REVIEW ARTICLE

# Pulse ideotypes for abiotic constraint alleviation in Australia

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## Abstract

*Background*  Pulses are cultivated across a range of soil and climatic conditions that often have many abiotic constraints to production. Whilst water stress has been identified as the greatest constraint in Australian pulse cultivation, other limitations include heat, frost, nutrient deficiency, and a variety of soil physiochemical constraints. Several studies on various pulses have examined shoot and root architecture and their ability to mitigate specific abiotic constraints. However, these studies have been conducted independently of each other, and there is a lack of amalgamated information combining both shoot and root responses that can address production constraints.

*Scope*  This review examines the shoot and root system architecture of key pulses used for human consumption grown in Australia including chickpea, lentil, faba bean, field pea and lupin; and where possible it provides a comparison with relevant research from other crops, especially cereals. It examines research conducted on adaptations to drought, waterlogging, temperature extremes, soil chemical toxicities and high soil strength.

*Conclusion*  The review utilises a physiological framework to identify trait combinations that define theoretical ideotypes of pulse crops that would be better able to mitigate abiotic constraints currently limiting Australian pulse productivity. This framework can be extended directly to other similar environments globally or be used to develop new ideotypes that are better adapted to a wider range of regions within Australia.

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## Introduction

Global pulse production is increasing due to its recognition as a valuable plant-based protein source and as an important component of many dryland cropping systems. When grown in rotation, pulses provide a break in disease cycles for cereals, allow for alternate weed control options and improve soil nitrogen as a result of nitrogen fixation (Angus et al. 2015; Evans et al. 2001; Kirkegaard et al. 2008; Zhao et al. 2022). Most of the pulse crops have a relatively shallow root system that can leave water at depth for subsequent deeper rooting crops such as cereals and oilseeds (Campbell et al. 2007). Additionally, this review found that research on abiotic constraints in pulses is lagging when compared to cereals, and to a lesser extent, oilseeds.

Pulses have an indeterminate growth habit and are grown in a broad range of environments, latitudes and altitudes; however, production is often limited by a range of climate and soil production constraints (Ambika et al. 2021; Bourgault et al. 2017; Deol 2018). For example, pulse cultivation in Australia is spread across the grain belt region which extends from central Queensland, down through to southern and western Australia. In north-eastern Australia, rainfall is summer dominant, and winter crops rely heavily on stored soil water profiles for yield. Earliness in phenology helps to avoid the rapid onset of terminal heat stress and needs to be combined with genetically deep roots that can chase a receding soil water profile to maximise productivity. Conversely, the higher rainfall zones in south-eastern Australia are better suited to long-season crops, as there are often opportunities for early sowing on the opening rains. On some occasions, growth can extend into early summer if seasonal conditions bring cooler temperatures and late rains.

In cereals such as wheat and barley, an ideotype that was proposed by Donald (1968) and Fischer (1981) facilitated the deployment of specific traits, especially *via* altering phenology such as flowering date, that increased yield potential by avoiding water stress needed for improved adaptation in Mediterranean type environments. Vernalisation also suits early autumn sowing where thermal accumulation and long days might normally induce a sub-optimal flowering time. Additionally, photoperiod sensitivity can allow the extension of the growing period into summer in more southern latitudes. These examples of specific traits facilitate better adaptation to target environments. Whilst there is a much wider combination of shoot morphological, phenological and physiological traits that have been suggested to optimise crop performance (Fang and Xiong 2015; Sehgal et al. 2017), research on roots has been much more limited. Provided that single physiological traits as described above can have small effects on addressing constraints, there is potential for more significant productivity gains to be realised by pyramiding traits to form a region-specific crop ideotype.

This review targets three distinct climatic regions in Australia where pulses are grown. It examines potential climate and soil constraints and assesses plant and crop physiological traits that may improve adaptation to overcome the constraints. This review focuses on key pulses used for human consumption in Australia including chickpea, lentil, faba bean, field pea and lupin; and where possible provides comparisons to other crops, principally cereals. A physiological framework was used to classify traits into specific categories, and by selecting appropriate traits from each category, new crop ideotypes are suggested to improve adaptation to a defined agroecological region. The second section presents the context of the framework, followed by the third section which outlines the conceptual framework and justifications are discussed in the fourth and fifth sections.

## Australian climate and soil in context

The Köppen-Geiger climate maps partition global landscapes into specific climatic regions (Peel et al. 2007, allowing the identification of similar climates around the world. These climate maps identify zones based on seasonality, amount of rainfall and maximum and minimum temperatures. Any extremes of these factors constrain crop production. Given the highly variable environments in Australia, constraints such as drought, waterlogging, heat, and frost can occur across the different crop production zones. These constraints and responses by pulse crops are discussed in "Climate constraints" section.

Climatic classifications serve two purposes in this review. Firstly, they allow environmental constraints to be identified, which can then be used to hypothesize trait combinations to define ideotypes that could be deployed for constraint mitigation. Secondly, by mapping out analogous regions on a global scale, the specific ideotype designs can be put into a global context. This also provides an avenue to target global regions for germplasm importation that are likely to have a base level of adaptation to regions within Australia. For the purposes of this review, we limit our ideotype design to three target regions outlined below.

Figure 1 shows the Köppen-Geiger climate map of Australia. In north-eastern Australia, the main cropping zone falls in the Cfa class, characterised by summer dominant rainfall, although there is no typical dry season due to its sub-tropical nature. This region has relatively high rainfall by Australian standards and a hot summer. Global regions that have a similar climate classification are Morocco and Portugal, vast areas of south-eastern USA, stretching from Virginia down to Florida in the east, and Oklahoma to Texas in the west, southwestern China, Taiwan, southern Japan, and parts of southwestern Brazil. Further south along the coast is the southern high rainfall region,

classified as Cfb. This is a temperate region with a warm summer and winter dominant annual rainfall of greater than 500 mm. Globally, similar regions include northern Spain, much of France, and further north into the Netherlands and western Germany, all the United Kingdom and parts of the western coast of the United States of America and Canada. The third region we investigate is the southern low rainfall region, classified as BSk. This cropping region is typically arid with rainfall below 350 mm per year with a mean annual temperature below 18 °C, with hot, dry summers. Analogous climate regions globally include inland of Esperance in Western Australia, much of southern Spain, sub-coastal Algeria, Inner Mongolia, and the western portion of the Great Plains in the USA, from south Dakota through to Texas and into northern Mexico. These three regions have been selected due to the high level of cropping that occurs and a diversity of environments to illustrate the potential of ideotype design specific to environments.

