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CROP & PASTURE SCIENCE

Chickpea and lentil show little genetic variation in emergence ability and rate from deep sowing, but small-sized seed produces less vigorous seedlings

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ABSTRACT

Context. Germination and emergence are key to successful annual crop establishment. Emergence rate depends on germination rate, sowing depth, and rate of pre-emergent shoot elongation. The rate at which a shoot grows prior to emerging from the soil becomes significant when crops such as chickpea (*Cicer arietinum* L.) and lentil (*Lens culinaris* Medik.) are deep sown to utilise moisture below the conventional sowing zone. **Aims.** In seeds of contrasting size, we aimed to compare the ability of chickpera and lentil varieties to emerge from deep sowing. Here we describe genetic variation for epicotyl growth rate, and phenotypic variation for epicotyl and root growth rates and biomass partitioning, of chickpea and lentil, as they relate to seed size. We further assess the impact of deep sowing and soil type on emergence, establishment and yield of the two species. **Methods.** Epicotyl elongation rates, root growth and seedling biomass partitioning were determined in controlled environment studies, using soil tubes. Field trials were conducted on two different soil types at two sowing depths. **Key results.** Most of the variance in epicotyl growth rate could be attributed to species rather than variety. Although epicotyl emergence was faster in lentil, chickpea epicotyl growth rates were higher than those in lentils and unrelated to seed size, whereas growth rates in lentils were weakly correlated to seed size ($r = 0.31$). Root development and epicotyl diameter appeared to be traded for maintenance of growth in smaller seeds of both species. In the field, sowing depth did not affect emergence, establishment or yield of chickpeas at either site. Deeper sowing resulted in minor reductions in emergence of lentil at one site, although biomass and yield were not affected. **Conclusions.** Emergence of both crops was unaffected by deep sowing (to at least 200 mm) under controlled environment and sandy field conditions. There was minimal genetic variation for the measured parameters within a species. Seed size was of little importance for emergence rate; however, shoot growth rate from small seeds was maintained by reducing seedling vigour. **Implications.** Seed size should be considered when deep sowing lentils in order to maintain high seedling vigour. Further work is needed to understand how environmental factors influence seedling emergence from depth.

Keywords: biomass partitioning, chickpea, deep sowing, emergence, epicotyl growth, legume, lentil, pulses, seed size, sowing depth.

Introduction

Establishment is a key phase in the life of a plant. Germination and emergence are important factors in successful annual crop establishment, particularly as farmers try to balance risk of heat and frost across the growing season and maximise yield via changes to traditional sowing times, particularly introducing early sowing to extend the growing season (Hunt *et al.* 2019). Complete and uniform emergence of healthy seedlings, leading to successful establishment of a crop canopy and root system, is vital for the rapid growth and development needed to attain yield potential. A crop that establishes poorly is at risk of competition from weeds and can be more susceptible to other abiotic stresses.

Emergence rate – the time it takes for a shoot to appear at the soil surface – is a combination of germination rate, sowing depth, and the rate of pre-emergent shoot growth. These three factors are influenced by temperature, moisture, and soil characteristics such as compaction and aeration; biotic factors such as soil microorganisms may also play a role (Gardarin *et al.* 2016; Lamichhane *et al.* 2018).

The rate at which a shoot elongates prior to emerging from the soil becomes significant when crops are deep sown. Predicting when a crop will emerge post-sowing can be integral to deciding when to sow and which variety to sow, or if sowing is even advisable. Deep sowing is of particular interest in rainfed environments as a method to manage seasonal rainfall variation and to utilise moisture below the conventional sowing zone (Siddique *et al.* 1998; Emenky and Khalaf 2008). In some growing regions such as south-west and south-eastern Australia, there have been distinct changes in rainfall patterns and a less predictable season break (Cai *et al.* 2012; Scanlon and Doncon 2020; Flohr *et al.* 2021). Declining autumn rainfall can lead to insufficient moisture for germination near the soil surface during the desired sowing window. However, summer rainfall or small early autumn rainfall events can result in subsurface moisture being available during the sowing window, even if surface soils are dry. In tropical environments where crops grow on shallow water tables of stored monsoonal soil water, deep sowing can be important to access stored soil moisture for germination (Polthanee 2001; Buakum *et al.* 2013). In addition to allowing growers to exploit subsoil moisture and achieve optimal sowing times, deep sowing can reduce seed predation and assist in avoiding phytotoxicity of pre-emergent herbicides.

Not all crops are suitable for deep sowing. Those crops with hypogeal germination (where cotyledons stay underground) tend to be more resilient to sowing deeper than 50 mm; however, the mechanism behind this is has not been clearly elucidated. The commonly held explanation is that pushing a thin epicotyl (pre-emergent embryonic stem) through the soil is less energetically demanding than pulling the cotyledons through the soil, and that more seed resources would need to be allocated to a hypocotyl (the stem-like organ between the radicle and the cotyledons) in order to support the cotyledons (Kluyver *et al.* 2013). Hypogeal monocotyledon crops such as wheat, barley and oats emerge from depth through the growth of a modified leaf called the coleoptile, and sometimes the extension of the first internode or mesocotyl. The potential length of these organs has been studied in detail across numerous varieties, and in all three species, significant genetic variation has been shown (Radford and Key 1993; Paynter and Clarke 2010; Mohan *et al.* 2013; Luo *et al.* 2020; Rebetzke *et al.* 2021). Emergence ability from depth has also been demonstrated in most hypogeal dicotyledonous crops (i.e. lentil, pea, chickpea, and faba bean); however, the extent of genetic variation for emergence ability from depth and shoot growth rates within these species is less well understood.

In hypogeal dicotyledon crops such as chickpea and lentil, the plumule (embryonic stem apex, bearing the first leaves) is pushed to the surface through the extension of the epicotyl. The epicotyl growth rate of these species is unknown and the effect of environmental conditions on emergence rate has not been well quantified. Time to emergence has been measured in both species, giving some indication of pre-emergent shoot growth rates; however, these rates cannot be separated from germination times. In addition, some publications report no intra-specific variation for emergence rate (Angus *et al.* 1980; Soltani *et al.* 2006; Safahani *et al.* 2017), whereas others found that variety influenced emergence rate (Gan *et al.* 2002; Richards *et al.* 2020). Many of these studies were larger field experiments, so potentially, these emergence rates are confounded with abiotic factors (particularly temperature and moisture availability), spatial variation and seed size or quality.

Seed size is considered important when sowing at depth and sowing guides generally recommend larger seed for deeper sowing. The supposition that larger seed, having greater carbohydrate reserves, would achieve higher successful emergence from depth than smaller seed seems logical; however, there is surprisingly little evidence to support this. In several smaller studies of 2–10 varieties of wheat, seed size has been shown to correlate with coleoptile length (Cornish and Hindmarsh 1988; Botwright *et al.* 2001*b*; Moussavi Nik *et al.* 2011), with small seed having reduced establishment at depth (French 2015). On the other hand, a large screening of 662 wheat varieties contradicts these studies, showing with both coleoptile length and emergence had little correlation with seed size (Mohan *et al.* 2013). A single study showed no difference in days to emergence in the field between large and small kabuli chickpeas (Gan *et al.* 2003). To our knowledge, no direct correlation with seed size and emergence ability or speed of emergence from depth has been shown for lentil or chickpea.

In grain crops, seed size is influenced by both genetic and environmental components. Farmers concerned with establishment exploit interactions of the two components by choosing varieties with a desirable seed size and then further grading these to select the largest seeds, although evidence supporting the impact of this practice on establishment is similarly sparse (Harker *et al.* 2014; Brill *et al.* 2016).

