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Some soil factors constraining buffel grass (*Cenchrus ciliaris* L.) seedling growth rate across a range of acid red Kandosols in Queensland, Australia

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ABSTRACT

Buffel grass (*Cenchrus ciliaris* L.) has passionate grazing industry advocates and biodiversity conservation detractors around the world due to its ability to readily establish and spread on certain soil types. A more detailed understanding of what soil factors influence the success of seedling establishment will offer guidance to anyone wishing to either encourage or discourage buffel grass establishment in a particular area. Twenty soils from land types where buffel grass had a varied history of successful establishment and persistence in south western Queensland, Australia were assessed in a pot trial for their influence on early seedling growth rate of buffel grass. Some currently had buffel grass growing there. Aspects of the chemistry of each soil were compared against the rate of seedling growth of buffel grass cv. Biloela that was sown with or without a phosphate coating on the seed. Available soil phosphorus had a major influence on seedling growth in the absence of a phosphate fertiliser coating, but levels of other factors such as exchangeable aluminium and calcium were also critical. Several multiple regression equations with differing soil parameters included proved equally good at predicting buffel seedling growth but they did not greatly improve on the strong correlation with available soil phosphorus. This seemed due to the interchangeability amongst soil pH, cation exchange capacity and degree of clay as controlling factors, over and above available phosphorus. Thus, where available soil phosphorus is marginal for rapid buffel seedling growth, soil pH, exchangeable aluminium and total exchangeable cation levels could have similar importance in determining whether buffel grass colonised or failed to gain a foothold in that area.

Keywords: aluminium saturation, aluminium toxicity, clay content, exchangeable acidity, exchangeable calcium, pH, phosphorus, red earth.

Introduction

Buffel grass (*Cenchrus ciliaris* L. or *Pennisetum ciliare* (L.) Link) is an important pasture grass in semi-arid rangelands in many parts of the world. Native to eastern Africa, Arabia and the Indian subcontinent (Tropical Forages 2020), buffel grass has been sown around the globe and supports the livelihood of many grazing businesses. Buffel grass is very well adapted to establishing, persisting and spreading in arid climates (Lawson *et al.* 2004; Franklin *et al.* 2006). However, due to its ability to invade some natural systems, buffel grass is regarded as a weed in some circumstances (Williams and Baruch 2000; Biosecurity 2012; Marshall *et al.* 2012). Buffel grass can alter flora and fauna abundance and fire regimes (Fairfax and Fensham 2000; Eyre *et al.* 2009; Smyth *et al.* 2009). It can be very difficult to eradicate once well established (Dixon *et al.* 2002; Scott 2014) but equally can be difficult to establish and persist on particular soil types (Fitzgerald 1955; Ibarra-F *et al.* 1995; Puckey and Albrecht 2004).

In semi-arid Australia, buffel grass dominates many pastoral lands but has invaded national parks and town gardens and footpaths (Jackson 2004; Friedel *et al.* 2007; Read *et al.* 2020). Cox (2013) says seasonality and amount of rainfall as well as minimum winter temperatures explain global buffel grass distribution, but Marshall *et al.* (2012) say there are scant published data about soil factors that provide support or resistance to its invasion. Eyre *et al.* (2009) say a combination of factors controls its ease of establishment and eventual persistence rather than a dominant factor.

In Africa, buffel grass grows mostly on sandy and other well-drained soils (Bogdan 1977; PlantZAfrica 2021), avoids clay-rich and calcium deficient soils (Bogdan 1977), and prefers soils with pH (1:5 in water) in the range of 7–8 (Zamundio 2009). Elsewhere, buffel grass has been noted to prefer loose or sandy-surfaced soils (Tropical Forages 2020). However, the species is so diverse that some ecotypes prefer clay soils (Grains 2014). Australian commercial pasture experience reflects that diversity, with robust Molopo, Biloela and Tarewinnabar cultivars performing well on heavy clays (Vertosols) while Gayndah and American cultivars perform best on sandy earths (Kandosols). The small West Australian cultivar grows well on the lower slopes of sand dunes (Arenosols) in the Pilbara and Gascoyne regions of Western Australia. A loose soil surface and soil disturbance has been found to assist in its establishment in many countries (Brenner and Kanda 2013). Extra localised moisture, such as along waterways and 'run-on' areas also enhances its presence, but not prolonged inundation or waterlogging (Anderson 1974; Weed Management CRC 2008).

Greater soil fertility under isolated deep-rooted eucalypt trees greatly enhances buffel grass colonisation beneath their canopy (Christie 1975*b*; Silcock 1980), and was correlated with available soil phosphorus (P). However, Johns (1981) did not find buffel grass to grow better under poplar box (*Eucalyptus populnea* F. Muell.) trees in the Nyngan–Cobar district of western New South Wales where the level of available soil P under trees was not appreciably higher than in the inter-canopy zone. Hence, other factors such as soil pH, available cations and soil microflora are possibly involved (Ebersohn and Lucas 1965; Silcock 1975). For example, Armstrong *et al.* (1992) found that buffel grass seedling growth in mulga soil (acid red earth now called a Kandosol) inoculated with VAM (Vesicular-Arbuscular Mycorrhiza) and amended with lime to pH 5.8 improved seedling growth at 35 days after sowing but only in the absence of additional P fertiliser. Native grasses had differing VAM responses. In Sonora, Mexico, where buffel grass has spread widely (De la Barrera 2008) soil phosphate was not well correlated with its existence (Ibarra-F *et al.* 1995). Abundant available soil P assists seedling growth of buffel grass on the acidic red Kandosols (mulga soils) of south-western Queensland (Christie 1970; Silcock 1980; Silcock and Smith 1984) and around Alice Springs (Schlesinger *et al.* 2013). Silcock and Smith (1982) demonstrated that the critical stage when buffel grass seedlings were most in need of a P 'stimulus' was between the 2 and 5-leaf stage prior to tillering. Edye *et al.* (1964) and Christie (1970) showed that fertiliser P enhanced seedling survival under severe moisture stress but had a far less dramatic influence on the growth of established buffel plants. Christie (1975*a*) hypothesised that about 25 $\mu g\ g^{-1}$ or more of acid extractable P (BSES method, Kerr and von Stieglitz 1938) was desirable for vigorous growth of buffel grass on the mulga soils around Charleville, Queensland.

Sanchez and Salinas (1981) report that the high level of exchangeable aluminium in very acidic red South American soil types was more detrimental to buffel grass growth than to certain *Brachiaria* species. Spain and Andrew (1978) also found buffel grass to be inherently more sensitive to free aluminium ions in water culture than many other tropical grasses.

Hence there are likely to be combinations of soil factors and rainfall constraints that limit where buffel grass will establish and persist in different parts of the world and thus where it might be a valuable grazed pasture or regarded as a weed.

This experiment sought to determine whether the soil available P constraint on the establishment of buffel grass seedlings on acidic soils from south-west Queensland was exacerbated or moderated by other soil factors such as pH, exchangeable calcium (Ca), aluminium (Al) and potassium (K), and cation exchange capacity (CEC).

Materials and methods

During the period May to July 1982, dry surface (0–10 cm) soil was collected at a restricted location from 20 red soils (many carrying some mulga, *Acacia aneura* F. Muell. ex Benth. trees) in south-west Queensland, and screened onsite through a 2.5 mm sieve to remove stones and vegetation litter. Sieving and mixing the soil was necessary to allow similar soil to be placed in each pot from a site, to allow soils of differing sandiness to be sensibly compared for their nutritional effect on seedling growth, and to allow a similar degree of compaction in each pot, even though it no longer emulates a field ecosystem. It is a recognised scientific procedure for an experiment with our stated aim (Birch 1958; Ross *et al.* 1985; Cabrera 1993; Wäldchen *et al.* 2012), and any alteration to soil chemistry that may result should apply to all soils. A mobilisation of mineralised nitrogen is a near-universal effect of soil sieving (Craswell and Waring 1972; Stenger *et al.* 1995) and is usually proportional to the organic carbon content of the soil (Birch 1958; Wäldchen *et al.* 2012.) The location of the collection sites, mapped Western Arid Region Land Use Survey land type (WARLUS 1974, 1978, 1990) and the existing vegetation are given in Table 1.

The sieved dry soil was put into 20 × 20 cm plastic pots lined with a polythene bag which had been perforated at the base with a few small holes for drainage. All pots were filled as closely as possible to the same level with the same degree of compaction. The filled pots were individually weighed

Table 1. Sandy Kandosols collected for a pot trial to assess the importance of soil factors other than available phosphate in influencing buffel grass seedling growth rate.