Soil type also plays a major role in constraining pulse production. Supplementary Fig. 1 shows the main soil types in Australian grain production regions. Deep sands, sand over clay, Sodosols and Chromosols dominate soils in the west. Calcarosols
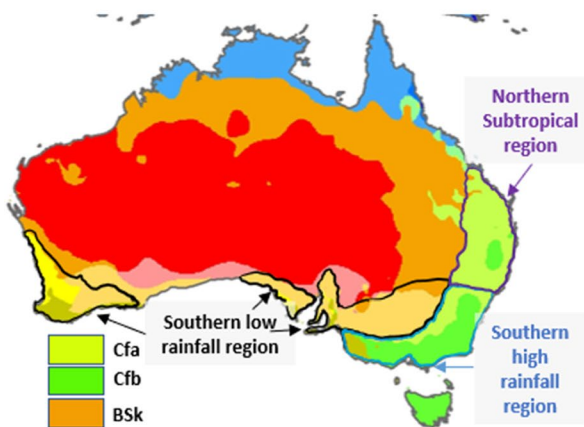


| 1st | 2nd | 3rd | Description | Criteria* |
|-----|-----|-----|-------------|-----------|
| **B** | | | **Arid** | $MAP < 10 \times P_{threshold}$ |
| | W | | Desert | $MAP < 5 \times P_{threshold}$ |
| | S | | Steppe | $MAP \geq 5 \times P_{threshold}$ |
| | | h | Hot | $MAT \geq 18$ |
| | | k | Cold | $MAT < 18$ |
| **C** | | | **Temperate** | $T_{hot} > 10$ & $0 < T_{cold} < 18$ |
| | s | | Dry Summer | $P_{sdry} < 40$ & $P_{sdry} < P_{wwet}/3$ |
| | w | | Dry Winter | $P_{wdry} < P_{swet}/10$ |
| | f | | Without dry season | Not (Cs) or (Cw) |
| | | a | Hot Summer | $T_{hot} \geq 22$ |
| | | b | Warm Summer | Not (a) & $T_{mon10} \geq 4$ |
| | | c | Cold Summer | Not (a or b) & $1 \leq T_{mon10} < 4$ |

*MAP = mean annual precipitation, MAT = mean annual temperature, $T_{hot}$ = temperature of the hottest month, $T_{cold}$ = temperature of the coldest month, $T_{mon10}$ = number of months where the temperature is above 10, $P_{dry}$ = precipitation of the driest month, $P_{sdry}$ = precipitation of the driest month in summer, $P_{wdry}$ = precipitation of the driest month in winter, $P_{swet}$ = precipitation of the wettest month in summer, $P_{wwet}$ = precipitation of the wettest month in winter, $P_{threshold}$ = varies according to the following rules (if 70% of MAP occurs in winter then $P_{threshold} = 2 \times MAT$, if 70% of MAP occurs in summer then $P_{threshold} = 2 \times MAT + 28$, otherwise $P_{threshold} = 2 \times MAT + 14$). Summer (winter) is defined as the warmer (cooler) six month period of October-March and April- September.

**Fig. 1** Köppen-Geiger climate type map of Australia with climate symbol criteria definition and the agroecological regions of the proposed framework highlighted as Northern Subtropical, Southern high rainfall and Southern low rainfall. Figure adopted from Peel et al. (2007)

and Chromosols are dominant in the main cropping regions of central-southern Australia. Sodosols and Vertosols are more common in the high rainfall region further south, whilst the eastern cropping area is composed of Vertosols and Sodosols (Isbell 2002). The deep sandy soils of the west have rapid drainage and various mixtures of clay and sand in the subsoil. Chromosols characteristically have a sandy or loamy horizon overlying a clay-textured subsoil with pH greater than 5.5 and are not sodic. Sodosols are also texture-contrast soils but have a sodic top 20 cm of the B horizon with an abrupt or clear textural difference between the A and B horizons. Vertosols lack texture contrast and have a high clay content, resulting in a large capacity to store water, with vertic (shrink-swell) properties that produce large cracks when dry, thus, commonly called cracking clay. Calcarosols also lack texture contrast in the profile but characteristically contain high calcium carbonate ($CaCO_3$) throughout the profile and often have saline and sodic subsoils (Agriculture Victoria 2019a, c). Each soil order has its unique characteristics and its own set of physiochemical constraints.

The following section presents the ideotypes based on the physiological framework, followed by details of how the framework was developed based on the crop physiology categories and adaptation traits of climate and soil constraints. These soil constraints and pulse crop responses are discussed in "Soil constraints" section.

## The physiological framework of constraint-based region-specific ideotype

The framework describes four categories of traits: photosynthetic, phenological, morphological, and performance traits. Photosynthetic traits include measures such as $CO_2$ assimilation, stomatal conductance, radiation use efficiency, chlorophyll content, canopy temperature and carbon isotope discrimination. Morphological traits refer to components of aerial and root branching such as height, depth, angle etc., along with leaf shape and area, and other structural components such as pubescence or aerenchyma. Phenology relates to temporal aspects of different growth stages with the key ones in pulses being time to flowering, time to podding, flowering duration and time to maturity. Performance

traits are yield and yield related traits, such as plants per square metre, pods per plant, seeds per pod, seed weight, harvest index (HI) and yield potential. Yield potential (YP) is the highest expected yield achieved when varieties best adapted to constraints are grown in ideal conditions with best management practices (Fischer et al. 2014; Fischer and Edmeades 2010). Water limited potential yield (YPw) is the expected yield with the best variety and management practice under ideal conditions given the specific water availability (Passioura 1977).

The identification of specific traits from each of the different categories of the physiological framework would support the optimisation of productivity in light of specific constraints. To illustrate this process, we identify the range of traits likely to provide the best adaptation to diverse climatic zones and soil types in each of three cropping zones (Table 1) (Supplementary Fig. 4). These are the Southern low rainfall region (southern, south-eastern and western Australia), Southern high rainfall and Northern subtropical region (Fig. 1). These regions differ markedly in the amount and pattern of rainfall, temperatures as well as latitude and its effect on day length. Because soils are highly variable throughout Australia; generalisations are used to illustrate contributions to ideotype design.

### Southern low rainfall region

The southern low rainfall region of Australia typically has annual precipitation of less than 350 mm per year, occurring mainly in winter. This region typically has hot, dry summers that limit subsoil water recharge. Sowing time is often dictated by the opening autumn rains and the region has a hot, dry finish, potentially with mid-season, intermittent droughts. Dominant soil groups include deep sands, sand over clay, Calcarosols, Sodosols, Vertosols and Tenosols (Isbell 2002). The main pulses grown are vetch and field pea; however considerable research effort has been invested in reducing production risk associated with other higher value crops e.g., lentil. The focus here would be on an ideotype based on maximising water use efficiency through the shoot and root architecture, optimising phenology and addressing soil constraints that are common and often severe, through genetic tolerances (ideotype (a) Table 1).