This study focuses on genotypic and phenotypic variations with respect to seed size of both lentil and chickpea, in order to address the knowledge gaps identified and understand how these factors influence emergence. Understanding pre-emergent shoot phenotypic variation in relation to seed size is valuable to management decisions for released varieties and in defining breeding targets around emergence and establishment.

In this paper we report the results of two controlled environment experiments, and a third experiment comprising field trials at two locations. In the first experiment, we looked for genetic variation by determining epicotyl growth rates in 10 commercial varieties of lentil (*Lens culinaris* Medik.) and nine varieties of chickpea (*Cicer arietinum* L.). In the second experiment, we studied phenotypic variation by grading seeds of a single variety of each of lentil and chickpea into size groups and assessing seed size effects on epicotyl growth rate and biomass partitioning. We hypothesised that seed size would drive emergence rate but not ability to emerge from depth, and that biomass partitioning would be affected by seed size when these species are sown at depths <150 mm. In the third experiment, we examined the effect of soil type and sowing depth on emergence and establishment by sowing one variety of each species at two sites with contrasting soils, at standard (50 mm) and extreme (200 mm) sowing depths.

Materials and methods

Seed sources

Seed for Expt 1 (genetic variation) was sourced from well-watered glasshouse trials for commercial varieties of both lentil and chickpea, such that the two species did not have the same maternal conditions. Seed used in Expt 2 was sourced from single plots from field trials in Esperance in 2018; this provided a larger range of seed size from a single origin, avoiding confounding maternal effects. All seeds for the controlled environment experiments had seed moisture standardised to ~10% by incubating for 3 weeks in humidity chambers (Gold and Hay 2008); the exact water content of individual varieties or size groupings was estimated using a hygrometer (HC2-AW probe; Rotronic, Bassersdorf, Switzerland). Bulk seed for field trials was sourced from commercial seed suppliers. Chickpea seed had been pre-treated with the fungicide P-Pickle T (Nufarm, Mebourne, Vic., Australia).

Controlled environment experiments and conditions

Several methods of measuring epicotyls were prototyped: growing through air, soil or within a roll of germination paper. The three methods produced significant differences in elongation growth rate (Supplementary materials Fig. S1). We chose to measure seedlings in soil tubes because it was the protocol most representative of field conditions.

Soil used was a 3:1 mix of sand and loam potting mix (Richgro, Perth, WA, Australia). Starting soil moisture was 11.0% (±0.4%), which is ~60% of the field capacity of 17.4%. This provided non-limiting water to the seeds and therefore soil moisture did not affect emergence time or germination percentage (Hosseini *et al.* 2009). Bulk density across both experiments was 1.26 (±0.02) g cm^{-3}. Prior to the start of each experiment, dry soil was mixed with water in 50-kg batches by using a cement mixer, and no further moisture was added during the experiments.

Controlled environment experiments were conducted at 20°C constant room temperature, and soil temperature within the soil tubes was 20.0°C (±0.7°C) across all experiments. Degree-hours were calculated using 20°C and a base temperature of 0°C for both species (Covell *et al.* 1986; Ellis and Barrett 1994; Sleimi *et al.* 2013; Rohban *et al.* 2018).

Experiment 1: genetic variation in epicotyl growth rate and diameter within and between pulse species

The experiment was a randomised complete block design with four replicates of each variety. Each replicate consisted of two seeds in a single pot. Mean seed weight for each variety was determined and three seed groupings (small, medium, large) were defined for each species (Table 1). Lentil groups were 40, 50 or 60 (±3) mg; chickpea groups were 170, 220 or 300 (±10) mg. Individual seeds were then weighed and only those within the size range were selected for the experiment.

Capped plastic tubes 85 mm by 350 mm were used as pots. Moist soil was packed volumetrically in 50-mm layers, and seeds were sown to 250 mm. Once filled, the soil was topped with a 20-mm layer of plastic beads to inhibit evaporation over the experiment. Soil moisture in each layer at the end of the experiment did not deviate significantly from starting levels.

Four pots of each variety were destructively harvested at eight intervals of 20 degree-days from 40 to 180 degree-days. Soil was gently shaken onto a tray and the seedlings were washed out of the soil. Epicotyl diameter (20–30 mm above the seed) and length from the seed to the top of the plumule arch were measured by using a ruler or digital calipers.

Experiment 2: phenotypic variation with seed size within and between pulse species

Small, medium and large subsamples of individual varieties (chickpea cv. Striker and lentil cv. Bolt) were selected from a single maternal source, these species are widely grown in Western Australia, across a range of rainfall zones. Before sowing, three size groupings of each species were roughly grouped by seed diameter and then bought to a standard seed moisture in humidity chambers (see above). Individual seeds were then weighed and only those within the size ranges nominated were selected for the experiment. Three size groups were used per species: for lentils 20, 40 and 60 (±3) mg; and for chickpeas 100, 200 and 300 (±10) mg.

Table 1. Chickpea and lentil varieties used in this study.

Species	Variety	Type	Fresh seed weight (mg)	Experimental size group	Epicotyl elongation rate (mm degree-hour^{-1})
Chickpea	PBA Drummond	Desi	220	Medium	2.05
Chickpea	Genesis 090	Kabuli	300	Large	2.23
Chickpea	Genesis 114	Kabuli	300	Large	2.10
Chickpea	Genesis 836	Desi	170	Small	2.03
Chickpea	PBA HatTrick	Desi	170	Small	2.08
Chickpea	Jimbour	Desi	170	Small	2.05
Chickpea	Neelam	Desi	220	Medium	1.92
Chickpea	PBA Slasher	Desi	220	Medium	1.92
Chickpea	PBA Striker	Desi	300	Large	1.96
Lentil	PBA Ace	Red	50	Medium	1.39
Lentil	PBA Blitz	Red	60	Large	1.52
Lentil	PBA Bolt	Red	50	Medium	1.70
Lentil	PBA Flash	Red	60	Large	1.78
Lentil	PBA Greenfield	Green	60	Large	1.65
Lentil	PBA Hallmark	Red	50	Medium	1.48
Lentil	PBA Highland	Red	40	Small	1.51
Lentil	PBA Hurricane	Red	40	Small	1.59
Lentil	PBA Jumbo	Red	60	Large	1.65
Lentil	PBA Jumbo2	Red	60	Large	1.70

Seed weight is ±5 mg for lentils and ±10 mg for chickpea. Epicotyl elongation rates measured in soil-grown seedlings sown at 250 mm depth with soil moisture content 11.0% (±0.4%) at 20°C. Epicotly elongation rates are calculated using the slopes from regression analysis.

Because seeds were being sown deeper (to 350 mm) and root measurements were being taken in this experiment, longer capped plastic tubes (85 mm by 600 mm) were used as pots. Pots were filled volumetrically in 50-mm layers and topped with plastic beads as in Expt 1. Four replicate pots were filled for each seed size at each sampling time point, and each pot contained single seed of known mass and seed moisture.

Pots were harvested at six intervals of 40 degree-days from 80 to 280 degree-days. At harvest, soil was gently shaken onto a tray and the seedling was washed out of the soil. Epicotyl and primary root lengths were measured, secondary roots counted and the longest measured, and then the seedling was broken into component parts of seed, root and shoot (epicotyl and plumule). Seeds were dried at 130°C for 1 h (ISTA 2017), and shoots and roots were dried at 60°C for 24 h. An estimated initial seed dry mass was calculated from the initial seed mass and its seed moisture content; the difference between this value and the total seedling dry mass at harvest was assumed to be from loss via apparent respiration (Botwright *et al.* 2001*a*).