Site name	Location	WARLUS reference[A]	Site description
Angellala (Ang)	44 km down C'ville-Bollon Rd and 2 km N of Angellala Ck	III, S1 (unit 61)	Tall mulga – some *Hakea ivoryii* and dead cypress pine – very sandy top of a rise; very sparse ephemeral pasture
Arabella (Ara)	33 km E of C'ville – at site of grazing trial (Orr *et al.* 1993)	III, M1 (unit 38)	Tall mulga/poplar box/silverleaf ironbark/bitterbark trees over *Aristida*, *Digitaria*, *Monachather*, Malvaceae – sloping, high in landscape
Augathella (Aug)	6 km along Oakwood Rd W from old Augathella-Tambo Rd	IV, M1 (unit 52)	Sandy mulga/dead finish/wilga/poplar box over *Enteropogon acicularis*, *Thyridolepis*, *Aristida*, *Enneapogon* – on a rise; buffel beside road
Beechal (Bee)	5 km NNE of 'Beechal' house near pasture trial plot; 35 km ENE of Toompine	I, M1 (unit 46)	Sloping mulga/poplar box/dogwood on scalded mulga soil; sparse perennial pasture
Boatman (Boa)	At old mulga thinning trial – 9 km from Boatman house and 137 km from C'ville	III, H3 (unit 39)	Dense, slightly sloping mulga scrub with scattered poplar box trees at mulga thinning trial (Beale 1973); *Aristida*/mulga soil grasses
Bowra (Bow)	5.9 km up C'mulla – Humeburn Rd from Warrego River bridge	III, D1 (unit 62)	Linear sand dune; cypress pine, *Capparis* spp., *Acacia murrayana* surrounded by black clays; mixed pasture
Charleville (Cha)	7 km E of C'ville near Research Master Site – same soil as Silcock and Smith (1982) pot trial	III, S1 (unit 45)	Mulga/poplar box/ironwood – flat, sandy; sparse perennial grass and Malvaceae herbage
Cheepie (Che)	20.7 km W of Cheepie on N side of bitumen C'ville-Quilpie road	I, H4 (unit 50)	Open, stoney top of slope – mulga clumps, *Euc. terminalia*, occasional wilga and *Cassia* sp.; rock grass pasture
Glenbar (Gle)	70 km down Boatman Rd from C'ville-C'mulla Rd	III, N (unit 64)	Sandy heath/spinifex (*Triodia* sp.) rise with *Casuarina* spp., grasstrees and *Calytrix longiflorens* – no eucalypts
Kalanoa (Kal)	115.5 km SSE down Boatman Rd from C'ville-C'mulla Rd	III, M2 (unit 44)	Flat lowland, open tall mulga/*Eucalyptus* spp./false sandalwood/*Cassia* spp./*Eremophila glabra*; kangaroo grass, *Eriachne* spp.
Kanalba (Kan)	2 km W of 'Kanalba' house on cultivation area – approx. 32 km S of Morven	III, M1 (unit 49)	Almost flat mulga/poplar box/false sandalwood plus kangaroo grass. Buffel grass grows where sown. Oats and wheat grown in winter
Langlo (Lan)	4.1 km along Scrubby Crk Rd from Langlo-Tambo Rd and 2.4 km E of Langlo River	IV, M2 (unit 56)	Recently cleared mulga/silverleaf ironbark/grey turkeybush/mixed grass – sloping, some kurrajong
Maryvale (Mar)	3 km SW of 'Maryvale' house, 30 km SW of Morven	III, H1 (unit 38)	Gently sloping mulga/poplar box with wiregrass and some *Hakea sp.*
Maxvale (Max)	7.1 km past Ward River on Adavale – C'ville Rd	III, M3 (unit 28)	Poplar box/false sandalwood/green turkeybush/*E. acicularis*, *Aristida* spp. – occasional mulga and rosewood – flat, surface sealing soil
Ravenscourt (Rav)	6.8 km along Langlo Rd from Adavale Rd turnoff (70 km NW of C'ville)	III, M3 (unit 39) or A3 (unit 26)	Flat, run-on area, poplar box/false sandalwood/green turkeybush grading into gidyea/leopardwood one way and mulga/poplar box/false sandalwood other way
Rhondavale (Rho)	11 km S from C'ville airport entrance on Cunnamulla Rd	III, N (unit 64)	*Triodia marginata*/*Acacia gnidium*/*Calytrix longiflorens*/silverleaf ironbark/scattered mulga – flat, relatively high area; limited pasture
Rundalua (Run)	94.5 km down Boatman Rd from C'ville-C'mulla Rd	III, H3 (unit 46)	Upland, shallow duplex soil dominated by mulga – nearby *Micromyrtus* sp./poplar box; no ground herb layer
Turn Turn (Tur)	45 km down Hungerford Rd from Eulo-Thargomindah Rd – beside Cle-P2-WR exclosure	I, S2 (unit 61)	Flat, sandy, sparse mulga/poplar box/beefwood/ironwood/*Er. sturtii*/*Do. attenuata* with woollybutt and *Eremophila gilesii*/*Er. longifolia*
Winbin (Win)	66.4 km W of Cheepie on bitumen C'ville-Quilpie road – S side of road	I, S1 (unit 63)	Flat mulga/*Ac. brachystachya*/wiregrass/woollybutt – rel. sandy usually but not for this sample

(*Continued on next page*)

Table 1. (*Continued*)

Site name	Location	WARLUS reference[A]	Site description
Wittenburra (Wit)	1 km S of 'Wittenburra' house, Eulo beside pasture introduction site	I, M2 (unit 64)	Flat run-on area, mulga clumps plus poplar box, *Hakea* sp., *Ac. victoriae*, and saltweeds

C'ville, Charleville; C'mulla, Cunnamulla; Ac., *Acacia*; Do., *Dodonaea*; Er., *Eremophila*; Euc., *Eucalyptus*.
Botanical names conform to Henderson (1997).
[A]WARLUS = Western Arid Region Land Use Study (WARLUS Part I, III or IV). Reference is study part number, land system code and land unit code within that part, e.g. III, S1 (unit 45). Three-character site code used in figures is listed under each site name.

and arranged in three randomised blocks in a glasshouse in south-west Queensland. All pots were then spray-watered to excess with rainwater for 2 days while standing in dishes to ensure that the soil reached maximum water holding capacity. The dishes beneath were then removed and the pots were allowed to drain freely for 6 h before being weighed again (called field capacity (F.C.) here). This weight was recorded so that each pot could be returned daily to that moisture content to counteract evaporative loss while seedlings grew. Because the clay type of the red soils was non-swelling, the seedlings had the same volume of soil from which to later extract their nutrients in each pot. The pots were then left to dry out on their surface for 3 days in preparation for sowing the seeds.

Samples of the air-dry sieved soil from each site were analysed in a laboratory for pH in water, pH in 1 M KCl, electrical conductivity (EC), chloride (Cl), BSES acid P, Colwell bicarbonate P, effective CEC, exchangeable Ca, magnesium (Mg), sodium (Na), K and Al, and exchangeable acidity. The analyses methods used were those documented by Bruce and Rayment (1982), namely 1:5 in water for pH, EC and Cl, exchangeable cations and CEC in 1 M ammonium chloride at pH 7.0 and exchangeable acidity in 1 M potassium chloride. A more extensive analysis of soil parameters was not done due to budgetary constraints but numerous earlier trials with these soils in the Charleville environment by Christie and Silcock had shown that buffel grass seedlings up to the tillering stage did not require basal nutrients other than P for good growth. Also, Silcock *et al.* (1976) achieved no growth rate response from buffel grass seedlings to 34 kg N ha^{-1} equivalent on Charleville mulga soils presumably because sieving the soil stimulated sufficient mineralisation of soil organic matter (Franzluebbers 1999; Kristensen *et al.* 2000).

After-ripened, commercial buffel grass cv. Biloela seed of high purity and germinability was used. Half the required 'seed', technically fascicles, was wet with water-soluble methyl cellulose glue and then coated with powdered monosodium phosphate in a tumbling device and placed to dry in the sun. The mean dry coat weight resulting was 22.9 mg on fascicles that initially weighed an average of 3.2 mg each. This coat:seed ratio of 7:1 was fairly high compared to a theoretical minimal need of about 3:1 for healthy buffel seedling growth (Silcock and Smith 1982). Twelve 'seeds' were sown at 1 cm depth in a predetermined, even, well-spaced arrangement into the dry surface soil in each pot on 12 October, 1982. Thus, there were 60 pots sown with coated fascicles and 60 with uncoated fascicles, and 3 replicates of 20 soils for each. After all pots were sown, they were gently spray-watered with deionised water for about 1 h when all pots appeared well wetted. The surface of the pots was kept damp for the next 5 days by multiple sprayings each day and daily weighing to ensure the pots were kept at F.C. Thereafter, as the seedlings grew, pots were watered daily back to their appropriate F.C., determined earlier before seeds were sown. There was only one small rainfall event during the first 50 days of this trial, so all plants grew in typical warm, bright early summer Charleville weather (BOM 2022) but with maximum temperatures constrained to about 30°C by evaporative coolers.

The following data were recorded for each seed sown and subsequent growing seedling:

(i) Hours to coleoptile emergence from the soil surface;
(ii) Days from sowing to the appearance of the tip of Leaf 3;
(iii) Days from sowing until Leaf 4 was fully expanded (that is, ligule visible);
(iv) Length of Leaf 4 lamina (cm).

Individual seedling growth recording ended when the fourth leaf was fully expanded because prior research had shown that the major impact of P fertiliser on buffel grass seedling growth on acid mulga soils began as the tip of the third leaf appeared, and was over once the ligule of the fourth leaf was fully exposed (Silcock *et al.* 1976; Silcock and Smith 1982). To minimise any potentially confounding impact of nutrient rundown by large plants, each seedling was also harvested at ground level once it had a fully expanded fourth leaf.

Statistical analysis

Analysis of Variance (ANOVA) was conducted on the plant growth measures and time intervals between each development stage. Plant development rate variability within a pot was treated as a separate error term. Correlation matrices were calculated amongst all soil and plant parameters, and the MULCOV statistical package (McIntyre and Ward 1970) was used to derive multifactorial equations that best described the relationship between seedling growth rate and the most influential soil chemistry parameters.