Phenological adaptation could include early flowering which enables plants to set seed before growth is terminated by increasing (terminal) drought and heat,

**Table 1** Physiological framework of region-specific ideotypes for low, high and subtropical rainfall zones contextualised in Australian pulse production areas



Physiological framework of region-specific ideotype

| (a) Southern low rainfall region (BSk) | (b) Northern subtropical region (Cfa) | (C) Southern high rainfall region (Cfb) |
|---|---|---|
| **Pulse crops** | | |
| Main crops are field pea followed by chickpea then lentil. | Chickpea, faba bean and mung bean. | Mostly faba bean, a few field pea, and potential for lentil. |
| **Soil traits** | | |
| Ranges from deep sandy soils to calcareous, sodic, alkaline, acid soils and boron toxicity at depth. Absence of moisture at depth in the Victorian regions. | Mostly vertosol, compacted, alkaline, patchy sodic. Salinity and boron at depth. Soil moisture present at depth. | Mostly chromosols and sodosols, dense sodic subsoil or acidic (aluminium and manganese toxicity) topsoils, waterlogging and perched water table. Soil moisture present at depth. |
| **Rainfall** | | |
| Low, intermittent, winter dominant. | Summer dominant to year-round, full soil water profile at beginning of the season. | High, winter dominant. |
| **Other stresses** | | |
| Common heat and frost events during the reproductive phase. | Common heat and frost events during the reproductive phase. | Cold at the early part of the season, generally a milder season, cooler temperatures into summer. |
| **Phenology** | | |
| Short season, indeterminant to recover from heat and frost, early vigour to shade soil. | Early flowering and early maturity with determinacy to take advantage of the short growing season and terminal drought. | Late season, late flowering, and late maturity to take advantage of the long season and cooler temperatures into summer, are highly determinant with strong photoperiod-driven maturity. |
| **Morphology** | | |
| Dimorphic growth habit with prostrate growth early in the season to shade the soil, high plant and pod height later in the season for harvestability particularly as moisture limits overall plant biomass. Mechanism to stop flower and pod abortion during stress (thicker attachment or genetic mechanism), plant biochemicals to help stress events and high pollen viability. **Root characteristics**: Wide, shallow, combination of fine roots and roots with thick root tip, hypocotyl roots, boron, sodic and salinity tolerance. | Intermediate branch angle associated with high growth rates and larger leaves to still give good canopy coverage. Increased plant height later in the season for harvestability. Higher total biomass can lead to higher yield if harvest index is maintained. Mechanism to stop flower and pod abortion during stress (thicker attachment or genetic mechanism). Improved yield components such as seeds per pod and pods per peduncle. **Root characteristics**: Steep, deep, and cheap roots to access water down the soil profile as the plant grows. | Open canopy to help with physiological disease tolerance, narrow and more erect branch angle, larger leaves, thicker stems to prevent lodging, with more aerenchyma. Longer internodes and bigger more spaced-out leaves to improve light interception. More tendrils to hold the canopy upright. Higher total biomass can lead to higher yield if harvest index is maintained, high pod height. Improved yield components such as seeds per pod and pods per peduncle. **Root characteristics**: Hypocotyl roots with aerenchyma for waterlogging, bigger root biomass to support bigger aerial components, acid tolerance through aluminium and manganese tolerance mechanisms. |
| **Photosynthetic traits** | | |
| Low carbon isotope discrimination for greater water use efficiency. Efficient $CO_2$ assimilation rate. Less stomatal conductance to limit water loss, potentially leading to higher canopy temperatures, necessary when committed to shallow roots. Driven by fewer, smaller, or less open stomata. | Moderated canopy temperature, longer stay green to improve light interception. Plant plasticity to regulate high or low $CO_2$ assimilation rate, stomatal conductance and canopy temperature depending on water and solar radiation availability. Increased water use efficiency, plasticity in stomatal conductance depending on the environment. | High $CO_2$ assimilation rate and stomatal conductance with cooler canopy temperature to maximise photosynthesis to supply the sink. Longer stay green to maximise light interception. |
| **Performance traits** | | |
| Seed quality and size take priority over maximising pod number or seeds per pod. | Maximising grain number and yield through high biomass and HI, seed number, and size for quality. | Increasing seed, seeds per pod, pods per peduncle. Maximising grain and pod number to increase yield through high biomass and HI. Size for quality. |

although this needs to be balanced against the occurrence of late frosts. Indeterminacy coupled with an early onset of flowering would also be a useful trait to mitigate the impact of transient frost or heat events. These events and variable growing season rainfall can result in flower, pod, or seed abortion, and indeterminacy would allow plants to reflower should significant abortion events occur, or if there are late-season rains.

Architecturally, high early vigour associated with a prostrate growth habit could help reduce soil water evaporation *via* shading and partitioning of accumulated biomass/assimilates to greater yield. However, prostrate growth is undesirable for machine harvest, thus a dimorphic growth (prostrate then erect growth habit) would be better suited for the southern low rainfall region addressing architectural adaption for the environment and harvestability. Many of the true winter wheats exhibit this phenotype, however, dimorphic growth has not been observed in pulse cropping systems (Hyles et al. 2020).

Root architecture consisting of wide, shallow, and prolific fine roots could take advantage of small and ephemeral rainfall events throughout the season. In soils with high soil strength and compaction, presence of a few roots with thick root tips would aid in better soil penetration (Cairns et al. 2011). The intermittent winter rainfall in this region is quickly lost to evaporation or drainage in sandy soils. As a result, there is often a lack of moisture in the root zone (Nuttall et al. 2010; Verburg et al. 2020). Other factors the reduce subsoil moisture includes utilisation by previous crops in the rotation and subsoil constraints that limit root growth and extraction of soil water and nutrients. These subsoil constraints include sodicity, aluminium and boron toxicity, and salinity. Therefore, a shallow root system may be the most efficient use of resources in a crop that relies on in-season, ephemeral rainfall events for growth and productivity where moisture is absent at depth or root growth is limited due to physicochemical soil factors (Rao et al. 2021).

To address the soil toxicities in this region, genetic variation in tolerances can improve adaptation of pulse crops such as in lentil, where significant genetic variation in boron toxicity has been observed (Hobson et al. 2006). Conferring improved tolerance to these soil biophysical constraints in effect allows the plant to utilise a greater quantity of soil water. However, the simultaneous occurrence of multiple soil constraints in these subsoils (Nuttall et al. 2003) will require either a pyramiding of tolerances or ameliorating the soils to produce significant improvements in yields, although currently available methods can be expensive and logistically challenging, (Armstrong et al. 2022).