Experiment 3: field trials

Field trials were sown near Merredin (−31.451, 118.216) on a brown deep loamy duplex (Soil Groups of Western Australia, Soil Group 505; Schoknecht and Pathan 2013) and Dandaragan (−30.657, 115.768) on a pale deep sand (Soil Group 444; Schoknecht and Pathan 2013), Western Australia, during May 2019 (Table 2, Fig. S2). Chickpea cv. Striker and lentil cv. Bolt were sown at either standard (50 mm) or extreme (200 mm) sowing depths. Trials were of replicated (n = 4) split-plot design with depth treatment as the main plots and species as subplots. Plots were 10 m long with eight rows on 250-mm row spacing. Standard

Table 2. Field experimental conditions with sowing depths and dates for chickpea PBA Striker and lentil PBA Bolt.

Site	GSR (mm)	Sowing date	Soil moisture at sowing (%)		Soil pH(CaCl$_2$)	
			0–100 mm	100–200 mm	0–50 mm	100–200 mm
Dandaragan (calcareous pale deep sand)	221.3	27 May	1.6 ± 0.2	1.8 ± 0.3	6.5 ± 0.2	6.1 ± 0.5
Merredin (brown deep loamy duplex)	172.6	09 May	4.1 ± 1.2	8.1 ± 0.5	4.7 ± 0.2	4.6 ± 0.3

Growing season rainfall (GSR) is rainfall from sowing to harvest; daily rainfall graphs are available in Fig. S2.

sowing density for the region was used: for chickpeas 80 kg ha^{-1}; for lentils 50 kg ha^{-1}.

Emergence and establishment measurements were taken every 7–21 days from 14 days after sowing (DAS) at Merredin and 21 DAS at Dandaragan. In two 1-m^2 quadrats per plot, emergence time and number were counted by hand. This was continued until no more new seedlings appeared (5 weeks post-seeding) and was checked at 10 weeks post-seeding. Establishment was monitored as canopy cover increase, measured by counting green pixels in digital images using Canopeo within MATLAB (MathWorks, Natick, MA, USA) (Patrignani and Ochsner 2015).

Time to 50% flowering of plot was recorded. Two 0.5-m^2 biomass cuts were collected at anthesis and at full maturity. Harvested material was dried at 40°C for 72 h.

Data analyses

The controlled environment experiments (randomised complete block designs) were analysed using replicates as blocks. Data was collated and analysed in the R (ver. 3.5.1) environment (The R Foundation, Vienna, Austria). Nested ANOVA and regression models were used to partition variance between species, between varieties within seed-size grouping within species, or between seed size within a species. Factorial linear and quadratic regressions were used to model changes in epicotyl and root growth and diameter and biomass accumulation over time. Residual plots were used to identify outliers and ensure that errors were normally and independently distributed.

Results

Genetic variation in epicotyl growth rate and diameter between and within species (Expt 1)

All sown seeds were close to emergence or had emerged from the sowing depth of 250 mm by the final harvest at 180 degree-days. So as not to use any data from emergent seedlings, only points from 80 to 160 degree-days were used in the analysis of epicotyl growth rate. Epicotyl appearance from the seed was slower in chickpea; at 40 degree-days, lentil epicotyls were 2–9 mm, whereas no chickpea seeds showed epicotyl growth. However, once epicotyls broke through the seed coat in chickpeas, they had a significantly faster ($P < 0.001$) rate of growth than lentils (Fig. 1*a*). Epicotyl growth rate differed significantly between ($P < 0.001$) and within species (Table 1); linear regression explained 96.5% of the variation, with the species effect being by far the largest, accounting for 94.5% of variance. There was a time × species × seed size interaction ($P = 0.011$) such that epicotyl growth rate and seed size were weakly positively correlated ($r = 0.31$) in lentils, but not in chickpeas (Fig. 1*b*).

Epicotyl diameters were measured at each harvest and varied significantly ($P < 0.001$) both between and within species over time (Fig. 2). Linear regression over the harvests explained 91.4% of the variation, with the species effect again being the largest, accounting for 88.1% of variance. Epicotyl diameters were significantly larger in chickpeas than in lentils. Within species, chickpea epicotyl diameters did not differ ($P = 0.64$) over time, whereas lentil epicotyl diameters reduced ($P < 0.001$) over time. Epicotyl diameters differed significantly ($P < 0.001$) with variety within species, but this was not related ($P = 0.198$) to seed size.

Phenotypic variation with seed size within and between species (Expt 2)

Effect of seed size on epicotyl growth rate and diameter

Sowing seeds at extreme depth (350 mm) resulted in growth rates slowing over time in some seed-size treatment groups (Fig. 3). Linear regression of the epicotyl growth rates prior to any slowing of growth (80–160 degree-days) accounted for 96.8%, with species alone explaining 96.6% of all variation, with no seed-size effects within species ($P = 0.403$). Chickpea growth rates were higher ($P < 0.001$) than those of lentils within this mostly linear phase (Fig. 3). Extending the analysis of epicotyl growth over the entire, non-linear measurement period (80–280 degree-days) explained 97.5% of total variation, and although species remained the most significant factor (explaining 96.6% of the variation), the interaction with seed size within species became highly significant ($P < 0.001$); beyond 160 degree-days, shoots from larger seed continued to elongate linearly, whereas epicotyl growth rates from smaller seed slowed as seed reserves were exhausted (Fig. 3*a*).

Effect of seed size on root growth

The experiment was run in long soil tubes (600 mm deep) so that primary roots did not reach the pot base, allowing for unimpeded root length to be measured at all harvests. Unlike the shoots, root growth was negatively affected by smaller seed size from the beginning of the growth period. Polynomial linear regression of root growth with time over the entire growth period (80–280 degree-days) explained 86.1% of total variation. The species effect accounted for 56.7% of variation, and within species, the seed size × time interaction was highly significant ($P < 0.001$, Fig. 3*b*). Root growth rates were much more rapid in chickpeas than in lentils (particularly up to 160 degree-days, Fig. 3*b*). Differences between seed-size groups were larger in lentils than in chickpeas. In lentils, root growth rates were linearly related to seed size, whereas in chickpeas, only the small-seed group grew significantly slower than either the medium- or large-seed group (Figs 3*b* and 4).