Results

Soil properties

Percent moisture when air-dry and at F.C. (Table 2) was inversely proportional to the visual sandiness of the soil, which reflects the proportion of clay in the soil (not explicitly determined but many published works report this broad relationship – WARLUS 1974; Wäldchen *et al.* 2012; Kirkham 2014; Soil Quality Pty Ltd 2021). The sandiest soils with F.C. of about 10% were Bowra and Glenbar and the most clayey ones visually were Wittenburra and Ravenscourt with F.C. almost 50% higher at 15%. The latter two had the highest moisture content when air-dry and at F.C. which conforms with the findings of Ahern (1990) and Wäldchen *et al.* (2012). Most soils were strongly acidic to very strongly acidic ($\text{pH} < 5.5$) (Table 3), the exceptions being Kalanoa and Wittenburra, which were slightly acidic (pH 6.1–6.5) (Turner *et al.* 1993). All had very low salinity and sodicity levels based on their EC, Cl and exchangeable Na levels (Tables 3, 4; WARLUS 1974; Bruce and Rayment 1982). Maxvale, Ravenscourt and Bowra had the highest available soil P, especially Bowra ($24\,\mu\text{g g}^{-1}$ bicarbonate test) but most had low ($10\text{–}20\,\mu\text{g g}^{-1}$) or very low ($<10\,\mu\text{g g}^{-1}$) levels of available P (Table 3). Degree of red hue in the damp soil varied from a bright red-brown (2.5YR) at many sites to a pale pinkish-red (7.5YR) at Rundalua, and a very pale yellow hue (10YR) at Glenbar.

Table 2. Moisture holding properties and relative density of the soils used.

Soil source	Air dry soil in pot (g)	Added water for field capacity (g)	Effective field capacity (%)	Air-dry moisture (%)
Angellala	7410	820	11.1	0.6
Arabella	6910	880	12.7	1.5
Augathella	6260	820	13.1	1.8
Beechal	6710	860	12.8	2.0
Boatman	6810	730	10.7	1.9
Bowra	7510	750	10.0	0.4
Charleville	7100	840	11.8	1.3
Cheepie	6910	880	12.7	1.6
Glenbar	7310	770	10.5	0.7
Kalanoa	6810	870	12.8	1.9
Kanalba	6560	850	13.0	1.7
Langlo	5910	840	14.2	1.4
Maryvale	7360	920	12.5	1.1
Maxvale	6910	950	13.7	2.1
Ravenscourt	6560	970	14.8	2.2
Rhondavale	7410	780	10.5	0.7
Rundalua	7310	850	11.6	1.0
Turn Turn	7410	850	11.5	1.2
Winbin	6960	820	11.8	1.2
Wittenburra	6010	910	15.1	3.1

Pots were filled as closely as possible to the same level and degree of compaction with sieved, air-dry soil.

The degree of Al saturation of the exchangeable cations was high (>26%) for Angellala, Arabella, Charleville, Cheepie, Glenbar, Rhondavale and Turn Turn (Table 4). These are all relatively sandy soils but with diverse vegetation cover ranging from dense mulga to spinifex (*Triodia marginata* N. T. Burb.) or treeless rock grass (*Eriachne mucronata* R. Br.) grassland. Those with a low proportion of exchangeable Al did not conform to any simple vegetation category. Of them, Kalanoa and Wittenburra were the least acidic of all 20 soils, Ravenscourt was from an alluvial area with higher clay content, but Augathella, Boatman, Bowra and Langlo did not have any consistent vegetation or soil feature, except that their pH values in water were medium acidic (5.4–5.8, Table 3).

The detailed soil reports in WARLUS (1974, 1990) propose that exchangeable Ca was comparatively high at Kalanoa and Wittenburra, (4.7 and $4.6\,\text{meq}^{-100\text{g}}$ accompanied by relatively high Mg levels ($3.3\,\text{meq}^{-100\text{g}}$). Calcium levels were extremely low at Glenbar ($0.1\,\text{meq}^{-100\text{g}}$), and very low at Angellala and Rhondavale, all very sandy soils. Exchangeable K levels were low ($0.1\text{–}0.2\,\text{meq}^{-100\text{g}}$) on the very sandy soils of Bowra, Angellala, Glenbar and Rhondavale (Table 4) while Kalanoa, Langlo and Wittenburra soils rated high ($>0.6\,\text{meq}^{-100\text{g}}$; Bruce and Rayment 1982). Sodium levels were all very low except in the Wittenburra soil with $0.15\,\text{meq}^{-100\text{g}}$ and it also had a much higher K level ($1.1\,\text{meq}^{-100\text{g}}$) than all other soils. The ratio of exchangeable Al to exchangeable Ca was very high for the Glenbar soil (6.2) due to its very low Ca content, with Angellala and Arabella soils the next highest at just above 1.0 (Table 4).

Soil/soil correlations

There were some strong, highly significant ($P < 0.001$) correlations ($r > 0.68$) amongst the soil parameters measured (Table 5). Available P by acid extraction, as used in Queensland for acidic soils (Bruce and Rayment 1982), was closely correlated with the values from the Colwell bicarbonate P method ($r = 0.94$) which is used more widely around the world. Available P levels (by either method) were not well correlated with any other soil factor for these soils, the best being -0.34 with percentage Al saturation. However, available P was strongly correlated with buffel seedling growth (see below) as reported in published Australian research (Christie 1970; Silcock 1980).

Soil pH by the 1:5 in water method was strongly correlated with soil pH using the 1 M KCl method ($r = 0.89$)

Table 3. Soil chemical properties expressed on an air-dry basis and Munsell soil colour of some with a distinctly different shade of red when wet.

Soil	pH 1:5 Water	pH 1:5 1 M KCl	Elec. Con. (mS cm^{-1})	Cl$^-$ (μg g^{-1})	Extr. Phos (μg g^{-1}) Acid P	Extr. Phos (μg g^{-1}) Bicarb P	Munsell Colour[A]
Angellala	5.0	4.1	0.010	9	5	6	2.5YR 4/6
Arabella	5.1	4.0	0.011	7	2	4	
Augathella	5.4	4.6	0.013	7	5	5	5YR 3/3
Beechal	5.1	4.1	0.014	8	9	11	2.5YR 3/6
Boatman	5.4	4.5	0.009	7	3	4	
Bowra	5.8	5.4	0.026	8	35	24	10YR 6/4
Charleville	5.5	4.1	0.007	8	6	5	
Cheepie	5.0	3.9	0.012	6	7	6	
Glenbar	4.9	3.9	0.010	6	2	3	
Kalanoa	6.4	5.9	0.034	13	5	3	2.5YR 3/6
Kanalba	5.5	4.4	0.032	9	6	6	2.5YR 3/6
Langlo	5.7	4.9	0.022	8	3	5	5YR 3/4
Maryvale	5.0	3.9	0.018	11	7	8	
Maxvale	5.3	4.1	0.010	7	17	19	
Ravenscourt	5.5	4.5	0.011	9	18	19	
Rhondavale	5.4	4.1	0.004	6	3	4	2.5YR 3/4
Rundalua	4.7	4.1	0.061	26	6	5	7.5YR 3/2
Turn Turn	5.2	4.0	0.016	8	12	11	2.5YR 3/6
Winbin	5.2	4.1	0.008	6	8	9	
Wittenburra	6.2	5.1	0.020	15	8	9	

[A] A greater prefix number before YR indicates a paler red colour.

although generally about 1 unit higher towards neutral (Table 3). Soil pH was significantly negatively correlated ($P < 0.01$) with exchangeable acidity (-0.71), exchangeable Al (-0.64) and percentage Al saturation (-0.63) (Table 5). Exchangeable Al was inversely related to soil pH below 5.5 but it became zero once pH rose above 5.5 (Fig. 1*a*) whereas there was a moderate positive linear fit between exchangeable Ca and pH over the whole range recorded ($r = 0.77$, Fig. 1*b*). The relationship between exchangeable Al and exchangeable Ca was negative but still had a significant correlation of -0.65 (Table 5) for Ca levels up to 4.6 meq^{-100g}. These inter-relationships resulted in a strong inverse correlation ($r = -0.79$) between percentage Al saturation and exchangeable Ca (Fig. 2*a*).

Other notable high correlations (>0.84) were found between the soil air-dry moisture content (an indicator of relative clay content) and effective CEC and exchangeable K. There was also a high positive correlation between effective CEC and its main components of exchangeable Ca (Fig. 2*b*), Mg and K (Table 5). Effective CEC also had a significant negative correlation ($P < 0.05$) with exchangeable acidity (-0.49), exchangeable Al (-0.47) and percentage Al saturation (-0.63) (Table 5). The relationship between exchangeable Ca and effective CEC was very strong ($r = 0.96$, Fig. 2*b*) as also for exchangeable Mg (Table 5) but a moderate negative relationship (-0.65) existed between exchangeable Al and exchangeable Ca (Fig. 2*a*, Table 5). There was a strong correlation between electrical conductivity and Cl assay ($r = 0.86$, Table 5).

Omission of the two most extreme examples, Bowra and Glenbar

The soil results in tables and figures show that extreme or outlier values may greatly influence the correlation coefficients calculated. Thus, more correlation calculations were done with the two most extreme soil types from Bowra and Glenbar omitted. This had little effect on the correlation coefficients for most pairs tested but the correlation coefficient for bicarbonate available P against soil F.C. was increased from 0.13 (n.s.) to 0.48 ($P < 0.05$). Conversely, omitting the five soils with zero exchangeable Al reduced the significance of the correlation between exchangeable Ca and exchangeable Al from -0.65 (**) to -0.40 (n.s.).

Table 4. Concentration of the major cations and the exchangeable acidity of the soils used.