Alternatively, root growth can be restricted by low plant available water, especially in the subsoil, as a result of insufficient precipitation and high evapotranspiration. This scenario is more likely to occur if soils have a high clay content or when fallowing, which increases subsoil water, has been replaced by continuous cropping thereby depleting water (O'Leary and Connor 1997). Given the presence of many physicochemical constraints in the subsoil, and an increasing absence of subsoil water due to reduced precipitation and increasing evaporative losses resulting from climate change, a strategy to 'avoid' subsoils may be appropriate. The production of plant roots is physiologically expensive (Ma et al. 2010), especially where potential benefits are limited so the development of shallow root system may be the most efficient use of plant assimilate to increase yield (and water use efficiency) (e.g. (van der Bom et al. 2020). This root form combined with proteoid roots such as those found in lupins, would also be beneficial for environments with low phosphorus as it can readily improve foraging of immobile nutrients such as phosphorus in the topsoil layer (Lynch 2019). The genetic variation in soil water extraction and use also contributes to root growth and survival in growth limiting soil environments. Improving water use efficiency is a key goal for crop improvement in this region and carbon isotope discrimination (CID) may be a useful tool to select better varieties.

Southern high rainfall region

There are highly productive cropping regions in southern Australia where rainfall exceeds 500 mm per year and spring/summers are generally cooler and wetter, allowing a longer growing season than in the southern low rainfall regions. The most common soil types used for cropping are textured contrast soils (70%) with clay subsoils that have high bulk densities such as Chromosols and Vertosols (MacEwan et al. 2010). Water deficit is much less of a limitation in these high rainfall zones (HRZ) – indeed temporary water logging occurs frequently

during winter so it would be important to optimise pulse phenology based on flowering and maturity to take advantage of the longer growing season (ideotype (c) Table 1).

Expansion of wheat into these regions occurred in the 1970s through the incorporation of various degrees of vernalisation and photoperiod sensitivity; these traits would similarly be useful to improve adaptation of pulses (Devitt et al. 1978; Eagles et al. 2010). Late maturity may also help to overcome the trade-off related to early phenological events, such as frost damage (Lake et al. 2016, 2021) and low yield potential in high resource available environments (Kaloki et al. 2019). Plants also need to have a determinate habit, as unregulated growth could compromise seed production, quality, and harvest index (Sangma and Chrungoo 2010; Samuel et al. 2022). The southern high rainfall region generally has low photo-accumulation and colder temperatures resulting in slow plant growth. Depending on the crop species, late flowering and maturity would be beneficial in such an environment as it would provide a greater opportunity for continued growth over a longer season and associated accumulation of photosynthate leading to high yield.

The low light intensities and short-day lengths occurring during winter in the southern high rainfall region combined with ample water suggest that maximising light interception to increase photosynthesis would be highly beneficial. This could be achieved with a tall, upright canopy and large leaves. Although high biomass would be desirable, it needs to be structured in such a way as to avoid high humidity within the canopy and ensure there are high levels of genetic resistance to foliar disease in cultivars. This could be achieved with taller plants, high initial branching, and narrow branch angles. However, the taller plants would need stronger and possibly thicker stems to support greater biomass, to prevent lodging. This upright nature would allow airflow between plants to reduce humidity and allow better penetration of fungicides deeper into the canopy and for a longer period (Ando et al. 2007; Smart 1985). It would also assist in reducing the severity of waterlogging events *via* increased evapotranspiration. Larger leaves with high chlorophyll content, stomata numbers and high stomatal conductance would maximise photosynthesis, which is important in this region where extensive cloud cover can limit light. Such an outcome could

be measured through the level of canopy temperature depression as water evaporates through the transpiration processes.

The more temperate growth conditions are likely to cause less reproductive organ abortion and a higher yield could be achieved in plants that can better develop a larger carbon sink. Production-associated traits such as more seeds per pod, more flowers per node and more nodes per plant would help to provide larger sink for increased photosynthesis. A high harvest index would also need to be achieved to maximise production (Zhang et al. 2006). Chickpea provides a unique challenge in this region due to its susceptibility to moderate chilling and waterlogging, leading to reproductive organ abortion; genetic tolerance to this would also be highly desirable.

We propose that a physiological framework comprising a root architecture consisting of a large root system with hypocotyl roots would be ideal for the southern high rainfall region. The profuse roots with low water use efficiency can extract excess soil water without compromising plant health. Soil acidity and phytotoxic concentrations of aluminium and manganese are common in topsoils in this environment and maintaining root biomass and function could improve productivity (Khabaz-Saberi and Rengel 2010; Zhang et al. 2006). Genetic tolerance to high concentrations of aluminium and manganese has been identified in other crops and would expand the current range of soils available for production of pulses in this region. Waterlogging is also a problem and crops that form aerenchyma in the root cortex thereby allowing bulk diffusion of air into root tips would be beneficial. Gladish and Niki (2000) found that the field pea variety Alaska produced lysigenous cavities under high respiratory demand such as in waterlogging situations and concluded that these worked as a form of aerenchyma. Several other pulses and forage legumes have been shown to produce aerenchyma and lysigenous cavities (Erskine et al. 1993). In addition, profuse roots also provide better anchorage, and prevent lodging with hypocotyl roots further enhancing as a support structure while providing access for root respiration to help in moderating effects of waterlogging.

Northern subtropical rainfall region

This subtropical region is characterised by summer dominant rainfall averaging greater than 500 mm

per year, combined with hot summer temperatures. The maximum temperature rarely falls below 20 ℃ and often exceeds 30 ℃ in the summer months. The most common soil type are deep grey vertosol clays, which have a large capacity to store soil water accumulated during fallows. Other major edaphic features are the salinity, sodicity and high chloride content that limit root growth preventing access to stored subsoil moisture (Dang et al. 2006, 2008). The optimal sowing time for temperate pulses is late April and heat risk at flowering increases significantly beyond mid-September (Grains Research & Development Corporation 2017). This can be a highly productive agroecological zone and is a key production area for chickpea but can experience high variable rainfall between years. Defining a new pulse ideotype such as ideotype b in Table 1, for this region may not only aid the productivity of chickpea but also facilitate the production of other pulse crops that could be grown in this region.

Grain growers ideally plant winter crops in this region into either a full or partially full soil water profile. As rainfall during the winter growing season is often low, crops deplete the soil water at the surface and roots progressively extract water from deeper in the profile. Crop growth would be supported by deep roots being able to access the receding water profile which has led to the proposed "steep, deep, and cheap" root ideotype (Lynch 2013). This root system is well adapted to the shorter seasons imposed by terminal heat stress as access to deep water later in the season helps to maintain a cooler canopy and ensure adequate grain filling. A less dense root system is therefore proposed to limit the drain on assimilates on the plant, while still being sufficient to maintain uptake of nutrients required by a smaller crop biomass.