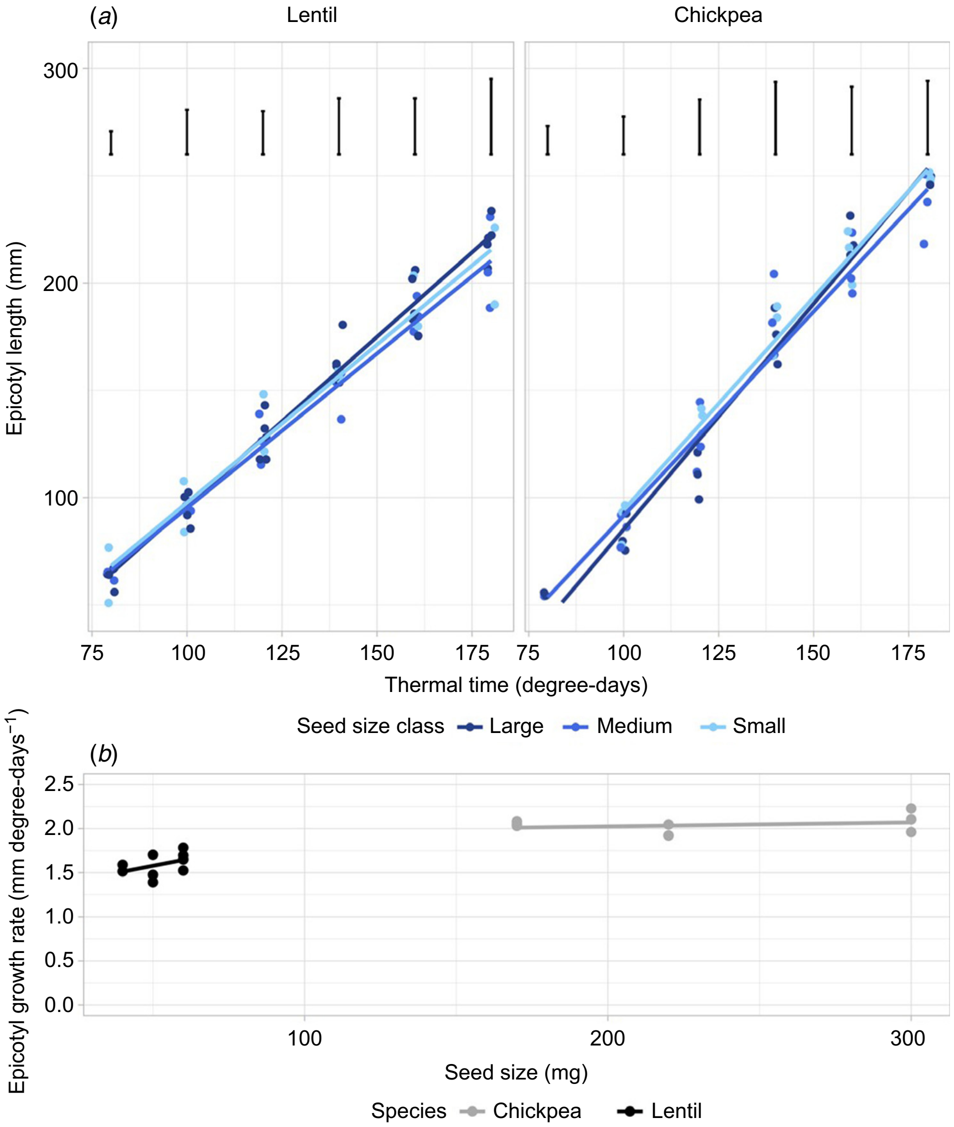

Fig. 1. Chickpea and lentil epicotyl growth with time. (*a*) Epicotyl elongation (length) over time presented as variety means with a linear regression by seed-size group; (*b*) growth rate as estimated from the regression by seed size. Epicotyl elongation was measured from 19 varieties ($n = 3$) in staggered destructive harvests of soil-grown seedlings sown at 250 mm in 11% moisture content soil (~60% of field capacity) at 20°C. Varieties were grouped by seed size with three seed-size groups per species: lentils 40, 50 or 60 (±3) mg; chickpeas 170, 220 or 300 (±10) mg. Vertical lines represent l.s.d. ($P = 0.05$) values for comparing varieties at individual harvests.

Lateral root growth (roots emerging off the primary root) followed a similar trend to primary root growth. Bolt lentils produced very few lateral roots, whereas Striker chickpeas started producing lateral roots from 80 degree-days (Fig. 4). Chickpea lateral root numbers followed a similar trend over time to that of root length, increasing rapidly in both large- and medium-size seeds and much more slowly in small seeds ($P < 0.001$, Fig. 4*c*). This had large effects on final lateral root development. In seedlings from small seeds, no more than 12 lateral roots were observed, all of which had developed by 160 degree-days (Fig. 4*c*). Thus, chickpea plants developing from small seeds traded off both primary root length and lateral root number to maintain epicotyl growth.

Biomass partitioning in pre-emergent seedlings

Until the plumule arch breaks the soil surface and the first leaves expand and start to photosynthesise, the growing seedling is reliant on seed reserves for growth; these reserves will be partitioned between the seed remnant, shoot, root and respiratory losses.

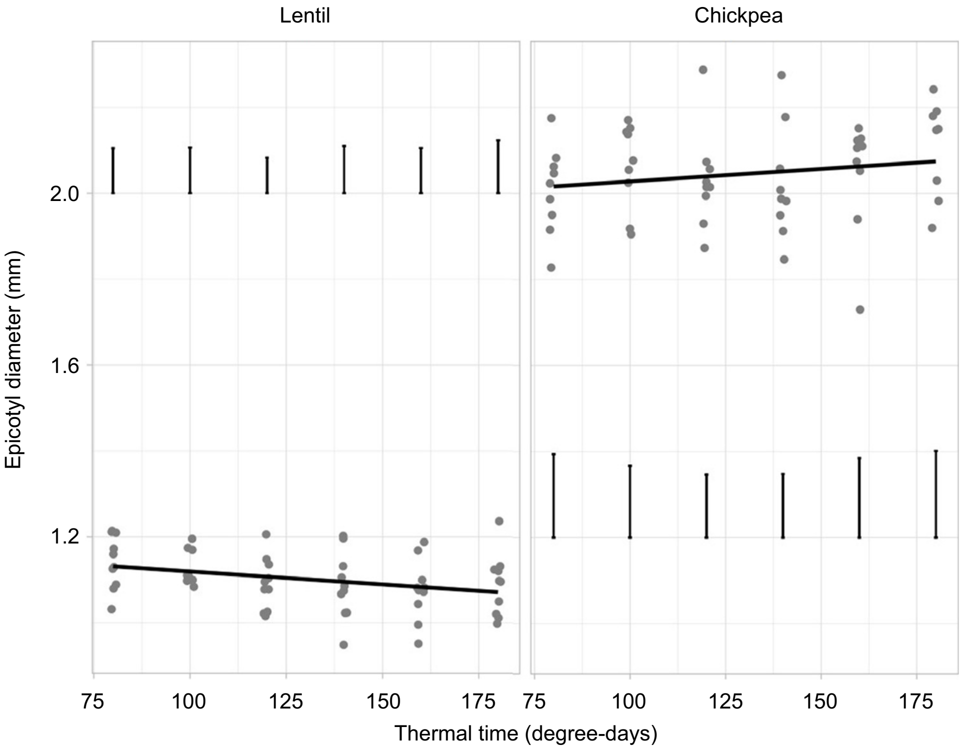

Fig. 2. Chickpea and lentil epicotyl diameter. Changes in epicotyl diameter over time are presented as variety means with a linear regression. Epicotyl diameter was measured with digital callipers on 19 varieties ($n = 3$) in staggered destructive harvests of soil-grown seedlings sown at 250 mm in 11% moisture content soil (~60% of field capacity) at 20°C. Vertical lines represent l.s.d. ($P = 0.05$) values for comparing varieties at individual harvests.

As expected, seed reserves declined over time as shoot and root systems elongated and started respiring, using mobilised seed reserves (Fig. 5). By 200 degree-days, dry weight of all seeds had reduced by at least 50% (Fig. 5), and in small seeds the remnant seed biomass was as low as 25% of the initial seed weight (Fig. S3). Linear regression of seed reserve over time explained 90.4% of the variation. The species effect was significant, explaining 78.3% of the variation. Chickpea seed reserves declined faster than lentil seed reserves. The interaction of seed size within species with time was also highly significant ($P < 0.001$), with seed biomass proportion declining at slower rates over time in large seeds of both species (Fig. 5).