Soil	meq^{-100g}								
	Eff. CEC	Exch. Ca^{2+}	Exch. Mg^{2+}	Exch. Na^{+}	Exch. K^{+}	Exch. Al^{3+}	Exch. acidy	% Al satn	Al/Ca ratio
Angellala	1.14	0.4	0.03	0.02	0.16	0.44	0.53	38.6	1.10
Arabella	2.75	0.9	0.2	0.03	0.53	0.92	1.09	33.5	1.02
Augathella	4.71	3.2	0.8	0.03	0.56	0.05	0.12	1.1	0.02
Beechal	3.93	2.0	0.8	0.04	0.52	0.41	0.57	10.4	0.21
Boatman	3.68	2.3	0.7	0.04	0.47	0.10	0.17	2.7	0.04
Bowra	1.56	1.2	0.2	0.03	0.13	0	0	–	0.00
Charleville	2.17	0.7	0.4	0.02	0.33	0.66	0.72	30.4	0.94
Cheepie	2.90	1.0	0.5	0.03	0.48	0.76	0.89	26.2	0.76
Glenbar	1.53	0.1	0.6	0.02	0.08	0.62	0.73	40.5	6.20
Kalanoa	8.78	4.7	3.3	0.03	0.74	0	0.01	–	0.00
Kanalba	3.53	2.1	0.5	0.04	0.65	0.15	0.24	4.3	0.07
Langlo	3.95	2.3	0.8	0.03	0.79	0	0.03	–	0.00
Maryvale	1.99	0.7	0.3	0.03	0.36	0.39	0.60	19.6	0.56
Maxvale	4.69	2.3	1.1	0.03	0.58	0.53	0.68	11.3	0.23
Ravenscourt	5.34	3.1	1.5	0.05	0.49	0.11	0.20	2.1	0.04
Rhondavale	1.11	0.4	0.2	0.02	0.10	0.29	0.39	26.1	0.73
Rundalua	2.48	1.1	0.4	0.04	0.41	0.35	0.53	14.1	0.32
Turn Turn	2.86	0.9	0.5	0.03	0.47	0.82	0.96	28.7	0.91
Winbin	2.71	1.3	0.6	0.03	0.38	0.26	0.40	9.6	0.20
Wittenburra	9.17	4.6	3.3	0.15	1.10	0	0.02	–	0.00

Note: All soils were nett negatively charged, based on pH calculations.
Effective CEC = sum Ca + Mg + Na + K + Exch. Acidity} These expressed on an oven dry basis.
% Al saturation = 100 × Exch. Al/Effective CEC}.
Exchangeable Acidity = by titration (Bruce and Rayment 1982); effectively exch. $Al^{3+} + H^{+} + NH_4^{+}$.

Seedling growth

Emergence and survival

An average of 7.3 of the 12 sown seeds emerged (61%) for each pot, with the range from 4 to 11. Differences in total numbers emerging for individual soils were random and unrelated to soil chemistry, texture or seed coating. Total seedlings emerging from the six pots of a soil ranged from 52 for Kanalba to 36 for Boatman. Speed of seedling emergence was slowed slightly ($P < 0.01$ overall, Table 6) when the seed had a P coating, on average 0.6 days, and it was never significantly improved for any soil. Such slight delay in emergence from seeds with a water-soluble coating is well documented (Silcock and Smith 1982). Three quite sandy soils (Charleville, Rundalua and Turn Turn) had emergence delayed an average of more than 1 day (Table 6).

Plant numbers emerging in each soil × coating group ranged from 14 to 26 out of a possible 36. Emerging numbers were similar for coated and uncoated seed (22.2 versus 21.4 seedlings per treatment respectively) and the average number of survivors was also similar, 21.6–20.3 respectively. Hence, once emerged, a P coating did not enhance early survival under well-watered conditions. Emergence was best from Kanalba, Rundalua and Angellala soils (>25 seedlings from all three reps) and worst from Boatman, Cheepie and Winbin (<20). Survival was much worse on the Glenbar soil than all others (eight deaths) with seven of these from the uncoated seeds after leaf 3 appeared. The worst survival from other uncoated seeds was three deaths on Kanalba soil.

Emergence to leaf three appearance

The phosphate seed coatings very significantly ($P < 0.001$) shortened the time that it took seedlings to exsert the tip of their third leaf (Table 6). Only the Bowra soil had a high enough soil available P level to mask the expected stimulation of early seedling growth that the phosphate coating provided. By contrast the soil with slowest seedling growth was Glenbar with Rhondavale not much better (Table 6). Both are very acidic, have very low amounts of Ca, K and exchangeable cations and a high level of exchangeable Al (Tables 3, 4). Both have spinifex as the dominant grass cover species where the

Table 5. Correlations between the various soil parameters measured for the 20 soils collected. High correlations (>0.84) are shown in bold font, italics used where no meaningful correlation.

Parameters	F.C.	Air-dry H_2O	pH water	pH 1 M KCl	EC	Cl^-	Acid Phos	Bicarb Phos	Eff. CEC	Exch. Ca^{2+}	Exch. Mg^{2+}	Exch. Na^+	Exch. K^+	Exch. Acidy	Exch Al^{3+}	% Al satn	Al^{3+}/Ca^{2+}	% Base saturn
F.C.	1																	
Air-dry H_2O	0.812	1																
pH in water	0.363	0.460	1															
pH in 1 M KCl	0.215	0.277	**0.893**	1		*Strong correlation between pH in water & in 1 M KCl [expected]												
Elect. Condy (EC)	*0.053*	*−0.034*	*0.068*	0.343	1													
Chloride (Cl)	0.139	*0.106*	*0.001*	0.193	**0.864**	1		*Strong correlation between Cl & EC [expected]										
Acid P	*−0.055*	*−0.091*	0.217	0.318	0.082	−0.043	1											
Bicarb P	0.133	*0.070*	0.142	0.177	*−0.049*	−0.101	**0.945**	1		**V. strong correlation between acid & bicarb P [expected]								
Effective CEC	0.717	**0.854**	0.735	0.655	0.197	0.266	*−0.020*	*0.038*	1		*Strong correlation between Eff. CEC & air-dry% moisture							
Exch. Ca^{2+}	0.682	0.813	0.769	0.740	0.218	0.229	*0.062*	0.103	**0.962**	1		***Strong correln between Eff. CEC & exch. Ca^{2+}						
Exch. Mg^{2+}	0.584	0.729	0.761	0.680	0.186	0.291	*−0.014*	*0.014*	**0.957**	**0.886**	1		**Exch. Mg^{2+} & exch. Ca^{2+}					
Exch. Na^+	0.558	0.709	0.458	0.335	0.150	0.372	*0.057*	0.121	0.676	0.610	0.670	1		*Eff. CEC & exch. K^+				
Exch. K^+	0.830	**0.859**	0.558	0.442	0.245	0.265	−0.158	*−0.066*	**0.855**	0.814	0.723	0.689	1		*Exch K^+ & A.D.% wtr & Eff. CEC			
Exch. Acidity	−0.216	−0.253	−0.708	−0.803	−0.260	−0.171	−0.222	−0.153	−0.490	−0.665	−0.492	−0.361	−0.336	1		***pH & exch. Al^{3+} v exch. Acidity		
Exch. Al^{3+}	−0.232	−0.257	−0.640	−0.750	−0.292	−0.213	−0.208	−0.159	−0.473	−0.653	−0.465	−0.356	−0.332	**0.991**	1		*% Al satn & exch. Al^{3+}	
% Al saturation	−0.462	−0.531	−0.629	−0.707	−0.342	−0.205	−0.342	−0.340	−0.630	−0.786	−0.519	−0.413	−0.589	0.825	**0.846**	1		
Al^{3+}/Ca^{2+}	−0.393	−0.396	−0.397	−0.383	−0.222	−0.206	−0.267	−0.284	−0.370	−0.487	−0.208	−0.245	−0.481	0.423	0.449	0.666	1	
% Base saturn	0.475	0.557	0.681	0.746	0.313	0.165	0.361	0.349	0.662	0.812	0.550	0.423	0.614	−0.821	−0.826	**−0.992**	−0.646	1
															***Ratio of Al^{3+} to % Base satn & % Al satn			

For $P < 0.05$ $r >$ abs. 0.43 and for $P < 0.01$ $r >$ abs. 0.55.

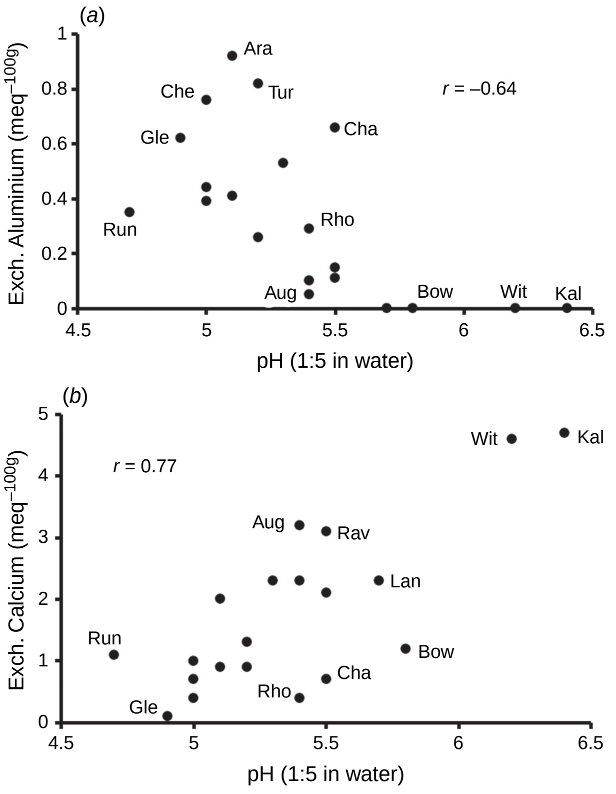

Fig. 1. Effect of soil pH on the level of (*a*) Exchangeable aluminium and (*b*) Exchangeable calcium in the soils collected. Note the critical effect of soil pH below 5.5 on the presence of exchangeable aluminium. Labels are the first three letters of the soil collection site name – see Table 1.