Aerially, the crop would require high early vigour to facilitate rapid ground cover to limit evaporative losses of soil water. Stay green has been identified as a useful

**Table 2** Drought tolerance targeted traits in pulses with future potential

| Physiological Framework Grouping | Target trait | Crop | Reference |
|---|---|---|---|
| Phenology | Early flowering and maturity | Chickpea | Singh et al. (1995) |
| Photosynthesis | Sustained carbon isotope discrimination | Chickpea Peanut Faba bean | Buddenhagen and Richards (1988) Hubick et al. (1986) Khan et al. (2007) |
| Photosynthesis | Lower canopy temperature / leaf temperature / stomatal conductance | Chickpea Faba bean | Ramamoorthy et al. (2016) Khan et al. (2007) |
| Photosynthesis | Sustained osmotic potential | Alfalfa, Faba bean, Chickpea | Kang et al. (2011), Khan et al. (2007) Basu et al. (2007) |
| Photosynthesis | Sustained, relative Water content | Chickpea | Basu et al. (2007) |
| Photosynthesis | Sustained $CO_2$ assimilation rate, reduced transpiration | Chickpea | Basu et al. (2007) |
| Photosynthesis | Sustained chlorophyll fluorescence | Chickpea | Rahbarian et al. (2011) |
| Morphology | Sustained plant height | Chickpea | Singh et al. (1995) |
| Morphology | Reduced number of branches | Chickpea | Siddique and Sedgley (1985). |
| Morphology | Sustained biomass | Chickpea | Ramamoorthy et al. (2016) |
| Morphology | Sustained crop growth rate | Chickpea | Ramamoorthy et al. (2016) |
| Morphology | Pubescent leaves, stems, and pods | Soybean | Ghorashy et al. (1971) |
| | Absence of canopy wilting/low plant turgor | Soybean | Abdel-Haleem et al. (2012) |
| Morphology | Deeper roots and large surface area per unit of root weight | Chickpea and field pea | Benjamin and Nielsen (2006); Kashiwagi et al. (2006) |
| Morphology | Longer taproot | Faba bean Lentil | Belachew et al. (2018) Idrissi et al. (2015) |
| Morphology | Conservative pattern of water use and root growth | Chickpea | Zaman-Allah et al. (2011) |

**Table 3** Summary of below-ground traits for different constraints and their potential gains

| Trait | Crop | Gain |
|---|---|---|
| Phosphorous deficiency | | |
| Proteoid Roots | White lupin | 100% biomass retention in plants with proteoid roots at low P (10 mmol m$^{-3}$) compared to plants without proteoid roots at high P (100 mmol m$^{-3}$) (Keerthisinghe et al. 1998) |
| Organic acid extrusion and shallow rooting depth | Narrow leafed lupin | Large and deep rooting genotype had a 69% reduction in AGB and increased acid production by 35%, short and sparse rooting genotype had 54% AGB reduction and 54% increased acid production under P deficit (Chen et al. 2014) |
| Shallow root with wide root angle | Common bean | Deep rooting genotype had ~19% greater reduction in shoot biomass compared to shallow rooting genotype under P deficit (Ho et al. 2005) |
| | Common bean | Deep root genotype had 11.1% reduction in AGB, shallow root 0% reduction under P deficit (Liao et al. 2001) |
| | Common bean | Deep rooting genotypes had 14% greater yield loss than normal genotypes under P deficit (Henry et al. 2010) |
| Dense long Root hair | Lentil | 15% more P, 147% K, 143% Ca, 184% Mg and 178% Sulphur absorbed by genotype with denser root hair (Gahoonia et al. 2006) |
| Salinity | | |
| Active salt exclusion by organic solute accumulation | Wheat | 77% more Na + in xylem parenchyma of normal genotype compared to the tolerant genotype (Läuchli et al. 2008) |
| Compartmentalisation | Barley | Compartmentalisation in tolerant varieties had reduced Na accumulation by 26% in the cytoplasm, 3% more biomass and 100% more survival under excess NaCl (Flowers and Hajibagheri 2001) |
| Boron toxicity | | |
| Compartmentalisation | Canola | Tolerant lines had a 19% and 13% reduction in root length compared to 69% and 59% reduction in sensitive lines under toxic B conditions (Kaur et al. 2003) |
| Exclusion by organic salt accumulation | Wheat | No significant difference in yield between the two genotypes under normal conditions. Tolerant genotypes had a 3% average yield advantage with a max yield of 11% under toxic b conditions (Moody et al. 1993) |
| | Field pea & Annual Medics | 21% and 38% less shoot biomass loss in tolerant varieties of field pea and annual medics respectively under toxic B conditions (Paull et al. 1992) |
| Antioxidant system | Chickpea | 27% less reduction in root biomass in genotypes with high antioxidant activity (SOD, CAT, POX) under toxic B conditions (Ardıc et al. 2008) |

**Table 3** (continued)

| Trait | Crop | Gain |
|---|---|---|
| Aluminium toxicity | | |
| Active Al exclusion by organic solute accumulation | Wheat | Malic acid regulated the toxic effects of Al on root length by 92% under Al toxicity in comparison to roots with no malic acid (Delhaize et al. 1993) |
| | Arabidopsis | The release of citrate or malate increased relative root increment by 23% compared to lines that released pyruvate under Al toxicity 20 μm (Larsen et al. 1998) |
| | Wheat | The sensitive genotype had a 96% reduction in RL, while tolerant genotypes increased RL by 40% compared to control under Al toxicity; the addition of 20 μm malate increased RL by 88% in the sensitive genotype (Ryan et al. 1995) |
| High pectin cell wall and Compartmentalization | Faba bean | Under excess Al, faba bean accumulated ~ 14% less Al than maize, (Marienfeld et al. 2000) |
| High pectin cell wall | Field pea | Under normal conditions, the presence of border cells with pectin had 11% more RL than plants with border cells stripped off. Under excess Al, there was no significant loss of RL in plants with border cells while plants without border cells had ~ 13% reduction in RL and accumulated ~ 71% more Al (Yu et al. 2009) |
| Drought | | |
| Narrow LR angle | Wheat | 6–28% yield advantage over normal genotype under water limiting conditions (Manschadi et al. 2010) |
| Deep taproot | Common bean | In normal conditions, there is no significant difference with shallow rooting genotypes. Shallow rooted varieties had ~ 19% greater shoot biomass loss under drought compared to deep-rooted genotypes (Ho et al. 2005) |
| Few long LR | Maize | In the field under drought conditions few and long roots had 144% greater yield with deep water capture and 51–67% greater shoot biomass compared to many and short LR (Zhan et al. 2015) |
| Thin xylem | Wheat | 3–11% increase in yield under drought conditions in genotypes with thin xylem (Richards and Passioura 1989) |
| Waterlogging | | |
| Porous roots | Forage Legumes | ~ 25% more growth in tolerant varieties than sensitive under waterlogged conditions (Striker and Colmer 2016) |
| | Lentil | ~ 28% more root mass retention in genotype with higher porosity in comparison to low porosity genotype lentil under waterlogged conditions (Malik et al. 2015) |

Above−ground biomass (AGB), Nitrogen (N), Boron (B), Aluminium (Al), Root length (RL), Lateral root (LR), Root length density (RLD)

trait in wheat in these regions as it allows continued photosynthesis after flowering in both well-watered and droughted conditions (Christopher et al. 2016). As there are typically high levels of water availability early in the season, it is proposed that high levels of photosynthetic capability would be beneficial and this could be achieved

by high chlorophyll content, high levels of $CO_2$ fixation driven by high rates of gas exchange and hence, cooler canopies. This region often experiences terminal heat and drought, and this would best be avoided through early flowering and pod set. Crop growth models have been deployed under these conditions and leaf elongation rate has been identified as an important growth parameter in maize (Hammer et al. 2006). Highly determinate growth habits would be useful in this region as it rarely experiences late-season rains.