Shoot growth was allocated the highest percentage of mobilised seed reserves in both species (Fig. 5). Linear regression of shoot elongation over time explained 91.1% of the variation, with 88.3% of this being explained by species alone; chickpea shoot biomass proportion increased more rapidly than lentil shoot biomass (Fig. 5). The interaction of seed size within species with time was again highly significant ($P < 0.001$), with large seeds allocating less seed reserve to the shoot over time.

Tissue maintenance via respiration consumed a considerable amount of mobilised seed reserve (~5–10% of initial seed mass; Fig. 5). Regression of estimated seed reserve partitioning to respiration over time accounted for 69.3% of the variation, species differences explaining 52.3%. Within species, seed size was highly significant ($P < 0.001$). In chickpeas, large seeds allocated less to respiration than small and medium seeds, whereas in lentils, the three size groups had a linear size-group relationship, with seedlings from small seeds allocating a higher percentage of reserve to respiration in order to maintain growth.

Roots constituted by far the smallest proportional partitioning of seed reserve (Fig. 5). Root biomass results were highly variable, and regression captured only 43.0% of variation, with species accounting for 33.2%. Highly significant interactions of seed size within species with time ($P < 0.001$) support the primary root length and lateral root initiation data (Figs 3*b* and 4). Small seeds and to a lesser extent medium-sized seeds of both species show a very flat biomass to root allocation curve, effectively trading off root development to maintain respiration and epicotyl growth (Fig. 5). By contrast, seedlings from larger seeds of both species slowly increased partitioning to roots over time. Root:shoot dry weight ratios reflect these patterns, with seedlings from small seeds having consistently lower ratios that those from large seeds (Fig. S4).

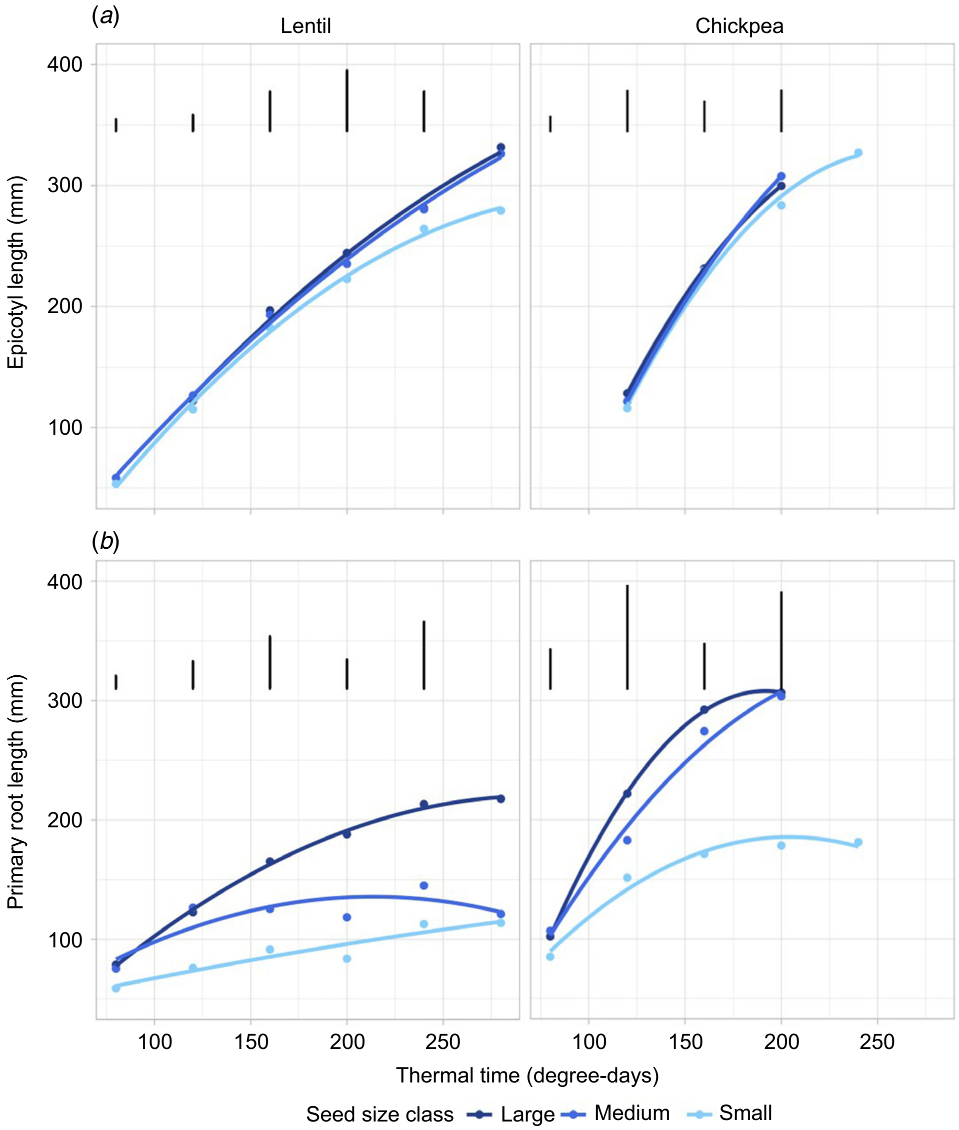

Fig. 3. (*a*) Epicotyl and (*b*) primary root lengths with time. Means of each variety are presented with a regression by seed-size group. Data are not presented for large- and medium-seeded chickpeas at 240 degree-days because epicotyl had emerged. Length was measured from three seed sizes of a single variety of each species (Striker chickpea and Bolt lentil; *n* = 4) in staggered destructive harvests of soil-grown seedlings sown at 350 mm in 11% moisture content soil at 20°C. Lentil seed size groups were 20, 40 and 60 (±3) mg; chickpea groups were 100, 200 and 300 (±10) mg. Vertical lines represent l.s.d. (*P* = 0.05) values for comparing seed-size classes at individual harvests.

Establishment and growth in the field (Expt 3)

Crop emergence rate in the field was measured by weekly counts (Fig. 6). Regression of emerged plant number over time explained 95.1% of the variation, with species accounting for most of this (90.3%) because lentil emerged faster than chickpea regardless of depth or site interactions. The two species' emergence responses differed at the different sites ($P = 0.032$) and with sowing depth ($P = 0.003$). Lentils showed a reduced emergence rate from 200 mm depth on the heavier soils at Merredin, whereas chickpea emergence was not impacted by either site or depth ($P = 0.91$).

Establishment of the crop was measured as canopy cover over time (Fig. 7). Regression of canopy increase over time explained 95.7% of the variation, with species accounting for most of this (86.3%). There was contrasting establishment ($P < 0.05$) of the two species at the different sites, the slower emergence of lentils at Merredin being reflected in slower canopy cover increase. Depth of sowing did not affect ($P = 0.95$) canopy cover over time.

