Premier Digit and Progardes Desmanthus compete effectively for applied phosphorus under mixed sward conditions

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Abstract
Grasses generally dominate the pastures of northern Australia. This may be associated, in part, with varietal differences in critical phosphorus (P) requirements that influence the competitive ability and persistence of the legume component. However, the effect of plant competition on shoot yield responses to soil P supply remain unquantified in tropical pasture swards. Micro-swards of Premier Digit and Progardes Desmanthus were grown, both as monocultures and mixed plantings, in soil amended with five rates of P fertiliser to determine the influence of sward conditions on shoot yield and tissue P. The shoot yield and tissue P concentrations of both species increased in response to soil P supply, with the shoot yield of Progardes Desmanthus in mixed plantings representing between 33–47% of the total yield of Digit and Desmanthus combined. The critical external P requirements of Progardes Desmanthus were generally equal to or lower than that of Premier Digit, yet both species competed effectively for applied P. Therefore, Premier Digit and Progardes Desmanthus may be suitable companion pasture species for establishment in the low-P soils of northern Australia.

Keywords
Critical P requirements, *Desmanthus* spp., *Digitaria eriantha*, sward competition, tropical pastures

Introduction
The extensive grazing systems of northern Australia are dominated by C_4 grasses and are generally established in nitrogen (N) and phosphorus (P) deficient soils. Under these conditions, there has been a gradual decline in pasture productivity (Robertson et al. 1997). It is expected that incorporating tropical pasture legumes into these systems will improve pasture productivity and quality (Jones and Rees 1997). However, the persistence of tropical pasture legumes is relatively poor (Peck et al. 2012). This phenomenon may be associated with the relatively high palatability of pasture legumes, when compared to constituent pasture grasses, which results in preferential grazing of the legume component (McCaskill et al. 2019). Alternatively, nutrient limitations such as P deficiency may lead to poor legume persistence because grasses generally forage more efficiently for available nutrients than legumes (Evans 1977). These interactions among tropical pasture species remain poorly understood.

Improved legume persistence may be achieved by combining tropical pasture species that have similar growth requirements. Preliminary research has indicated that there are substantial differences in yield potential between tropical grasses and legumes. This means that the grass component of a mixed pasture sward is likely to overwhelm the legume component. Nevertheless, varietal differences in yield potential and P requirements have not been investigated under mixed-sward conditions. A greater understanding of how tropical pasture species respond to limited soil P supply, particularly between constituent grasses and legumes, may help elucidate aspects of legume productivity. The objective of the current study was to determine the yield potential and critical P requirements of a tropical grass and legume when grown under monoculture and mixed-sward conditions.

Methods
Plant growth conditions
Premier Digit (*Digitaria eriantha*) and Progardes Desmanthus (*Desmanthus* spp., cvv. JCU 1–5) were grown to determine shoot yield and tissue P concentrations under monoculture and mixed-sward conditions. These pasture species are considered to be suitable companion species (Boschma et al. 2021). Both species were grown in a sandy soil (Grey Tenosol; Isbell 1996) that was collected from the upper 2–15 cm soil layer of a field at Armidale, NSW, Australia. The soil had a Colwell extractable P concentration of 5 mg P kg^{-1} soil, a phosphorus buffering index (PBI) of 29, and a pH ($CaCl_2$) of ~5.3. The soil was passed through a 5 mm sieve before 2 kg of oven-dry soil was weighed into plastic bags. Basal nutrients were applied to the individually

bagged soil as a solution, and included 15 mg N kg^{-1} (as CH_4N_2O), 5.5 mg S kg^{-1} and 13.5 mg K kg^{-1} (as K_2SO_4), and 1 mg kg^{-1} Liberal BMX (which included boron, copper, iron, manganese, molybdenum and zinc). Five P treatments were established by adding P fertiliser (as KH_2PO_4) to the basal solution at rates of 0, 10, 30, 45 and 90 mg P kg^{-1}. After the nutrient solution was applied, the soil was mixed thoroughly and packed into plastic pots (height = 15 cm, diameter = 13 cm) with a total soil depth of ~13 cm and a bulk density of ~1.2 g cm^{-3}.

Micro-swards of Premier Digit and Progardes Desmanthus were established by sowing seed to achieve a target density of ~15 plants pot^{-1}. Prior to sowing, the Progardes Desmanthus seeds were heat-treated by immersing in 85ºC water for 8 sec to break seed dormancy. Four replicate pots of both species, as monocultures and mixed plantings, were prepared for each P treatment. Transparent mylar screens (0.5 mm thick) were used to separate the species when grown in mixed-sward conditions, to minimise above-ground light competition. After planting, the pots were moved to a glasshouse (natural daylight; 35/25ºC, day/night) in Armidale, NSW, Australia. Plants were grown between August–September 2019. Pots were arranged in a randomised complete block design (blocks comprised the different replicates). Soil moisture was maintained by watering daily and by watering to 90% field capacity once per week.