## Crop physiology

In this section, we examine traits related to photosynthesis, morphology, phenology, and performance and how they are related to the ideotypes of the framework.

Phenological traits

Basic crop adaptation is related to an appropriate range of plant phenological traits for a particular growing region. As stated earlier, improvements in wheat yields in Australia resulted in part from breeding for early maturity through vernalisation and photoperiod sensitivity, which resulted in early flowering and grain filling to avoid high temperatures later in the growing season in a temperate environment (Devitt et al. 1978; Eagles et al. 2010). Further advances were made in the late 1900s with the introduction of semi-dwarf varieties insensitive to vernalisation and photoperiod (Richards et al. 2014). A similar situation occurred in some legumes; a study comparing the response of phenology in the tropical legumes soybean, green gram, black gram, cowpea, lablab bean and pigeon pea during the dry season in semi-arid tropical Australia showed that in general, early-maturing cultivars yielded better than late-maturing cultivars (Muchow 1985).In lentil, early phenology has been attributed to higher yields in newer genotypes that had early flowering, podding, and a reduced thermal time from flowering to maturity (Sadras et al. 2021). Muchow (1985) also showed that water deficit had a small effect on the days to flowering, but duration of flowering, pod-filling, and days to maturity were reduced (Muchow 1985). Impact of water

deficit in relation to chickpea phenology showed that there was an inverse correlation of normalized evapotranspiration deficit experienced by the crop with durations of emergence to flowering, flowering to beginning of pod-fill and beginning of pod-fill to physiological maturity. Water deficit before flowering had a greater negative impact on canopy development, light interception, and dry matter production than after flowering. Water deficit during the reproductive stage in chickpea increased biomass allocation to reproductive organs relative to an increase in shoot dry weight (Singh 1991).

Morphological traits

Various studies have examined how different morphological traits including plant height, number of branches, hypocotyl length, leaf area, stem length, number of internodes, pod type, and grain size are related to the impact of constraints (Tables 2 and 3). Access to a range of diverse morphological traits enables the development of an ideotype that can increase yield potential, especially when combined with specific agronomic management. For example, long coleoptile wheats utilise alternative dwarfing genes that produce the desired crop height but allow the development of long coleoptiles. Such genotypes can then be combined with agronomic practices such as early sowing. In this situation, the early vigour helps to shade the soil, reducing evaporation while the soil is still relatively warm (Richards et al. 2014). Such an ideotypic trait could be applied to pulses where early sowing may be advantageous. Wheat plants with high vigour demonstrate improved leaf area and specific leaf area (SLA), or the inverse dry leaf mass per unit area (LMA) (Rebetzke et al. 2004), highlighting how different physiological characteristics can be correlated with morphology.

Other morphological traits such as plant height, branching and branch angles are responsible for creating micro-climates with various degrees of canopy cover. Several branches at a wide angle would produce a prostrate growth habit that can help reduce soil moisture evaporation by providing substantial canopy cover. However, prostrate growth habits would make machine harvest difficult, particularly in water stress environments where shoot biomass can be low. Silva-Perez et al.(2022), identified that between 1993 and 2020 selection of higher yielding

lentil genotypes indirectly selected for taller and sprawling to very upright canopies compared to the older genotypes. Hence, it would be useful to identify a dimorphic growth habit such as that of true winter wheat where prostrate plants become more erect later in the season, either through the growing tips turning upwards or through new vertically inclined basal branches (Marone et al. 2020).

Photosynthetic traits

Environmental conditions such as fluctuations in light intensity, light duration, soil water content and temperature directly impact on rate of photosynthesis (Pan and Guo 2016; Xu and Zhou 2011) and low photosynthate production contributes to low yield (Farquhar and Sharkey 1982). Traits such as regulated stomatal conductance, chlorophyll content, radiation use efficiency and stay green influence photosynthesis in constrained environments, helping the plant to maintain optimum water potential, temperature, and functioning photosynthetic structures. These traits can be incorporated in pulses to sustain yield production in constrained environments. For instance, at a leaf level, controlled stomatal conductance in low rainfall environments allows the plant to adjust the flow of water and regulate internal temperature. In hot dry conditions, controlled stomatal opening limits the amount of plant moisture lost *via* transpiration, whilst simultaneously helping the plant to cool and maintain physiological functioning (Sehgal et al. 2017). Other transpiration-related traits, such as transpiration use efficiency and evaporation, also contribute to photosynthesis and subsequently yield under water stress (Passioura 1977). However, the capacity of a plant to photosynthesise depends not only on optimum water and temperature but also on the chlorophyll content and its viability (Bishop 1971) as well as biochemical reactions that induce oxidative stress (Reddy et al. 2004). The stay-green trait enables plants to maintain chlorophyll content in the late growth stages and has been shown to improve the adaption of cereal plants experiencing water deficit (Christopher et al. 2016; Thomas and Ougham 2014). In barley, the stay-green trait and greater yield have been associated with deep root length and delayed root senescence (Williams et al. 2022). Stay-green has not been investigated in pulses and may be a useful trait under certain circumstances.

Yield potential can be described as the multiplied effect of cumulative intercepted solar radiation with radiation use efficiency and harvest index (Monteith et al. 1977). Whilst a plant may have a high chlorophyll content and stay green trait, shading or low intercepted solar radiation and low radiation use efficiency (amount of aboveground biomass produced per unit of intercepted light that is available for photosynthesis) can limit its photosynthetic potential. In lentils selection for yield has selected for genotypes with increased light capture as a result of increased leaf size and reduce branching (Silva-Perez et al. 2022). Hence, an open canopy accompanied by high radiation use efficiency would enhance photosynthetic activity (Kiniry 1999; Muchow et al. 1993).