Biomass accumulation at anthesis was not affected by site ($P = 0.20$), species ($P = 0.20$) or sowing depth ($P = 0.71$); however, by maturity there was a strong biomass

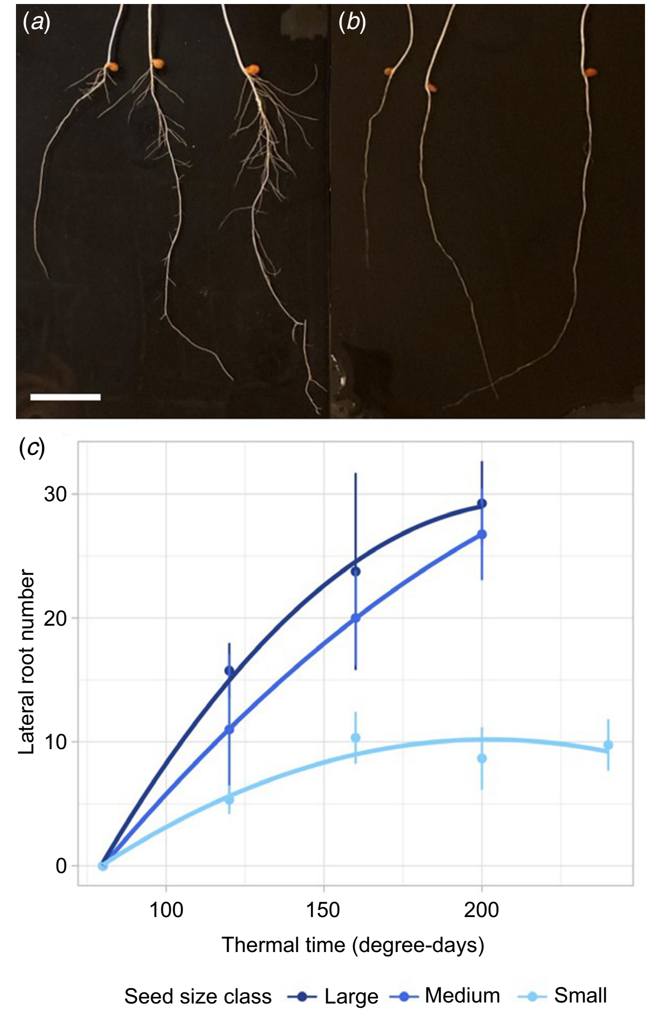

Fig. 4. (*a*) Chickpea cv. Striker and (*b*) lentil cv. Bolt roots harvested at 160 degree-days from soil-grown seedlings sown at 350 mm in 11% moisture content soil at 20°C. From left to right: seed size 100, 200, 300 mg for chickpeas and 20, 40, 60 mg for lentils. Scale bar 10 mm. (*c*) Lateral root number over time for Striker chickpea; lateral roots were counted in seedlings from the three seed sizes in staggered destructive harvests of soil-grown seedlings sown at 350 mm in 11% moisture content soil at 20°C ($n = 4$); vertical lines are standard errors.

accumulation interaction with site ($P < 0.05$), both species at Merredin producing significantly more biomass in the latter part of the season than plots sown at Dandaragan (Table 3). Depth of sowing did not significantly influence final biomass of either crop ($P = 0.64$), although there was a minor interaction with site; at Dandaragan harvest biomass of both crops was slightly lower in crops sown to 200 mm, whereas at Merredin the opposite occurred, with deeper sown crops producing slightly more biomass (Table 3). Final yield showed a strong interaction ($P < 0.05$) between species and trial site; chickpeas yielded slightly higher at Dandaragan than at Merredin, whereas lentil yields did not differ (Table 3). Although sowing depth did not influence yield ($P = 0.76$), as with harvest biomass, sowing depth did interact with site, such that deeper sown seed tended to yield slightly higher at Merredin and slightly lower at Dandaragan (Table 3).

Discussion

We demonstrated that under favourable soil conditions chickpea and lentil crops are very tolerant of extremely deep sowing. Across 19 commercial varieties, we found that both species could successfully emerge from depths as extreme as 350 mm, although successful establishment from these depths was not ascertained. However, under sandy field conditions, both species established well from sowing depths of 200 mm. We found that varietal differences in germination time and pre-emergent epicotyl growth rate were much smaller than differences between species under controlled conditions. Under the limited field conditions we tested, emergence time did not significantly differ, although emergence number was affected in lentils. In contrast to our hypothesis, seed size did not impact epicotyl elongation rate and emergence time in chickpeas and had only a slight impact in lentils, unless sown at extreme depths (>200 mm). However, this prioritisation of shoot growth rates across seed size groups was sustained in seedlings from small seeds at the cost of thinner epicotyl diameters and highly reduced root length.

Emergence rates from depth in these species have received little attention. This is surprising given that farmers in many tropical regions elect to sow these crops deep to access stored soil moisture (Saxena 1987). For example, in Queensland, chickpea crops are sown annually on up to 170 000 ha, and in this region it is not unusual to sow these crops to 100–200 mm deep (Cumming and Jenkins 2011). There has been some research into emergence rates of these crops from standard sowing depths. Thermal time to emergence has been shown to be 90–115 degree-days for chickpeas emerging from 50 mm (Gan *et al.* 2002; Soltani *et al.* 2006). Safahani *et al.* (2017) studied six lentil varieties, which had a mean of 94 degree-days to emerge from 40 m. We found slightly faster, but comparable, times for shoots to reach these lengths (see species-level regression in Fig. 1*a*; to emerge from 50 mm sowing depth in chickpea 80.9 degree-days and lentil 69.7 degree-days.

Emergence times will be impacted by abiotic factors such as temperature, soil moisture and soil type/bulk density (Nasr and Selles 1995). In our field results, the emergence of deep-sown lentils sown into a heavy loam at Merredin was at a slower rate than deep-sown lentils in a sand in Dandaragan (Fig. 6). The heavy loam did not affect the emergence of deep-sown chickpeas, likely due to the large diameter of chickpeas and sturdy epicotyls (Fig. 2). Although existing soil bulk density can be a concern in a sown system, much