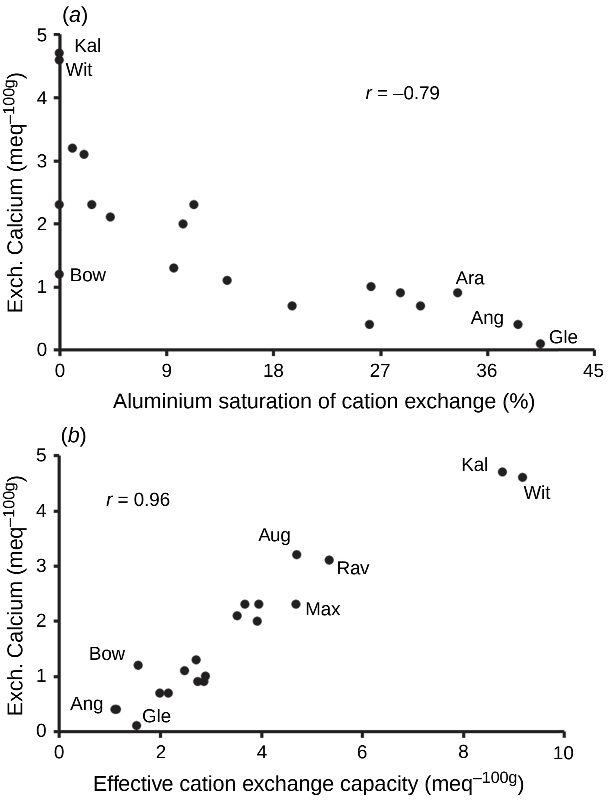

Fig. 2. The contrasting relationship strength between the level of exchangeable calcium present in the range of soils tested and (*a*) Exchangeable aluminium concentration and (*b*) the Effective cation exchange capacity exhibited. Labels are the first three letters of the soil collection site name – see Table 1.

soil was collected (Table 1). By this growth stage and beyond, there was a significant soil × P interaction on buffel seedling growth rate (Table 7). The magnitude of the statistical differences amongst the main factors for each seedling development stage is shown by the ANOVA *F* values in Table 8.

Leaf 3 appearance to leaf 4 full expansion

The beneficial effects of the applied phosphate ($P < 0.001$, Table 8) continued past the leaf 3 appearance stage for all soils, but were not as marked by day 18 on some of the higher available P soils like Kanalba and Ravenscourt (Tables 6, 7). The more favourable soils (more clay, less acidic and greater basic cation levels) grew seedlings at a greater rate at most times (Table 7). By day 26, seedlings in the Charleville soil were showing some signs of inadequate nutrition (paler green leaves) and were then amongst the slowest growing. They had fallen behind since day 18 when many from coated seeds were at a comparable growth stage (Table 7) to those in other more favourable soils.

Length of leaf 4 lamina

Only Bowra soil showed no P-coating response on leaf length (Table 6). The less hostile, more clayey soils from run-on areas with greater water holding capacity (Table 2) mostly grew slightly bigger plants in the absence of the P seed coating. For example, the average length of leaf 4 on non-P supplemented plants from Kanalba, Wittenburra, Maxvale and Ravenscourt soils ranged from 8.6 to 10.5 cm compared to 5 to 7.6 cm long on many other soils (Table 6). Despite that, leaf length of seedlings from P-coated seeds on Kalanoa, Langlo and Wittenburra soils was relatively small (12.8–13.9 cm long) compared to those grown on Cheepie, Maryvale, Turn Turn and Angellala soil (15.4–16.2 cm) which would not be considered the most genial soils of the collection.

Correlations between soil and plant parameters

A summary of the strongest correlations between buffel grass seedling growth and soil chemistry is provided in Table 9. For comparison, the equivalent correlations for the length of leaf 4 and time to coleoptile emergence are included. Simple correlations for all parameters recorded are shown in the Supplementary Tables S1, S2. In general there was a far smaller percentage of highly correlated relationships between plant and soil parameters (3.1%) compared to soil-soil (6.5%) and plant-plant (15.7%).

Correlations between seedling growth rate (inverse of time to a growth stage) and single soil chemistry measures

Table 6. Effect of phosphate coatings on seeds on the subsequent early growth of Biloela buffel grass seedlings on 20 different red Kandosols from the south-west Queensland mulga region.

Soil source	Mean days from sowing to seedling emergence			Mean days from emergence to L3 appearance			Mean days from L3 appearance to L4 full expansion			Mean length (cm) of leaf 4 lamina		
	−*P*		+*P*	−*P*		+*P*	−*P*		+*P*	−*P*		+*P*
Angellala	4.9		5.7	12.3		6.7	19.8		6.0	6.0		16.2
Arabella	7.2		6.9	10.4		6.1	15.8		6.0	6.7		13.9
Augathella	6.9		7.6	9.3		5.9	13.9		6.1	7.1		13.8
Beechal	7.1		7.1	9.0		6.6	14.3		7.5	7.6		12.6
Boatman	6.6		6.8	10.0		6.6	22.4		6.9	4.9		13.1
Bowra	5.5		5.8	6.5	n.s.	6.0	6.3	n.s.	5.7	16.0	n.s.	16.8
Charleville	6.0	**	7.4	13.5		7.1	35.6		7.6	3.2		11.2
Cheepie	6.4		7.4	10.7		6.3	19.1		6.1	6.3		15.4
Glenbar	5.7		6.3	16.6		9.0	48.5		13.2	2.3		8.2
Kalanoa	7.7		7.6	9.1		5.8	20.3		5.6	5.0		12.8
Kanalba	6.7		7.4	8.9		6.1	10.7	n.s.	7.5	8.6		13.7
Langlo	6.0		6.4	9.8		6.1	11.5		5.8	7.6		13.0
Maryvale	6.6		7.1	10.7		6.3	16.1		6.0	5.6		15.7
Maxvale	6.7		7.4	8.7		5.8	10.0		5.9	9.7		15.2
Ravenscourt	7.1		7.7	8.2		6.2	8.4	n.s.	5.9	10.5		14.9
Rhondavale	7.0		7.0	14.0		7.3	45.9		7.3	2.8		12.0
Rundalua	6.7	*	7.8	9.9		5.9	20.7		6.1	5.1		12.7
Turn Turn	5.6	***	7.5	11.2		6.2	15.6		6.2	6.9		16.1
Winbin	7.2		7.3	8.8		6.1	14.1		5.9	7.4		14.6
Wittenburra	5.9		6.9	9.2		6.1	10.1		5.8	9.1		13.9
l.s.d. ($P < 0.05$)		1.09			1.30			3.57			1.43	

Unexpected statistical effects due to *P* stimulation are highlighted, ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, n.s. non-significant.

were not often high. Up until the tip of leaf 3 appeared, growth rate was best correlated with available P ($r = 0.66$, $P < 0.001$) followed by exchangeable Ca and Al at $r = 0.48$ ($P < 0.05$) and exchangeable K at $r = 0.42$ (see Supplementary Table S1). At later growth stages such correlations, positive or negative, never exceeded 0.6 and often became non-significant, $r < 0.43$, especially for Al (Supplementary Table S1). However, the F.C. of the soil assumed late importance with correlations over 0.5 for time to leaf 4 full expansion (Table 9). In general, correlations were not greatly altered by fitting polynomial relationships.

Much stronger correlations often existed when the ratio of certain soil chemistry parameters was compared to seedling growth rate. Such major correlations related to the ratio of exchangeable Ca and exchangeable Al to each other and to other soil parameters such as percentage Al saturation of cations, base saturation and CEC (Table 9, Supplementary Table S1). The most significant of these at different seedling ages was the ratio of exchangeable Al to Ca ($r = 0.91$), the proportion of Ca in the exchangeable cations ($r = 0.85$) and of exchangeable Al to total cations ($r = 0.80$, Fig. 3*a*). The other very high correlation was between available P and the length of leaf 4, $r = 0.85$ (Table 9). Thus, high levels of available P and Ca amongst exchangeable cations were beneficial while a high proportion of exchangeable Al was detrimental.

Percentage of base saturation by cations had exactly the reverse correlation to that of Al saturation for the same plant growth parameters (Table 9). Exchangeable K often had a similar degree of correlation with buffel seedling growth rate as Ca but the relationship was only occasionally significant ($P < 0.05$, $r >$ abs 0.45), whereas exchangeable Mg and Na levels were unimportant (Supplementary Table S1).

If the most extreme soils of Glenbar and Bowra are excluded, buffel seedling growth rate on Southwest Queensland red Kandosols was still significantly correlated with available P ($r = 0.49$, $P < 0.05$). Likewise exchangeable Al remained strongly correlated with detrimental seedling growth effects (data not shown). In contrast, the very strong

Table 7. Percentage of seedlings reaching 3 and 4 leaf development stages by a specified time after sowing as influenced by phosphate coating and soil source.