Performance traits

Performance traits include yield and yield-related traits such as biomass and its partitioning to grain as harvest index. Although grain yield is a key measure of performance, yield components can interact in many ways to achieve optimal yield. Yield is a function of grain weight multiplied by grain number per square metre (Willey and Heath 1969; Carvalho et Fischer et al. 2014). In wheat, traits associated with grain number per plant include number of fertile tillers per plant and grains per tiller. Pulses are somewhat different in that yield is related to the number of flowering nodes, pods per node and seeds per pod. Pulses however have varying levels of indeterminacy, blurring pre- and post- flowering growth stages. This can have impacts on how crops may recover from stress events and the effects these may have on the various yield components. These yield and yield-related traits provide many avenues and combinations by which production limitations can be addressed.

Much of wheat yield improvement has arisen from increased harvest index (Richards et al. 2014). The *Rht-B1b* and *Rht-D1b* dwarfing genes have contributed to reducing wheat height resulting in greater HI, whilst maintaining aboveground biomass (Borlaug 1968; Richards 1992). Increased HI also means that carbon partitioning to the ear has improved, resulting in more grains (Fischer and Stockman 1986). Whilst improving HI has been beneficial in cereals, unfortunately previous improvements seem to have plateaued at approximately 0.62 and further improvements will likely come from other strategies (Richards et al. 2014). Harvest index in pulses has not had the same

level of investigation as wheat and is likely a useful target for yield improvement (Hay and Porter 2006; Hay 1995). Sadras et al. (2021) found that in lentils the rate of genetic gain was established at 1.23% per year across environments, and despite having early phenology, newer genotypes had biomass similar to older genotypes and had higher grain number and harvest index. Moreover, HI is generally considerably lower in current pulse cultivars than in elite wheat cultivars, so there is potential for increasing HI in pulses (Hay 1995).

In dry environments, water-limited yield potential has been achieved through optimising phenology with early flowering, thus, ensuring enough moisture is retained in the soil for later stages of pod fill. Deeper roots that allow for greater soil moisture extraction (Lynch 2013), and higher transpiration and harvest index have also been proposed as a mechanism for achieving YPw in dry environments where moisture is available at depth. However, it can be difficult to achieve both early flowering and rapid root elongation for deep roots as they often involve trade-offs (Fischer et al. 2014). Achieving either Yp or Ypw depends on the presence of genetic variation to allow selection for traits that can work in synchrony in addressing constraints while possessing heritability for selection by breeders.

## Climate constraints

This section discusses the range of climate constraints that limit pulse growth and yield across the different cultivation regions of Australia. Corresponding plant traits that have previously shown benefit in improving adaptation to these constraints are critical to the proposed framework.

### Drought

Pulse productivity can be affected by drought in various ways. Much of southern and western Australia relies on the first autumn rains to commence sowing and early growth, and delays in these rains can mean that farmers may sow crops early into dry soil or sow late on the rains when temperatures are low, resulting in uneven germination and poor establishment. Conversely, much of the more arid cropping regions experience terminal drought which can affect

grain set and grain fill. Dry spells during the growing season can also affect many stages of crop growth from emergence, resulting in low establishment number, through to the reproductive stage, affecting pod set and grain filling. In some cases, good early rains may encourage excessive vegetative biomass growth which depletes soil water, leaving insufficient water to form and fill grain later in the season (van Herwaarden et al. 1998).

Pulses are particularly sensitive to drought stress during specific phenological stages. Lack of water can reduce germination and restrict growth and nutrient uptake (Nadeem et al. 2019). In the reproductive stages, water limitation has caused precocious flowering, increased pollen sterility, low pod set, and ultimately reduced grain yield (Nadeem et al. 2019). Yield losses of 45 and 71% in faba bean and lentil respectively, have been observed when water stress occurs during pod set and grain filling (Katerji et al. 2011; Sehgal et al. 2017). Between 50 and 80% of yield was lost in chickpea experiencing terminal drought in a rainfed vs. irrigated experiment, expressed as a reduction in both seed size and seed number (Davies et al. 1999; Leport et al. 1999; Nadeem et al. 2019). Nadeem et al. (2019) and Ullah et al. (2019) observed reduced rates of photosynthesis, stomatal conductance, transpiration and chlorophyll content in soybean, chickpea and faba bean experiencing drought. The impairment of physiological function due to water limitation is a major cause of the above-mentioned impacts of drought on plant growth and reproduction, and genetic diversity for these physiological traits would help in breeding for drought tolerance.

Above ground, many traits can affect responses to the rate, duration and severity of drought stress in plants. For example, early vigour genotypes with high transpirational efficiency in wheat resulted in reduced soil evaporation, thus saving water for later growth stages. This is potentially a good tactic in environments where terminal drought during grain filling is common (Sadras and Rodriguez 2007) as well as where soil conditions limits deep root growth (Watt et al. 2005). The presence of pubescent structures on leaves can trap transpiring moisture and reduce plant water loss. This morphological character could be a useful trait to select for environments experiencing high temperatures and drought. The benefit of pubescent structures has been observed in soybeans, where

pubescent isolines showed a lower transpiration rate than the glabrous genotypes (Ghorashy et al. 1971). Stomata closure is another drought adaptation trait as it is the first response from plants sensing water stress and can be assessed in the short term by measuring gas exchange, canopy temperature (Fischer et al. 1998) and carbon isotope discrimination over a longer term (Condon et al. 2004). Other potential traits that have been observed to reduce plant water loss and help regulate plant physiological functions under drought conditions include reduced stomatal density, leaf area index, electrolyte leakage and sodium-potassium ratio (Table 2). Relevant traits to study water and drought stress in pulses are summarised in Table 2. Biochemical traits that are potentially useful in screening for drought tolerance include total chlorophyll content, total soluble sugar content, anthocyanin content, proline content, methylglyoxal content, total phenol content (Sinha et al. 2020) and chlorophyll fluorescence (Rahbarian et al. 2011).

Pulse root systems experiencing water stress have reduced total root length, surface area, biomass, root length density (RLD) and diameter (Belachew et al. 2018; Gorim et al. 2018; Manschadi et al. 1998); (Ramamoorthy et al. 2017). To improve maize adaptation to water stress, Lynch (2013) proposed a deeper root system with a large diameter primary root, few first-order lateral roots with abundant branching and seminal roots with steep growth angles, to improve access to subsoil water when in-season rainfall was limiting. Whilst the ideotype proposed by Lynch (2013) is based on a monocotyledon plant, aspects of it can be adapted to pulses. For instance, the presence of a deep root system in pulses under terminal drought conditions allows the plant to avoid water stress by accessing stored subsoil moisture and has been observed to be an effective root trait in pulses. Benjamin and Nielsen (2006) and Kashiwagi et al. (2006) examined chickpea and field pea root growth under irrigated and rainfed conditions and observed deep root growth under water deficit conditions, which was positively correlated to yield. In a glasshouse trial, Belachew et al. (2018) also observed that accessions of faba bean from dry regions to have deeper roots with long tap roots and larger root systems compared to wet regions. Few and long roots as a root trait adaptation for terminal drought has been observed by Manschadi et al. (1998) on faba bean and Zhan and Lynch (2015) on maize where plants with few long lateral roots performed better in the Mediterranean and arid environments with increased shoot biomass and yield.