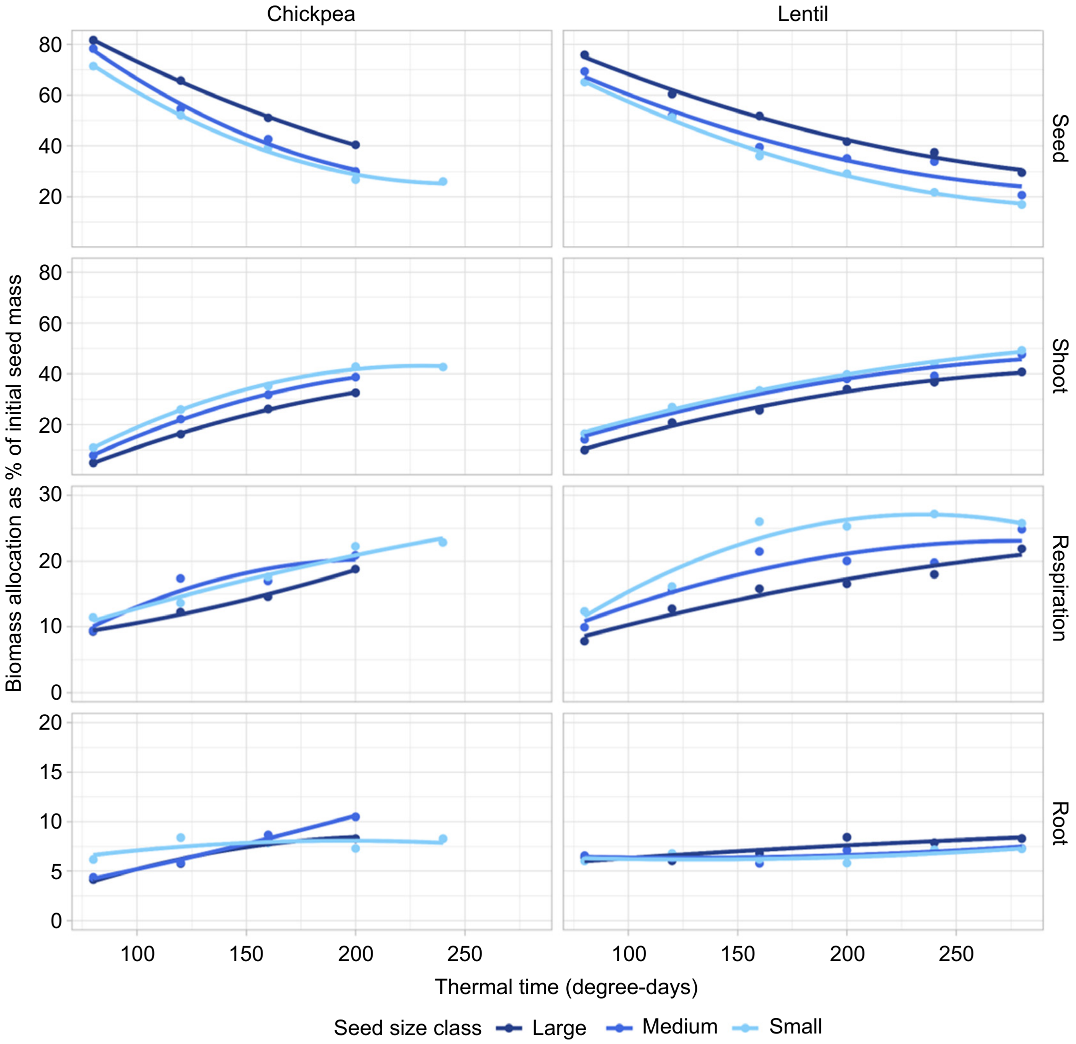

Fig. 5. Biomass partitioning by organ as a percentage of initial seed dry weight, in Striker chickpea and Bolt lentil. Means of each size grouping are presented with a regression by seed size; once shoots emerged, further data were not collected because shoots were no longer reliant on seed reserve alone. Biomass was measured from seedlings of three seed sizes ($n = 4$) sown at 350 mm in 11% moisture content soil at 20°C. Estimated initial seed dry mass was calculated from the initial fresh seed mass and seed moisture content; the difference between this value and total seedling dry mass at harvest was assumed to be from loss via respiration. Lentil seed size groups were 20, 40 and 60 mg; chickpea groups were 100, 200 and 300 mg.

of the compaction in the soil above the seed will be broken down by the seeding tines/discs. The type of seeding system, particularly the press-wheels, will have a significant impact on the final bulk density above the seed (Asoodar *et al.* 2006).

Our findings suggest that crops sown into warm soils to not show much time-lag in emergence from depth, whereas cooler soils would extend differences in emergence times. Interestingly in field trials, sowing into cooler soils has shown little delay to emergence of deep-sown lines (Australian late autumn/early winter sowing, soils 10–15°C, Siddique and Loss 1999; Canadian spring sowing, soils 9–13°C, Gan *et al.* 2003). Although measurement of precise emergence times in the field can be fraught with inaccuracies, comparing our controlled environment findings with those in the field gives an indication of the complex interactions experienced by pre-emergent shoots. Our field trial highlights this complexity; we compared emergence on a sandy soil and a heavier loamy duplex, however the sites also differed in soil temperature and moisture regimes and it is difficult to seperate the impacts of these factors on germination and emergence. At Merredin, the soils were also slightly acidic, which may be another factor affecting emergence rates. Analysis of these interactions between soil abiotic factors such as temperature, moisture and pH are needed to understand emergence times from depth. Many current pre-emergent

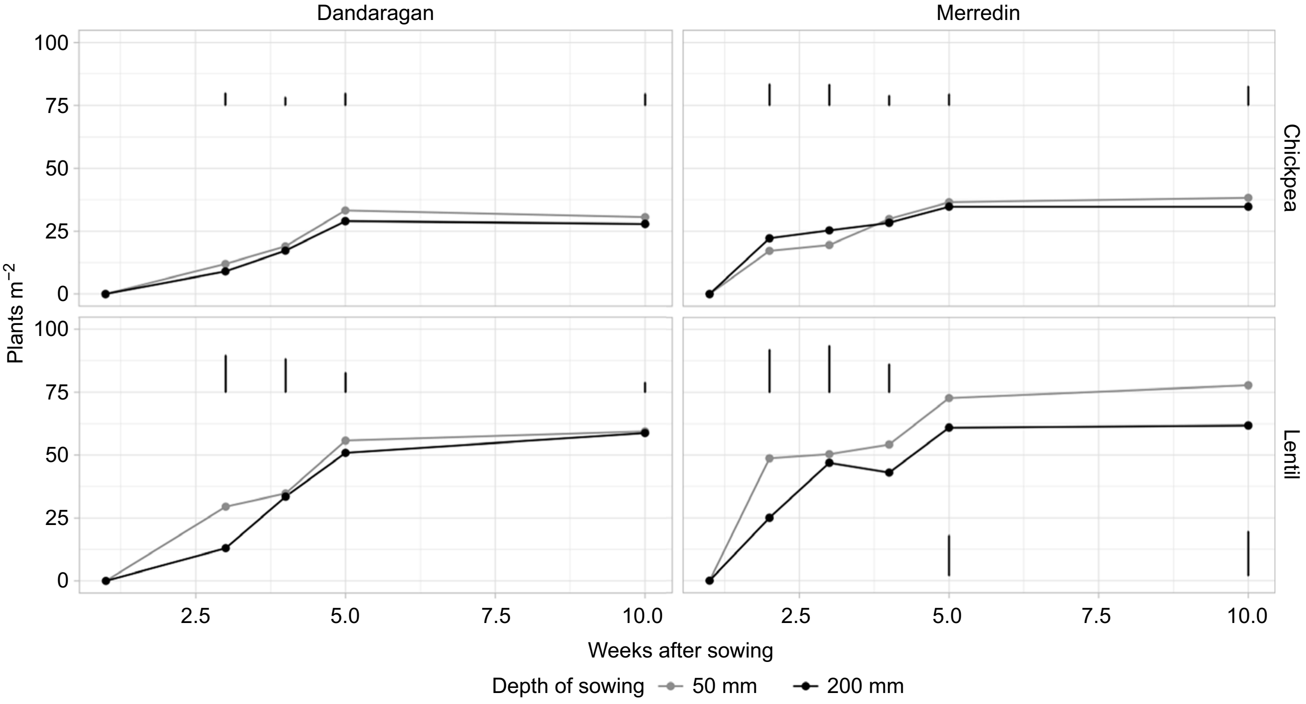

Fig. 6. Emergence of Striker chickpea and Bolt lentil from standard (50 mm) and deep (200 mm) sowing depths over the first 10 weeks after sowing. Counts were taken manually from two sections of 13-m^2 plots sown in May at Dandaragan and Merredin in Western Australia. Vertical lines represent l.s.d. ($P = 0.05$) values comparing sowing depths at individual count times.

