

Defining phosphorus efficiency in plants

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Abstract

The many different definitions for “nutrient efficiency” make the use of the term ambiguous. We evaluated nutrient efficiency using data from a study of response to phosphorus (P) supply in white clover (*Trifolium repens* L.) and lucerne (*Medicago sativa* L.). Application of various criteria identified in the literature as measures of nutrient efficiency did not clarify differences between purportedly P efficient and inefficient germplasm. Germplasm differed in maximum shoot and total dry mass and in solution P concentration ($[P]_s$) required to achieve 80% maximum yield, but not in P concentration of tissue ($[P]_t$), internal P utilization, or P uptake per unit of fine root dry mass. Differences in yield may have resulted from factors other than efficient use of P. To reduce the confounding effects that other factors have on nutrient efficiency, it is essential that *equivalent yields* of germplasm be demonstrated where nutrients are not limiting. Mechanisms that enable enhanced nutrient efficiency can be identified less ambiguously using this approach.

Introduction

Diversity among germplasm in the ability to acquire plant nutrients from the environment has been investigated for decades (Lyness, 1936; Godwin and Blair, 1991) and is the subject of many reviews (Gerloff, 1976; Gerloff and Gabelman, 1983; Glass, 1989; Blair, 1993). The term ‘nutrient efficiency’ has been used widely as a measure of the capacity of a plant to acquire and utilize nutrients for production of timber, crops or forages. Definitions of nutrient efficiency vary greatly (Clark, 1990) however, and in some cases may be misleading in the quest for increased productivity and identification of mechanisms for enhanced nutrient acquisition and utilization.

Identification of germplasm or species with differing nutrient efficiencies, generally includes investigation of potential morphological,

physiological, and biochemical mechanisms involved. These mechanisms have been well reviewed (Clarkson and Hanson, 1980; Sauerbeck and Helal, 1988; Caradus, 1990). However, it is often difficult to separate cause from effect when evaluating potential mechanisms of efficient nutrient uptake and utilization. The close relationship between root and shoot activities may mean that differences in yield or nutrient accumulation by plants, resulting from differences in metabolic activity, are incorrectly attributed to differences in root morphology and function.

Comparing P efficiency definitions: an example using lucerne and white clover germplasm

Five commonly used definitions of nutrient efficiency were used to differentiate the relative P efficiency of two lucerne germplasm, a low P tolerant (EG2) and an intolerant (IG2), second-

generation progeny of 'Rangelander', and two white clover cultivars, purportedly P efficient (Gandalf) and moderately efficient (Huia). Specific details of the pot experiments are presented by Gourley (1991). Plants were grown for 52 d in sand-alumina media with steady-state P concentrations of 2.9, 6.9, 40 and 88 μM . At harvest dry weights of shoots, fine roots (< 2 mm diam.) and coarse roots (> 2 mm diam.), and tissue P concentration were determined.

The measures of P efficiency used in this study to assess differences between germplasm were shoot dry mass (g DM pot^{-1}) (Blair and Cordero, 1978; Sauerbeck and Helal, 1988; Caradus, 1990), external P required to achieve 80% of maximum yield ($\mu\text{M P}$) (Föhse et al., 1988), P efficiency ratios (g DM mg P^{-1}) (McLachlan, 1976; Godwin and Blair, 1991), P utilization efficiencies ($\text{g DM}^{-2} \text{mg P}^{-1}$) (Siddiqi and Glass, 1981), and P uptake efficiencies ($\text{mg P g fine root DM}^{-1}$) (Blair and Cordero, 1978; Elliott and Läuchli, 1985). Fine root dry mass was used rather than total root dry mass because of the greater contribution of fine roots to P uptake (Barber, 1984).

Response curves for each germplasm were derived from the relationship between shoot dry mass (g pot^{-1}) and solution P (μM), using the Michaelis-Menten equation. Derived regression models for each germplasm were tested for invariance (Ratkowsky, 1983) to determine whether the two response curves were significantly different ($P < 0.05$). Phosphorus efficiency ratios, utilization efficiencies, and uptake efficiencies were analyzed by one-way analysis of variance at P concentrations of 2.9, 6.9, 40, and 88 μM to determine statistical differences between germplasm ($P < 0.05$).