Soil source	Percentage of plants with 3 leaves visible				Percentage of plants with 4 fully expanded leaves			
	−*P*		+*P*		−*P*		+*P*	
	Day 12	Day 16	Day 12	Day 16	Day 18	Day 26	Day 18	Day 26
Angellala	0	54	62	100	0	0	62	100
Arabella	0	35	35	96	0	0	35	100
Augathella	0	50	23	95	0	0	32	100
Beechal	0	63	9	100	0	16	5	95
Boatman	0	41	33	94	0	0	33	100
Bowra	62	96	78	94	67	96	78	100
Charleville	0	5	22	74	0	0	22	83
Cheepie	0	36	10	95	0	0	25	100
Glenbar	0	0	0	74	0	0	0	39
Kalanoa	0	33	8	100	0	0	33	100
Kanalba	0	71	8	100	0	50	4	100
Langlo	0	54	52	95	0	32	62	100
Maryvale	0	28	22	91	0	0	39	96
Maxvale	0	84	25	95	0	79	40	100
Ravenscourt	0	89	5	95	0	95	10	100
Rhondavale	0	4	25	90	0	0	15	95
Rundalua	0	37	16	88	0	0	52	96
Turn Turn	0	40	17	96	0	0	26	100
Winbin	0	62	14	100	0	6	18	100
Wittenburra	0	83	22	100	0	74	39	100

Table 8. Summary of statistical analyses (ANOVA) *F* values for seedling growth parameters.

Statistical parameter	Plant parameter				
	Days from sowing to coleoptile emergence	Days from emergence to leaf 3 appearance	Days from L3 appearance to L4 full expansion	Days from emergence to L4 full expansion	Length of Leaf 4 (cm)
			F values		
Soil source (19 d.f.)	4.79^{**}	20.05^{***}	51.72^{***}	62.33^{***}	41.05^{***}
Phosphate (1 d.f.)	21.57^{***}	722.43^{***}	938.25^{***}	1344.43^{***}	1820.06^{***}
Soil × Phos (19 d.f.)	1.07	6.66^{**}	34.47^{***}	36.72^{***}	10.09^{**}
Reps (2 d.f.)	0.30	1.50	2.42	2.56	13.92^{**}

$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

correlations with the ratio of exchangeable Al to exchangeable Ca when P was added ($r > 0.85$, Table 9, Supplementary Table S1) was reduced to nil if the Glenbar, Rhondavale and Charleville soils that support spinifex were excluded. Note that percent Al saturation of the CEC is most important at the earlier growth stage ($r = 0.80$, Table 9) and, while its importance diminishes later, it remains significant ($r > 0.50$). By contrast, available P and exchangeable Ca change far less with time and remain important positive growth factors at all times (Supplementary Table S1).

Inter-relationships amongst the seedling growth rates at different ages and then on leaf 4 size

The rate of early development of buffel seedlings was centred around the time taken between coleoptile emergence and the

Table 9. Correlation coefficients (*r*) between plant growth parameters and major soil parameters that are influential on buffel seedling growth on infertile soils in southwest Queensland. High correlations (≥0.80) are shown in bold font, italics used where no meaningful correlation.

Parameters	F.C. (%)	pH wtr	Bicarb P	Eff. CEC	Exch. Ca^{2+}	Exch. K^{+}	Exch Ca^{2+}/CEC	Exch Al^{3+}	% Al satn	Al^{3+}/Ca^{2+}	Base satn (%)
Sow to emerge −*P*	0.30	0.13	−0.14	0.36	0.39	0.27	0.23	−0.15	−0.37	−0.34	0.33
Sow to emerge +*P*	0.41	*−0.01*	*−0.09*	0.37	0.33	0.37	*0.05*	*0.09*	−0.22	−0.32	0.21
Sow to L3 appce −*P*	−0.35	−0.37	−0.66	−0.35	−0.48	−0.42	**−0.82**	0.48	0.72	0.72	−0.73
Sow to L3 appce +*P*	−0.14	−0.31	−0.39	−0.13	−0.23	−0.26	−0.62	0.37	0.42	0.60	−0.42
Sow to L4 F/exp −*P*	−0.53	−0.27	−0.58	−0.40	−0.49	−0.54	−0.71	0.35	0.65	0.70	−0.65
Sow to L4 F/exp +*P*	−0.32	−0.33	−0.35	−0.28	−0.36	−0.39	−0.63	0.32	0.48	**0.86**	−0.47
Length Leaf 4 –*P*	0.27	0.33	**0.85**	0.20	0.31	0.21	0.69	−0.37	−0.56	−0.47	0.58
Length Leaf 4 +*P*	0.14	*0.04*	0.57	*0.00*	*0.06*	*0.09*	*0.41*	*−0.05*	−0.21	−0.61	0.19
Emerge to L3 appce −*P*	−0.43	−0.39	−0.59	−0.45	−0.57	−0.49	**−0.85**	0.51	**0.80**	0.79	**−0.80**
L3 appce to L4 *F*/Exp −*P*	−0.55	−0.25	−0.56	−0.40	−0.48	−0.55	−0.68	0.32	0.63	0.69	−0.63
Emerge to L4 *F*/Exp −*P*	−0.54	−0.28	−0.57	−0.42	−0.51	−0.55	−0.72	0.36	0.66	0.72	−0.66
Emerge to L4 *F*/Exp Δ*P*[A]	−0.54	−0.26	−0.59	−0.41	−0.50	−0.54	−0.70	0.36	0.66	0.64	−0.66

For $P < 0.05$ r>abs 0.43 and for $P < 0.01$ r >abs 0.55.

[A] Δ*P* means the net effect of using a phosphate seed coating instead of no coating.

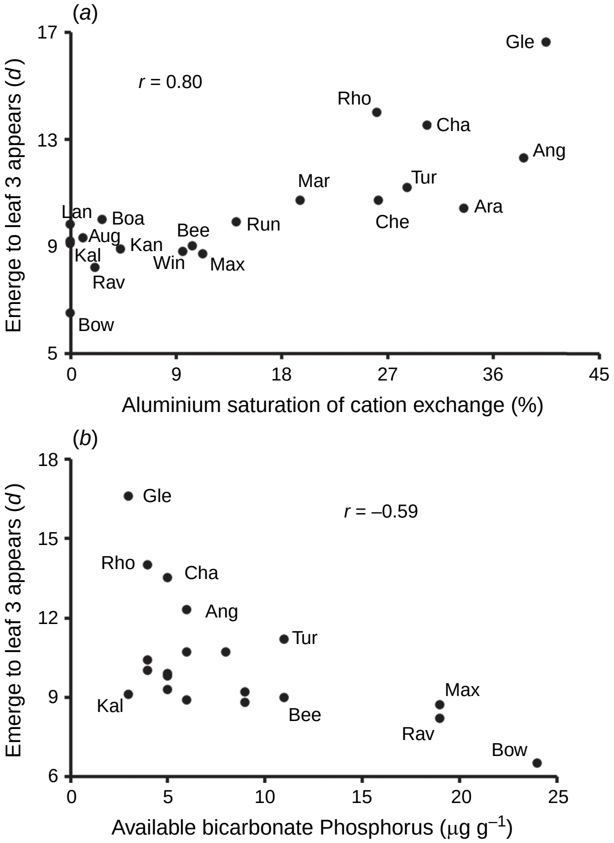

Fig. 3. Significant correlation between the time needed for the tip of the third leaf of buffel grass seedlings to appear in the absence of added phosphorus fertiliser and (*a*) percentage aluminium saturation of the exchangeable cations and (*b*) the level of available phosphorus in the soils tested. Labels are the first three letters of the soil collection site name – see Table 1.

appearance of the tip of the third leaf. The longer that took, the longer the time interval between then and full expansion of leaf 4 where no P seed coating was used (Fig. 4*a*). Most took just over 6 days to emerge under the prevailing glasshouse conditions and then another 6 days for the third leaf to appear if adequate P was available (Table 7) and then another 6 days to fully expand the fourth leaf under favourable soil P nutrition. Under very low available soil P levels this total 18 days increased to up to 70 days for some soils. Even when the seed was coated with P fertiliser, that critical growth phase of leaf 3 very clearly controlled the total time taken between seedling emergence and full expansion of leaf 4 (Fig. 4*b*, $r = 0.96$). The very strong correlations between early and later measures of seedling growth rate (Supplementary Table S2) would indicate no markedly greater lack of soil nutrition during the later stages of the seedlings' growth.

The length of leaf 4 in the absence of a P stimulus was inversely correlated with the time taken to grow leaf 3 and leaf 4 (Fig. 5) but it was a curvilinear relationship, with available soil P a key correlated factor. Soils from spinifex-dominated landscapes, Rhondavale and Glenbar, carried that effect to extremes.

