraction of soil nutrients and exploration of niche space in soil by the individual plant species [7]. If however the nutrient acquisition strategies of two or more plants are too similar, for example targeting the same niche space or nutrient pool in soil, competitive effects may limit the success of intercropping strategies. Therefore, the plasticity of root morphology and exudation under conditions of limited or heterogeneous nutrient sources is expected to minimize competition between plants and enhance the acquisition of nutrients by individual plants and intercrops [8].

The recovery of P from organic forms is achieved by the production of phosphatases by plants or microorganisms in the soil environment. The purple acid phosphatase and histidine acid phosphatase classes of phytase have been characterized in plants [9,10] and are reported to be expressed within the cell and exuded under conditions of P limitation [11]. Several species of grasses (e.g., *Brachiaria*, *Dactylis*) and legumes (e.g., *Stylosanthes*, *Medicago*, *Trifolium*) respond to P deficiency through the increased exudation of phytase from roots [11,12]. For example, wheat plants (*Triticum* L.) with greater root-associated phosphatase activity could assimilate more P from organic forms than plants with less or no activity [13]. When constitutively expressed in transgenic plants (e.g., *Nicotiana tabacum*, *Trifolium* L.), various fungal phytases (e.g., *Aspergillus* sp., *Peniophora* sp.) are shown to improve the assimilation of P from sparingly available P sources *in vitro* [14,15]. Whilst the modification of plants with single traits such as fungal phytase exudation has had a limited effect on P acquisition by plants grown in unfertilized soils [16], studies with model tobacco [17] and cereal/legume systems [8,18] suggest that the combination of phytase/phosphatase exudation and citrate efflux could improve the ability of plants to acquire P due to the combined action of these exudates on the solubilization and mineralization of soil P [19].

Organic anions/carboxylates represent a major component of root exudates, which directly affect the diffusivity and availability of P in soils [20]. A secondary effect of carboxylate exudation is the co-transport of counter ion species (e.g.,  $H^+$ ,  $K^+$ ,  $HCO_3^-$ ) to maintain cytosolic charge balance during exudation [21]. This exudation leads to the modification of rhizosphere pH with potential consequences on the solubility of nutrients, enzyme function, and cascading effects within the microbial community [22]. The genetic and environmental controls on carboxylate exudation (e.g., citrate, malate) have been studied extensively in cereals (e.g., *Triticum* L., *Hordeum* L., *Zea mays*) [23–25] and are known to depend on various nutrient deficiencies (e.g., P) [20], metal toxicities (e.g.,  $Al^{3+}$ ,  $Mn^{2+}$ ) [26], or as a mechanism for below ground C partitioning and the facilitation of microbial community symbiosis [27]. Phosphorus deficiency leads to increased citrate efflux in several legume species (e.g., *Medicago sativa*, *Lupinus* spp.) [28,29] and may be further enhanced when ammonium is supplied as the primary source of N due to rhizosphere acidification during ammonium uptake (e.g., *Lupinus albus*) [30,31]. In contrast, nitrate acts as a signal to induce the production of organic anions in tobacco (*Nicotiana tabacum*), which act as receptors of nitrate or counter ions for the maintenance of cytosolic pH [32]. Citrate efflux in barley (*H. vulgare* L.) is primarily studied with regard to its genetic variation across cultivars or role in  $Al^{3+}$  toxicity tolerance in acid soils and is therefore typically assessed under either P sufficient or deficient conditions

[33–35]. To our knowledge, there are no reports of citrate efflux among barley cultivars being affected by both P supply and N source ( $NH_4^+$ ,  $NO_3^-$ ).

Root plasticity in response to selective pressure (e.g., nutrient supply/source) allows plants to explore heterogeneous soil environments and forage for nutrients [7]. Common physiological responses of cereals and legumes to P deficiency include the partitioning of biomass to roots, increased production of fine roots, and the generation of 'low metabolic cost' roots, characterized by increased proportion of aerenchyma cells and greater root length relative to root biomass i.e., specific root length, SRL; [36–42]. The initiation or inhibition of root branching and elongation is also affected by N source ( $NO_3^-$ ,  $NH_4^+$ ). For example in barley and wheat, the localized application of nitrate initiates the growth and extension of seminal and lateral roots [43–45]. Plants provided with ammonium can suppress root branching and elongation in the absence of P, with these effects reversed and associated with improved seedling growth at higher rates of P application [46,47]. If yields in cereal and legume systems are significantly impacted by root architectural [5] and morphological traits, which affect the acquisition of soil mineral nutrients (e.g., lateral root angle, rhizosheath, SRL), the selection of plants with traits appropriate to a particular growth environment will be needed [48].

The effective combination of traits for the efficient recovery of P in complementary plant systems must also consider the genotypic variation of physiological and biochemical responses of plants to nutrient availability [49]. Therefore, the objective of this study was to take a systematic approach to the selection of barley cultivars and legumes species based on the morphological and biochemical response of genotypes to P supply and N source. We assessed root exudation (citrate efflux, phytase activity, pH change) and root morphological traits (root length, specific root length, root diameter size distribution) and identified plants with the greatest potential to access sparingly available or poorly soluble P in soil.

## 2. Materials and methods

### 2.1. Plant materials

Barley seeds (*Hordeum vulgare* L.) from a genome-wide association mapping collection (144 elite European germplasm) and previously assessed for P use efficiency and rhizosheath [50,51] were used for the initial screening in hydroponics, with a sub-set of these selected for further characterization following growth in sterile sand (Table A1). Seeds from six pasture legumes representing a range of root morphological [36] and exudation characteristics [52] were obtained from the New South Wales Department of Primary Industries, Wagga Wagga Agricultural Institute, NSW, Australia. These legume species, originally sourced from the southern Mediterranean and studied extensively in Australian pasture systems [53], were: Subterranean clover (*Trifolium subterraneum* cv. Leura), Purple clover (*Trifolium purpureum* cv. Electra), Biserula (*Biserrula pelecinus* cv. Casbah), Yellow serradella (*Ornithopus compressus* cv. Santorini), French serradella (*Ornithopus sativus* cv. Margurita), and Barrel medic (*Medicago truncatula* cv. Sultan; Table A1).

### 2.2. Chemical and enzyme sources

Standard nutrient salts were sourced from Sigma-Aldrich or BDH for all plant growth experiments. *myo*-inositol hexakisphosphate dodecasodium heptahydrate salt (InsP6; Sigma-Aldrich P8810; Gillingham, UK) was used for the determination of phytase activity in plant exudate solutions. Ammonium sulphate suspensions of lactic dehydrogenase (LDH; Sigma-Aldrich L2500), malic

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