The response curves of shoot dry mass and solution $[\text{P}]_s$ were significantly different ($P < 0.01$) for the lucerne germplasm EG2 and IG2, and the white clover cultivars Gandalf and Huia (Fig. 1). External P requirement to produce 80% of predicted maximum shoot dry mass was 19 and 32 μM for EG2 and IG2, and 15 and 29 μM for Huia and Gandalf, respectively (Fig. 1).

The plant $[\text{P}]_t$ increased with increasing solution $[\text{P}]_s$, while white clover was greater than that of lucerne. Because P efficiency ratio is equivalent to the reciprocal of $[\text{P}]_t$, differences in

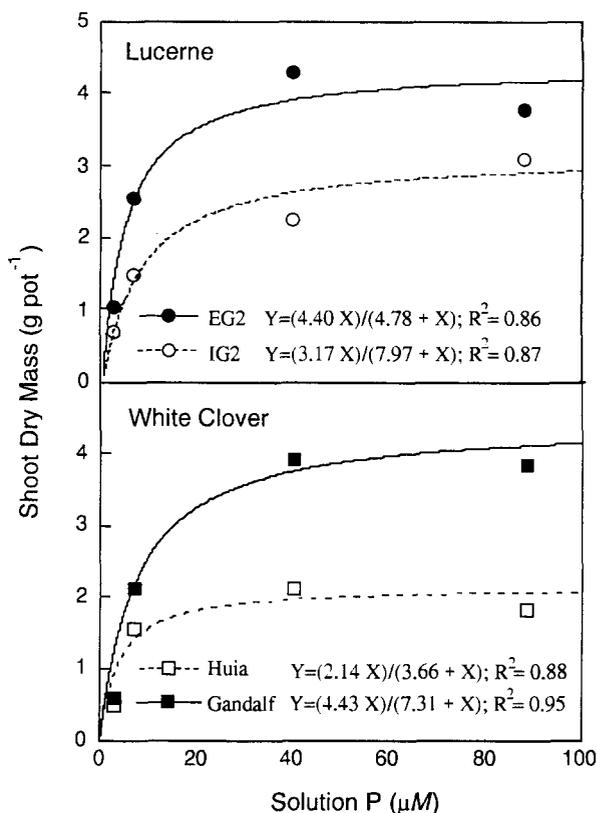


Fig. 1. Shoot dry mass response curves for lucerne and white clover germplasm over a range of solution P concentrations.

P efficiency ratio between germplasm corresponded to differences in $[\text{P}]_t$. Phosphorus efficiency ratio declined with increasing solution P concentrations, indicating a decline in the internal utilization of P to produce dry mass (Table 1). There were no significant differences in P efficiency ratios between the two lucerne germplasm, while the white clover germplasm Gandalf was significantly higher than Huia only at the highest $[\text{P}]_s$ (Table 1), where it appeared that Huia was accumulating luxury levels of P.

Utilization efficiency was not significantly different between EG2 and IG2 at any $[\text{P}]_s$ (Table 1). Gandalf had a significantly higher utilization efficiency than Huia at $[\text{P}]_s$ of 6.9 μM and above (Table 1). The similarity in $[\text{P}]_t$ between the two white clover germplasm in this experiment means that differences in P utilization efficiency were largely due to differences in yields.

Phosphorus uptake efficiency provided an

average value integrated over the entire plant growth period. The higher yielding germplasm had higher fine root dry mass and also higher total P accumulation than the lower yielding germplasm. There were no significant differences between EG2 and IG2, or between Gandalf and Huia in P accumulation per fine root dry mass (Table 1), indicating that the roots of each germplasm had a similar ability to absorb P from the solution.

Table 1. Mean phosphorus efficiency ratio, utilization efficiency and uptake efficiency for white clover and lucerne germplasm over a range of solution P concentrations

	White Clover		Lucerne	
	Huia	Gandalf	EG2	IG2
P Efficiency Ratio (g DM g P⁻¹)				
Solution P (μ M)				
2.9	430	458	655	740
6.9	306	313	570	536
40	170	189	314	317
88	146	175*	286	295
P Utilization Efficiency (g DM² g P⁻¹)				
Solution P (μ M)				
2.9	296	41	1034	736
6.9	626	876*	1959	1115
40	463	928*	1871	909
88	354	867*	1406	1203
P Uptake Efficiency (mg P g fine root DM⁻¹)				
Solution P (μ M)				
2.9	10.5	7.4	6.7	5.9
6.9	17.5	16.9	10.7	9.3
40	35.7	34.3	27.6	24.0
88	39.1	34.8	27.2	22.8

* Germplasm are significantly different ($P < 0.05$).