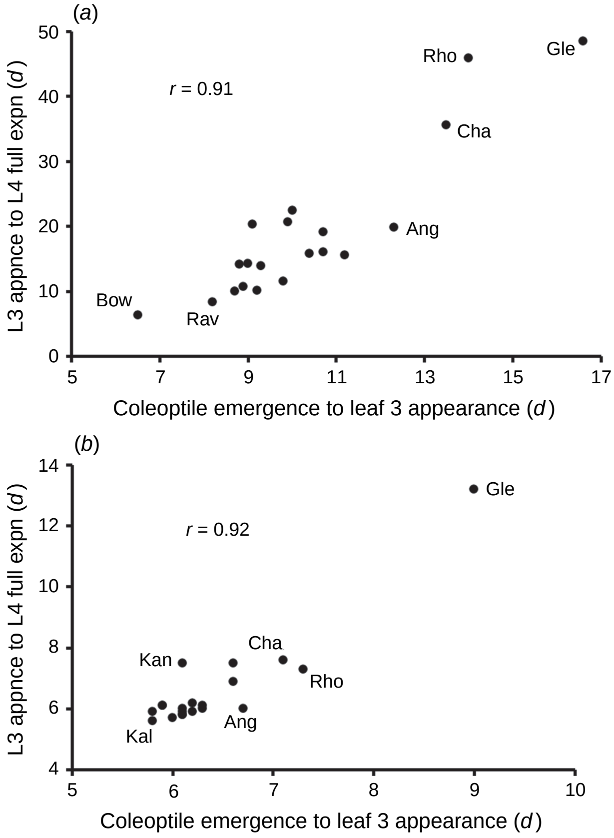

Fig. 4. Very close positive correlation between the rate of growth immediately after buffel grass seedling emergence and that at a later growth stage up until the fourth leaf was fully expanded for both (*a*) uncoated seeds and (*b*) seedlings grown with a phosphorus seed coating. Labels are the first three letters of the soil collection site name – see Table 1.

Fitted equations

Simple linear regressions relating soil parameters to speed of seedling growth were tested and some reached a significant R^2 ($P < 0.05$) in the range of 0.4–0.6. The best was

$$\text{Y \{Days to leaf 3 apex appearance\}} = 0.13\text{X \{\% A1 satn\}} + 8.4 \; (R^2 = 0.645)$$

Multiple regression

Numerous multiple regression relationships between seedling growth and soil parameters were tested, particularly involving available P, exchangeable Ca, pH, C.E.C, exchangeable Al and derivatives of the latter. When exchangeable acidity was included in the mathematical analyses, the exchangeable Ca parameter generally dropped out, indicating that these were fairly interchangeable and the latter of

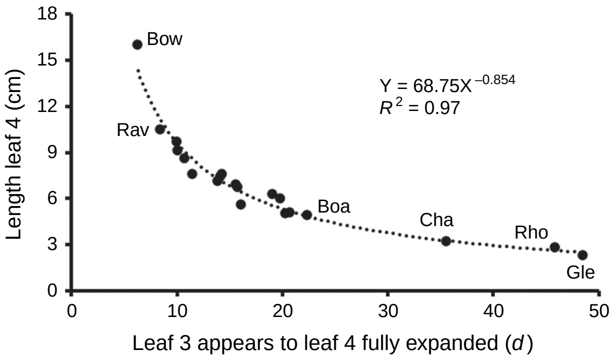

Fig. 5. Curvilinear relationship between the rate of buffel seedling growth in different soils and the length of leaf 4 where there had been no phosphate fertiliser coating applied to the seeds before sowing. Labels are the first three letters of the soil collection site name – see Table 1.

less predictive value. The best-fitting multiple regression equations were

$$Y1 = 9.90 + 0.183\,(\%\ \mathrm{A1\ satn}) - 3.36\,(\mathrm{Exch.\ acidy}) - 0.10\,(\mathrm{Bicarb\ P})\ (R^2 = 0.78)$$

where $Y1$ is days between coleoptile soil emergence and the appearance of the apex of leaf 3 in the absence of a P seedcoat.

For the next stage of growth up to full expansion of leaf 4, the same parameters were less useful at predicting buffel seedling growth rate ($R^2 = 0.55$) but still as useful as any other combination of the soil parameters assayed.

$$Y\,2 = 20.46 + 0.805\,(\%\ \mathrm{A1\ satn}) - 19.46\,(\mathrm{Exch.\ acidy}) - 0.59\,(\mathrm{Bicarb\ P})\ (R^2 = 0.55)$$

where $Y2$ is days between the appearance of the apex of leaf 3 and full expansion (ligule visible) of leaf 4.

The early growth rate of seedlings was almost as well explained by the ratio of exchangeable Al to the sum of exchangeable Ca plus Mg. The linear correlation coefficient was 0.76 and the fitted equation

$$Y\,3 = 8.7 + 5.18\,(\mathrm{Exch\ A1}/(\mathrm{Exch\ Ca} + \mathrm{Exch\ Mg}))\ (R^2 = 0.56)$$

where Y3 is the same as Y1.

Discussion

Two soil parameters were shown to be most influential in determining how readily seedlings of buffel grass might establish on a range of infertile, acid soils in south-west Queensland, available P and the ratio of exchangeable Al to exchangeable Ca (Table 9). Earlier studies had shown that buffel grass seedlings did not grow well on similar acidic soils unless P fertiliser was applied (Christie 1970; Silcock and Smith 1984). In the former case, a basal dressing of macronutrients (N, P, K, S) plus a pH-correcting level of lime ($CaCO_3$) were applied, while the latter grew seedlings without a basal nutrient application. Both studies used soil from the Charleville town common from whence one soil from the current experiment (Cha) was sourced (Table 1). Christie (1970) achieved a significant response by the Biloela cultivar to lime, nitrogen and K once the P deficiency was alleviated. Hence the marginal importance in the current trial of the level of exchangeable Ca and K agrees with those findings (Table 9) but Christie (1970) showed lime raised the soil pH to near neutral which disguised the potential deleterious impact of the appreciable level of exchangeable Al (see below). Other soil factors such as levels of Na, Mg, Cl and salts were unimportant (Supplementary Table S1) which is not surprising for sandy-surfaced soils in the region (Dawson and Ahern 1973). All soils were non-saline and non-sodic (Ahern 1990), and no significant correlation existed between buffel grass seedling growth rate and Electrical Conductivity, exchangeable Na, exchangeable Mg or Cl (Supplementary Table S1).

Phosphorus fertiliser stimulates shoot and root growth (Silcock 1975) and thus potentially enhances seedling establishment in arid environments where rapid access to deep soil moisture would correlate with greater establishment success. Christie (1970) also showed that enhanced availability of P in the substrate improved the moisture stress tolerance of buffel grass, as did Edye (1961) on spinifex soils at Yalleroi, central Queensland.

Critical soil nutrient levels for buffel grass

As seedlings on unfertilised Bowra soil grew as rapidly as those receiving P fertiliser, it appears that $1.2\,\mathrm{meq}^{-100\mathrm{g}}$ of exchangeable Ca is adequate for optimal seedling growth in a very sandy soil. So too was $0.13\,\mathrm{meq}^{-100\mathrm{g}}$ of K and a total effective CEC dominated by Ca of $1.56\,\mathrm{meq}^{-100\mathrm{g}}$ (Table 4), for the amount of available nitrogen that probably existed in the sieved soil. The very low levels of Na were non-toxic all round as was exchangeable Al except on those very acid soils with an appreciable percentage of the soil CEC provided by Al (Fig. 1*a*, Table 7 versus Table 4).

The role of soil pH

Soil pH *per se* was only weakly correlated with seedling growth rate (Table 9, maximum −0.39) irrespective of the quantification method used. However, it had a significant effect on other soil parameters such as exchangeable Al (Fig. 1*a*) and Ca (Fig. 1*b*), which in combination, strongly controlled seedling growth (Table 9). Likewise, CEC was only moderately correlated with seedling growth rate (Table 9, maximum $r = 0.45$) but was highly correlated with the level of exchangeable Ca (Fig. 2*b*) which, via its proportion to that of exchangeable Al, strongly controlled seedling growth (Table 9, Supplementary Table S1). Interestingly, the maximum correlation coefficient associated with exchangeable Al level was -0.51 for emergence to leaf 3 appearance if no P coating was used, yet as a proportion of all cations the correlation rose to 0.80 and to 0.79 for the exchangeable Al/Ca ratio (Table 9).

The chemistry of the Glenbar, Rhondavale and Charleville soils strongly controlled buffel seedling growth even after the phosphate deficiency was corrected, far more than was the case for all the other soils. The former two sites supported spinifex (*Triodia marginata*) and heath-type shrubs (Table 1) while anecdotal stories and the existence of dense spinifex nearby suggest that the Charleville town common site historically carried spinifex as well before very dense mulga and heavy grazing eliminated it. Insufficient nitrogen or soil microflora may have been the reason, despite the uncertainties discussed earlier based on the work of Silcock *et al.* (1976) and Armstrong *et al.* (1992).

Other soil fertility factors

In general, the 20 surface soils used were not fertile (Tables 3, 4) but, after sieving, sufficient soil nitrogen was seemingly mobilised in most soils so that small buffel grass seedlings grew quite rapidly, provided there was extra available P close to the germinating seed (Table 7). The exception was the Glenbar soil which had an extremely low level of available Ca and a very high level of exchangeable Al. Other soils which appeared to show late signs of nutrient insufficiency by virtue of a slowing seedling growth rate from P-coated seeds after leaf 3 appeared were Kanalba (only 4% of seedlings with 4 fully expanded leaves by day 18), Beechal (5% by day 18) and Ravenscourt (only 10%) against a mean of 38% for all other soils except Glenbar, and some were over 60% by this time (Table 7). Which nutrients may be involved is unclear but according to Ahern (1990) the measured levels of exchangeable Ca, K, and Mg were sometimes low, particularly Ca in the Glenbar soil. Assigning numbers indicative of likely suboptimal plant growth depends on soil type, plant species and associated nutrient levels but Ahern (1990) reviewed published reports and provided considered values for the soils of SW Queensland, namely 2 $\text{meq}^{-100\text{g}}$ for Ca, 0.5 $\text{meq}^{-100\text{g}}$ for Mg and 0.2 $\text{meq}^{-100\text{g}}$ for K. Hence Kanalba, Beechal and Ravenscourt soils would rate as adequate for these three nutrients, but not Glenbar (Table 4). Conversely, Angellala and Bowra would be regarded as having inadequate levels yet did not exhibit unduly slowed later growth.