Harvest and analysis

Plants were harvested after 35 days' growth. Shoots were cut at the soil surface and were oven-dried at 60ºC for 72 h and weighed. Shoot samples were then ground to <2 mm before a ~0.5 g subsample was pre-digested in a glass tube with 1 mL deionised water and 4 mL 70% (v/v) nitric acid for at least 2 h. Samples were digested using a Milestone UltraWAVE 640. The P concentration of the digested samples was determined using ICP-OES. Shoot P content was calculated by multiplying shoot P concentration and shoot dry mass. Measured parameters were analysed using R (R Core Team 2020). Critical external P requirements were calculated as the amount of P required to achieve 90% of maximum yield based on a Weibull growth function, with the 95% confidence intervals determined by bootstrapping the residuals. Critical internal P requirements were calculated as the shoot P concentrations that corresponded with the critical external P requirements.

Results

Shoot dry mass increased with P fertiliser application for both Premier Digit and Progardes Desmanthus ($P < 0.001$; Fig. 1). Under both monoculture and mixed-sward conditions, Premier Digit out-yielded Progardes Desmanthus. Nevertheless, the shoot yield of Progardes Desmanthus represented 33–47% of the total yield in the mixed swards.

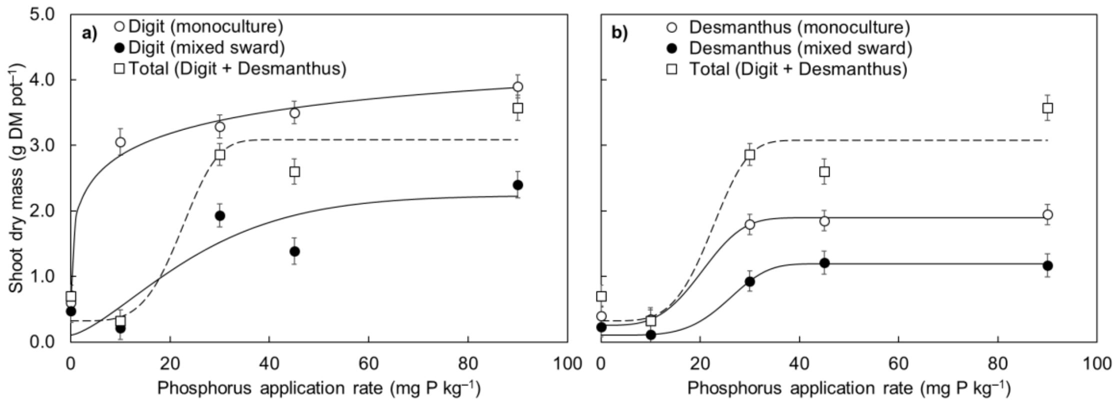

Figure 1. The shoot dry mass of Premier Digit (a) and Progardes Desmanthus (b) grown in response to five P application rates (0, 10, 30, 45 and 90 mg P kg^{-1} soil), under both monoculture and mixed-sward conditions. The total shoot dry mass of Digit and Desmanthus in the mixed swards is also shown in both panels (dashed line). Values show the mean ± se (n = 4). Fitted curves show Weibull growth functions.

The critical external P requirements of Progardes Desmanthus were either equivalent to or lower than that of Premier Digit, under both monoculture and mixed-sward conditions (Table 1). Mixed-sward conditions did not change the critical external P requirements of either species significantly.

Table 1. The critical P requirements of Premier Digit and Progardes Desmanthus. Critical external P requirements were calculated as the amount of P applied to achieve 90% maximum yield, with 95% confidence intervals shown in parentheses. Critical internal P requirements were the shoot P concentrations that corresponded with the critical external P requirements. * shows the values that could not be calculated.

Species	Critical external P requirement (mg P kg^{-1} soil)	Critical internal P requirement (mg P g^{-1} DM)
Premier Digit (monoculture)	**38.2** (24.6–50.8)	**4.30**
Progardes Desmanthus (monoculture)	**28.0** (24.7–38.2)	**2.38**
Premier Digit (mixed sward)	**49.2** (33.3–*)	**7.44**
Progardes Desmanthus (mixed sward)	**33.0** (30.2–*)	**2.02**
Total (Digit + Desmanthus)	**29.0** (24.6–34.7)	*

Shoot P content increased with P fertiliser application for both species (*P* < 0.001; Fig. 2). However, the shoot P content of Premier Digit was generally larger than that of Progardes Desmanthus.