These results indicate that different measures of nutrient efficiency can be obtained from the same experimental data. This supports the conclusions of others that ranking species and germplasm for nutrient efficiency can vary according to the definition used (McLachlan, 1976; Blair and Cordero, 1978; Blair, 1993).

An improved criteria for determining nutrient efficient germplasm

Screening germplasm for shoot dry mass or harvestable product in low P conditions may

provide the best estimate of productivity in low P soils, and in our example Gandalf and EG2 would be the preferred germplasm over Huia and IG2. However, before germplasm can be categorized as "P efficient" or "P inefficient", it is important to identify whether the superior performance in low P conditions is truly related to a specific mechanism enhancing P uptake or utilization. Many plant metabolic activities, such as phytohormone production, photosynthetic rate, photoperiodism, and production of ATP, can increase nutrient uptake and utilization by influencing root morphology and function (Wilkins, 1984). A superior metabolic activity, regardless of the mechanism, is likely to result in higher yields *independent* of P availability, and therefore should be identified as a superior rather than efficient genotype (Fig. 2). A mechanism

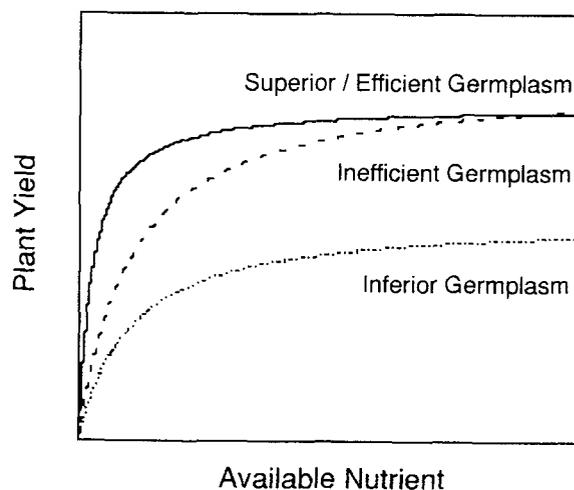


Fig. 2. Hypothetical yield response curves of three germplasm differing in nutrient efficiency and yield potential.

which leads to *true* P efficiency becomes unimportant when P is in excess of requirements. If the same maximum yield is not achieved, factors other than the nutrient under study are likely to be influencing plant growth.

It is essential therefore, that germplasm achieve similar yields when optimum amounts of P are available (Fig. 2). Differences in nutrient efficiency then can be related to the rates at

which the maxima are achieved (Fig. 2). Two of the previously discussed definitions, yield at low P availability and external P concentration required to achieve a percentage of maximum yield, both enable the designation of efficient and inefficient germplasm, as long as similar yield maxima are obtained.

Mechanisms of P efficiency should only be investigated after this criteria has been satisfied. A truly efficient germplasm could require less nutrient than an inefficient germplasm for normal metabolic processes. The use of nutrient efficiency ratios may therefore indicate a potential mechanism for enhanced nutrient efficiency. The calculation of utilization efficiency includes however, both yield and plant nutrient concentration, and is likely to complicate the identification of potential mechanisms associated with enhanced nutrient efficiency. Differences among germplasm in nutrient uptake per unit root dry mass or length, or differences in root morphological characteristics such as shoot:root ratio or root fineness, may also indicate mechanisms for increased nutrient acquisition at low nutrient availabilities (Caradus, 1990). An example of a specific mechanism that increases P efficiency is provided by Smith et al. (1993). Formation of greater amounts of vesicular-arbuscular mycorrhizal association increased the efficiency of P uptake and yields at low levels of P while similar yields are obtained between effectively and ineffectively inoculated plants when adequate P is available.

Conclusion

Our results and those from cited literature clearly indicate the importance of establishing sound criteria before designating germplasm as nutrient efficient or inefficient and associating efficiency with particular physiological and morphological characteristics. Similar yields at non-limiting

nutrient availability should reduce the possibility that differences in nutrient uptake are due to factors other than those associated with nutrient efficiency. Different maximum yields and similar P utilization and uptake by roots indicate that the germplasm assessed in this study should not be described as differing in P efficiency.

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