As described earlier, soil organic matter is readily mineralised to released nitrate nitrogen by drying and rewetting and by breaking up soil by sieving (Birch 1958; Craswell and Waring 1972). Thus, it was expected and has been shown by earlier pot studies using very similar soils (Silcock *et al.* 1976; Silcock 1975, 1980) and this experiment that sufficient soil nitrogen is available from most acid red kandosols to maintain healthy buffel grass seedling growth for at least several weeks in large pots of sieved soil, if adequate extra P is provided. Sieving may disrupt soil microbial ecosystems in the short term but the extent of that is unpredictable because it depends on the species of any organism (Tommerup and Abbott 1981) and the main state that organisms like VAM are in, spore or mycelial stage, at the time (Armstrong *et al.* 1992). VAM infection of roots can potentially augment the uptake of soil P from infertile soil (Hayman 1983; Thompson 1987) but Armstrong *et al.* (1992) were only able to achieve that outcome with buffel grass by liming Charleville soil to pH 5.8. Many of the soils now reported on were more acidic than that and no data about VAM was collected.

The current pot trial was not designed to re-examine that potential effect by micro-organisms for a wider range of acidic Kandosols, but it is a potential interacting factor in the field that may vary with the degree of clay in a soil (Rao *et al.* 1996). Against that, successful oversowing of grasses in the field almost universally requires appreciable surface soil disturbance and damage to existing herbaceous plants (Norman 1961; Cook 1980; DAF Qld 2022) thus nullifying, in practice, any effect of an intact soil microflora ecosystem.

Interpreting the correlation between buffel seedling growth rate and the soil chemical parameters

Simple correlation coefficients can provide a useful first look at complex data but often a graphical plot shows more clearly how causative a parameter is over the entire parameter range. Figs 3*a*, *b*, 4*a* data about the time between coleoptile emergence and the appearance of leaf 3 could be considered to have 'outliers' at both ends of the soil bicarbonate P extraction range – Glenbar and Bowra. The linear correlation for the 20 soils against available P is reasonable at -0.59 (Fig. 3*b*), but if only the eight soils labelled along a narrow corridor between these extremes are included in an analysis (Gle, Rho, Cha, Ang, Tur, Max, Rav and Bow), the correlation coefficient becomes extremely strong at -0.965 over a P extraction range of 3–24 $\mu\text{g g}^{-1}$. Then again, if only the 13 soils from the middle of the growth rate response range are considered (Kal to Tur), there is no correlation with bicarbonate P extraction in the range 3–11 $\mu\text{g g}^{-1}$, $r = 0.045$. There is no obvious collection-site factor that could facilitate either such soil grouping.

Most very high correlation coefficients (>0.85) between soil parameters and seedling growth rate and size involved ratios of exchangeable Al or exchangeable Ca, but were due primarily to the outlier effects of the Charleville, Glenbar and Rhondavale soils. Many other relationships surpassed a significant ($P < 0.05$) r value of 0.45, but only one exceeded 0.6, namely available P on time to leaf 3 appearance

($r = -0.66$, Table 9). Thus, the correlations with exchangeable K for different growth stages of between -0.49 and -0.55 and for exchangeable Ca between -0.48 and -0.57 were significant but not dominant.

Major soil parameter interactions

The F.C. of the soils was strongly correlated with their CEC (Table 5) which conforms to the general pattern of increases in both these parameters as the percentage clay increases (Ahern 1990). No data are directly available for clay content for these present soils but commonly lies between 15 and 30% (Dawson and Ahern 1973; WARLUS 1990), and the notes in Table 1 point to the very sandy nature of the soils with the lowest measured CEC, F.C. and air-dry moisture content, namely Glenbar, Rhondavale, Bowra and Angellala (Tables 2, 4). The soils with the greatest F.C. and air-dry moisture content, Wittenburra and Ravenscourt, had a relatively high CEC by contrast (Table 4).

The main interactions of importance were with soil pH and exchangeable soil cations. The lower the soil pH, the lower the total CEC of these soils in general (Table 5, $r = 0.735$) and concurrently the lower the amount of exchangeable Ca (Fig. 1*b*), K and Mg (Table 5). Conversely, lower pH meant much higher exchangeable Al (Table 5), but there is a clear lack of it when the pH was greater than 5.5 (Fig. 1*a*). Ionic Al only forms in soils at a pH below 5.5 (Rodríguez *et al.* 2009), but the consequence of that for growth of buffel depended on how much Ca existed to counteract aluminium's detrimental effects, mostly on root development (Kochian *et al.* 2005). In the 20 soils tested, there was a very strong inverse correlation between seedling growth rate and the ratio of exchangeable Al to that of Ca, $r = -0.86$ to -0.91 (Table 9). Hence the rate of seedling root penetration down a soil profile would be constrained and thus the risk of dehydration and death much increased on such soils in semiarid climates. Related measures of ionic Al content, exchangeable acidity and percentage Al saturation, had similar correlations with seedling growth rate suppression (Table 9, Supplementary Table S1).

Because the Charleville soil had a disproportionately high level of exchangeable Al for its pH, 0.66 $\text{meq}^{-100\text{g}}$ at pH 5.5 compared to the other soils (Fig. 1*a*), the huge responses to P fertiliser reported for this soil by Christie (1970) and Silcock and Smith (1984) are probably towards the extreme of what might be achieved by using P fertiliser on other mulga and red Kandosol soils. Conversely, the ability of buffel grass to naturally colonise or persist once sown on various red Kandosols in semiarid Australia may be better on other acidic soils with lower levels of exchangeable Al, independent of soil P level.

Broader environmental interactions

Other factors such as mean minimum temperature, seasonality and amount of rainfall (Cox *et al.* 1988), surface soil friability, woody plant density and subsoil chemistry (Pastures Australia 2007) will also have an effect on the invasive potential of buffel grass and its persistence once established (Friedel *et al.* 2007).

Mexican research has suggested that surface soil disturbance is a major factor in the incursion of the American cultivar of buffel grass (De la Barrera 2008) and that it established and persisted best on sandy soils (Ibarra-F *et al.* 1995). Australian experience would agree with both those conclusions (Friedel *et al.* 2007). Both these Mexican studies found total soil nitrogen to be well correlated with buffel spread, but De la Barrera (2008) was only studying an area with high available P soils. Both studies dealt with neutral pH soils, so no assays were done for exchangeable Al and a major parameter controlling buffel seeding growth in our study was thus irrelevant. An Australian study by Eyre *et al.* (2009) found no correlation between soil nitrogen level and the presence of buffel grass, and buffel pasture rundown studies would suggest that lack of available nitrogen does not lead to persistence problems, merely reduced productivity of the pasture (Peck *et al.* 2011). Ibarra-F *et al.* (1995) found that buffel grass spread more and persisted better on more infertile soils based on 167 sites in Texas and Sonora. Likewise, the present results from soils such as Bowra would also suggest that, climatic factors ignored, low fertility *per se* is not a major issue for buffel grass colonisation and survival provided soil available P is adequate ($>10\,\mu\text{g}\,\text{g}^{-1}$, Cook 2007), Ca is the dominant cation and exchangeable Al is negligible.

Climatic factors were also shown by Ibarra-F *et al.* (1995) to be important in determining where buffel grass was invasive or persistent, but again that was irrelevant in the present restricted study area. Different multifactorial models generated by Ibarra-F *et al.* (1995) to explain where buffel grass thrived did highlight exchangeable Ca and K, both of which showed significant correlations with seedling growth in the present study. A potentially important difference however, is that their Ca levels were mostly considerably greater than the soils reported here – 35.9 ± 26 $\text{meq}^{-100\text{g}}$ compared to 1.8 ± 1.3. However, these results are derived from different cultivars of a species that is genetically quite diverse (Scott 2014; PlantZAfrica 2021) and hence some genotypes may differ in their nutrient requirements. That may partly explain why nutrition studies from the cultivar commonly grown in Texas and Mexico produce results that seem at variance to those from Australia where a range of cultivars exist.

Conclusions

Adequate available soil P is always essential for buffel grass to establish from seed but excessive levels of exchangeable Al in such soil can still slow seedling growth appreciably. If the soil lacks exchangeable Al and available P is above about

$20\,\mu g\,g^{-1}$, buffel grass seedlings can still grow very well on quite low fertility, acid soils provided Ca dominates the exchangeable cations at a concentration of at least $1.2\,\text{meq}^{-100\text{g}}$. Strong surface soil acidity below pH 5.5 in water is not an inherently big constraint on buffel grass seedling growth but, it usually is because it is normally associated with high levels of exchangeable Al and often a low proportion of Ca in the exchangeable cations. Whether buffel grass is regarded as desirable or not in any part of the sub-tropical world depends on many factors but it is most likely to be regarded as potentially weedy if there is a combination of the soil chemical factors described above along with soil disturbance, a relatively friable, loamy or sandy soil surface texture and low woody plant cover.

Supplementary material

Supplementary material is available online.

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Data availability. The original data are retained in the Queensland Department of Agriculture Archives, Salisbury, Brisbane and may be viewed by applying to the General Manager of Animal Science of that organisation.

Conflicts of interest. I declare that there are no conflicts of interest associated with this research and its reporting.

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