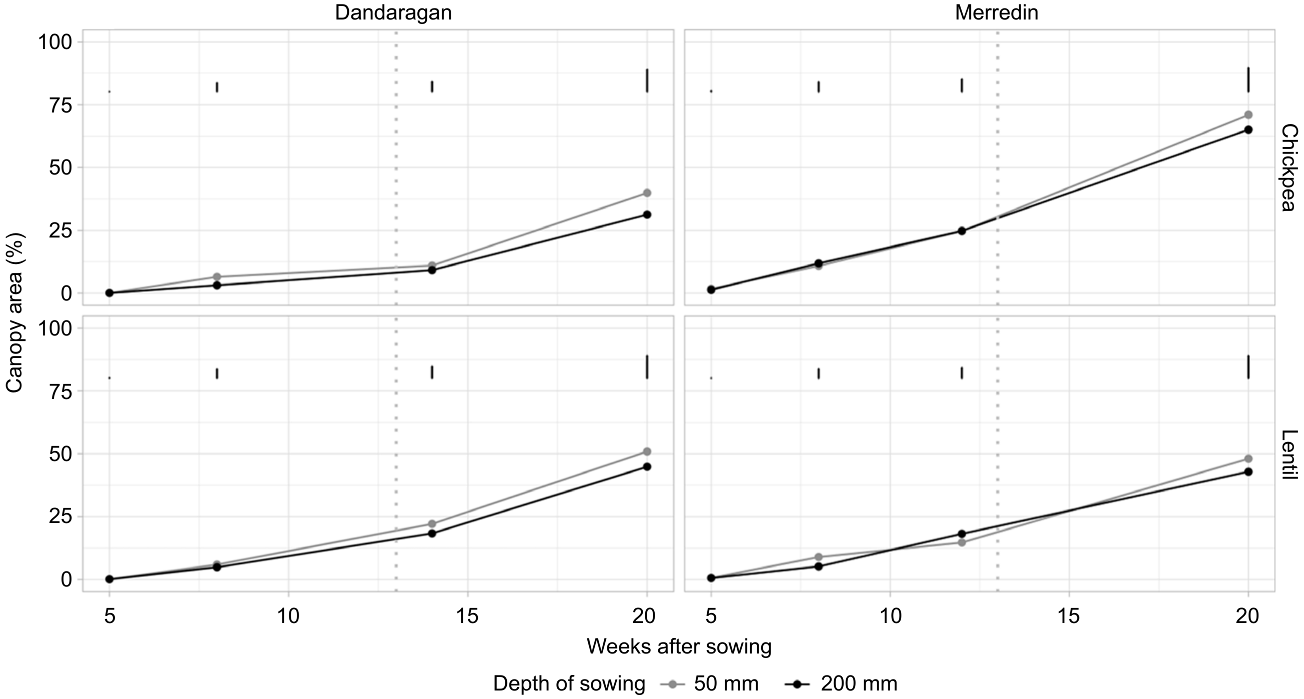

Fig. 7. Canopy development of Striker chickpea and Bolt lentil from standard (50 mm) and deep (200 mm) sowing depths measured as canopy cover over the first 20 weeks after sowing. Dashed line indicates flowering time (50% plot flowering). Canopy cover was measured by counting green pixels in digital images using Canopeo within Matlab. Images are from plots sown in May at Dandaragan and Merredin in Western Australia. Vertical lines represent l.s.d. ($P = 0.05$) values comparing sowing depths at individual measurement times.

Table 3. Biomass and yields (±s.e.) from sowing depth trials at Dandaragan and Merredin.

Site	Crop	Depth (mm)	Anthesis biomass (g m^{-2})	Harvest biomass (g m^{-2})	Yield (t ha^{-1})
Dandaragan	Chickpea	50	124.70 ± 18.40	124.71 ± 12.76a	1.45 ± 0.11a
		200	124.90 ± 12.76	101.60 ± 16.63a	1.17 ± 0.16ab
	Lentil	50	160.00 ± 21.90	91.30 ± 7.20a	0.99 ± 0.09bc
		200	146.10 ± 8.43	82.82 ± 7.14a	0.75 ± 0.13c
Merredin	Chickpea	50	148.62 ± 10.56	240.33 ± 21.29bc	0.83 ± 0.09c
		200	157.53 ± 16.03	287.41 ± 12.61c	1.05 ± 0.05bc
	Lentil	50	147.99 ± 15.43	219.43 ± 23.00b	0.98 ± 0.09bc
		200	173.49 ± 35.49	275.56 ± 36.35bc	1.18 ± 0.12ab

Within columns, means followed by the same letter, or no letter, are not significantly different at $P = 0.05$.

screening protocols do not even occur in soil (Raveneau *et al.* 2011; Gardarin *et al.* 2016), which makes transferring their findings to the field problematic because they do not necessarily reflect rates in soil. With both species in this study, we found large differences in epicotyl growth rates when trialling method prototypes in which shoots grew through air, in germination paper rolls or through soil (Fig. S1).

Anecdotally, seed size when sowing at depth has been considered of great importance, with growers often preferentially sowing large seed. However, there is limited evidence to support this, especially for larger seeded species. We found that seed size did not significantly affect epicotyl growth rate and emergence time, unless sowing was at extreme depths (>200 mm). However, as hypothesized, biomass allocation differed with seed size. In seedlings emerging from small seeds of both species (20 mg for lentils and 100 mg for chickpeas) and medium seeds in lentil (40 mg), maintaining shoot growth rates came at the cost of smaller epicotyl diameters and highly reduced root length. The impact of deeper sown seeds having a thinner/weaker shoots may result in seedlings being more susceptible to pest or fungal damage or being less able to push past soil resistance. Conversely, a thinner epicotyl may be easier to push through the soil, therefore being less energetically demanding on the seed reserves. Our field trials were sown with commercially sourced seed from which the smallest seed had been graded out; however, there was still significant variation in seed size. From our controlled environment studies, we hypothesise that a lower number of emerged plants in lentils may be due to smaller seeds not emerging from 200 mm.

Reduced root growth was one of the most evident changes in seedlings from smaller sized seeds. Roots can be energetically expensive to produce and can also have high respiration rates, making them metabolically expensive to maintain (Amthor 1984; Lambers *et al.* 2002); therefore, the reduction in root length/branching is possibly a combination of reduced utilisation of seed reserves for growth and lowering consumption via respiration, which constitutes a significant draw on seed reserves. Intuitively, it makes sense for pre-emergent seedlings to prioritise shoot growth. As soon as the plumule emerges from the soil, the first leaves will unfurl and photosynthate can be produced, ending the reliance on seed reserves, and potentially quickly making up for lower vigour in the roots and stem. On harvesting of emergent seedlings (data on these seedlings not included in analysis), it was observed that within hours of photosynthesis starting, root proliferation had increased. We did not follow root growth post-emergence, but sowing small seed at depth may continue to affect root growth and subsequent crop growth. Noting the slightly higher harvest biomass and yields achieved by deep-sown plots at Merredin (Table 3) where the season ended in severe terminal drought (Fig. S2), one could hypothesise that a deeper root system on the plants sown at 200 mm allowed for more access to moisture later in the season; this warrants further investigation.

Successful emergence of chickpea and lentil from depths as extreme as 350 mm has not previously been recorded. Although it is unlikely that depths as extreme as this would be of benefit (or even logistically possible) for growers, this finding, along with the relative lack of varietal difference in emergence ability and timing, offers confidence when considering sowing these crops to 150–200 mm. In chickpea, reductions in root and shoot vigour were significant only in extremely small seeds. These small seeds would likely not make it through the grading process and so their weaker performance would be unlikely to affect a grower. However, in lentil, the overall smaller seed size resulted in significant reduction in root length and shoot diameter, even in the medium size grouping, which would indicate that deeper sowing could result in less vigorous seedlings being produced from smaller seeds. Vigour is an important consideration in successful establishment (Finch-Savage and Bassel 2016), and further detailed work on the impact of deep-sown seedling growth in the days and weeks post-emergence is needed to understand the full implication of our findings.

Supplementary material

Supplementary material is available online.

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Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

Conflicts of interest. Andrew Fletcher is an Associate Editor of Crop & Pasture Science, but was blinded from the peer-review process for this paper.

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