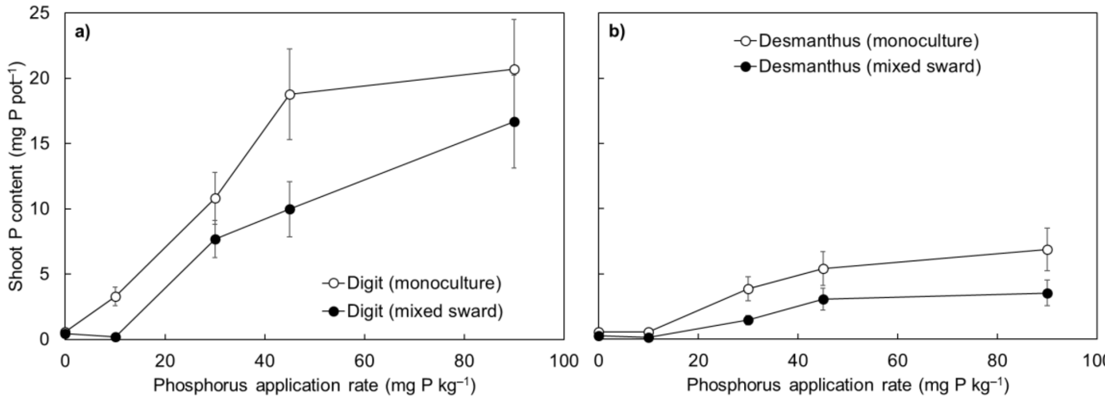

Figure 2. The shoot P content of Premier Digit (a) and Progardes Desmanthus (b) grown in response to five P application rates (0, 10, 30, 45 and 90 mg P kg^{-1} soil), under both monoculture and mixed-sward conditions. Values show the mean ± se (n = 4).

Shoot P-use efficiency declined in response to P fertiliser application for both species (*P* < 0.001; Fig. 3). Premier Digit was particularly efficient at producing dry matter in the P0–P10 treatments. In contrast, Progardes Desmanthus used acquired P relatively efficiently in the higher P treatments as well. On average, Progardes Desmanthus used acquired P more efficiently under mixed-sward conditions than under monoculture conditions; no difference was observed for Premier Digit.

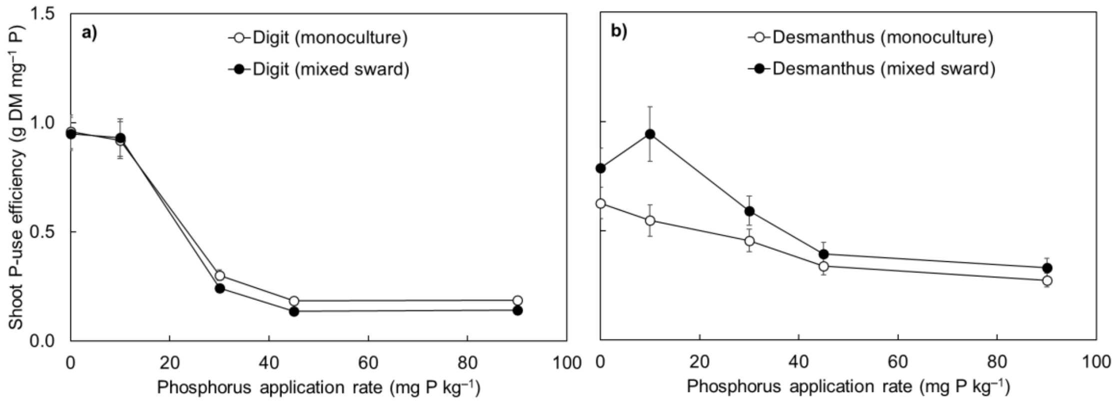

Figure 3. The shoot P-use efficiency of Premier Digit (a) and Progardes Desmanthus (b) grown in response to five P application rates (0, 10, 30, 45 and 90 mg P kg^{-1} soil), under both monoculture and mixed-sward conditions. Values show the mean ± se (n = 4).

Discussion

Premier Digit and Progardes Desmanthus were both responsive to P fertiliser when grown in the low-P soil. In general, the critical external P requirements of Progardes Desmanthus were equal to or lower than that of Premier Digit, under both monoculture and mixed-sward conditions. This indicates that Progardes Desmanthus is relatively efficient at acquiring P, and maintains this efficiency when grown with a constituent pasture grass. The shoot P-use efficiency of Progardes Desmanthus was also comparatively high across the P treatment range and increased in response to mixed-sward conditions. Nevertheless, Premier Digit had a much larger biomass potential which indicates that the grass component is likely to out-yield the legume component regardless of soil P supply, provided adequate N is available (although this is unlikely in many pastures where the relationship will be determined by legume N-fixation). This difference in productivity may be associated with varietal differences in root morphology, because grasses generally forage the soil more efficiently than legumes (Evans 1977). Indeed, the root morphology of *Desmanthus* spp. genotypes is known to be relatively poor because roots are short and thick while root hairs are short and mostly absent (McLachlan et al. 2021).

Legumes generally improve the quality of mixed pasture swards which leads to an improvement in animal production. However, the relatively high critical internal P concentrations for Premier Digit, in conjunction with its larger biomass potential, meant that this species achieved larger shoot P contents than Progardes Desmanthus. This result suggests that the primary function of the legume component in tropical pasture swards may be the fixation of atmospheric N for improved pasture productivity.

Conclusion

Premier Digit and Progardes Desmanthus competed effectively for applied P fertiliser, suggesting that they may be suitable companion species for the mixed pastures of northern Australia. Further research is required to determine how these species perform under field conditions, as further constraints such as drought and grazing will influence long-term productivity and persistence. Nevertheless, the critical internal P concentrations will be useful in tissue P interpretation.

Acknowledgements

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