Another possible adaptation is a narrower root system (Richards and Passioura 1989) and a higher number of metaxylem, traits which have been observed to improve water use and acquisition under water stress conditions in maize and soybean, respectively (Prince et al. 2017; Richards and Passioura 1989). There is wide genetic diversity in metaxylem conductance amongst pulse species and this trait works synergistically with root depth to access deep soil water (Strock et al. 2021). Other adaptations under water limiting conditions include rhizosheaths, suberized and lignified exo- and endodermis to reduce water loss from roots, and a large diameter root tip to enable better root penetration as soil strength increases as the soil dries (Lynch et al. 2014). The collection of traits listed above have been phenotyped in 400 maize genotypes to maturity and the best performing lines under water stress had traits of greater aerenchyma, high number and narrower metaxylem, along with thicker nodal roots (Klein et al. 2020). These traits enabled greater soil exploration (increased aerenchyma content, fewer cortical cell files and larger cortical cells), conserved soil moisture by restricting uptake (reduced hydraulic conductance and narrow metaxylem), and improved root penetration of hard and dry soil (thick roots with a large proportion of stele, and smaller distal cortical cells) (Klein et al. 2020). Hence, in regions such as subtropical northern Australia where moisture is often available at depth, the proposed root structure is of a few roots with steep root angle and deep root growth which have high aerenchyma, porosity in the cortex to access the subsoil moisture while having a low resources demand on the plant (ideotype B Table 1).

Whilst deep roots contribute to better water acquisition or drought adaptation in cereals and pulses under terminal drought when subsoil moisture is present, this trait also has disadvantages. In well-watered conditions plants with a deep root system might still invest in deep root growth instead of allocating assimilates to aboveground biomass and especially grain (El Hassouni et al. 2018). Also, rapid deep root development at an early growth stage may exhaust the water available during vegetative growth, leaving less water for grain filling, so slower deep root growth may be more beneficial (Zaman-Allah et al. 2011).

In regions such as the southern low rainfall areas of Australia, there is often an absence of stored subsoil moisture and deep roots would place a negative resource demand on the plant. Ramamoorthy et al. (2017) investigated chickpeas under drought conditions and found that a prolific root distribution in the topsoil was positively correlated to crop performance. Hence, under conditions of intermittent drought and absence of subsoil moisture such as in the southern low rainfall region, a shallow, wide, and cheap root ideotype provides a possible adaptation (ideotype A Table 1) (Rao et al. 2021; van der Bom et al. 2020). This form of root system architecture allows plants to maximise capture of the in-season rainfall before it is lost to evaporation or drainage and avoid water stress.

Waterlogging

Excess soil water can create anaerobic conditions and limit root respiration. The southern high rainfall region in temperate Australia constitutes areas that receive greater than 550 mm average rainfall a year, leading to frequent periods of temporary waterlogging over winter (July and August) when precipitation exceeds evaporation rates (Fig. 1). However, pulses can also experience transient subsurface or perched water tables in lower rainfall zones, promoting anaerobic growth conditions (Henschke and Yound 2015). Excess water in the soil reduces gas diffusion, causing hypoxia (low oxygen tension) or anoxia (complete lack of oxygen), resulting in a reduction in nutrient uptake by the plant, plant wilting, lower carbon dioxide diffusion, cessation of growth, and leaf and root senescence starting from the tips (Mustroph 2018; Stoddard et al. 2006). Pulses are most susceptible to waterlogging at emergence and flowering (Grains Research and Development Corporation 2018a). Anaerobic conditions result in increases in ions such as $Mn^+$ and $Fe^{2+}$ to potentially toxic concentrations (Patrick et al. 1985), as well as more acute damage from salinity (Barrett-Lennard and Shabala 2013). Waterlogged hypoxia is also detrimental to nodulation, subsequently reducing nitrogen fixation and supply (Striker and Colmer 2016). The cumulative effect of these unfavourable conditions is reduced root biomass, chlorophyll content, $CO_2$ assimilation, transpiration rate, stomatal conductance, efficiency of photosystem II and eventually reduced shoot yield (Smethurst and Shabala 2003; Watson et al. 1976).

In south-eastern Australia, waterlogging soon after plant emergence in winter results in "pruned" roots (Dickin and Wright 2008). Excess water has generally disappeared by spring when the daily evaporation rate exceeds rainfall but plants with pruned roots have been shown to be unable to recover, as the roots had insufficient depth to access the subsoil water (Mac-Ewan et al. 2010; Malik et al. 2002). Bramley et al. (2011) demonstrated that waterlogging produced fewer and shorter lateral roots as well as shallower tap roots in yellow and narrow-leafed lupin species. Yellow lupin recovered from the waterlogging by root growth near the base equivalent to that of non-waterlogged plants, but the new root growth did not compensate for the loss of lateral roots. A similar effect was observed in chickpea plants subjected to transient waterlogging, whereby overall root biomass was reduced, resulting in a 44 to 54% reduction in seed yield. Once the waterlogged conditions had stopped, the production of new roots was observed; old roots however did not resume growth (Palta et al. 2010). Palta et al. (2010) found that the root growth of both Kabuli and Desi genotypes of chickpea were affected by waterlogging, however, nodulation was only reduced in the Kabuli genotype, and this resulted in lower seed yield.

Lamb and Podder (2008) found that faba and broad bean had greater tolerance to waterlogging amongst Australian pulses, followed by yellow lupin and field pea. Solaiman et al. (2007) also observed faba bean to have the least reduction in shoot and root growth when subjected to waterlogging followed by yellow lupin, grass pea, narrow-leafed lupin, chickpea, lentil, and field pea. The study found that faba bean roots had more aerenchyma formation in the hypocotyl roots than other legumes and this aided their greater level of tolerance (Solaiman et al. 2007).

Root porosity (large gas-filled aerenchyma) has been identified as a key trait for improving tolerance to waterlogging in pulses (Malik et al. 2015; Solaiman et al. 2007; Striker and Colmer 2016). Striker and Colmer (2016), when examining root system architecture (RSA) in waterlogged forage legumes, observed that while root growth was reduced, genotypes with higher root porosity performed better than roots with low porosity. Under waterlogged conditions, anaerobic conditions affected internal $O_2$ levels, resulting in an accumulation of sugars. In highly porous roots, the internal $O_2$ levels were maintained, which allowed

nodulation and nitrogen fixation. Malik et al. (2015) compared lentil and field pea productivity under water-logged conditions. They found that field pea had higher root porosity and, in contrast to Solaiman et al. (2007) showed lower losses of root and shoot biomass to waterlogging compared to lentil. Field pea also recovered better after waterlogging. This study only investigated a single variety of each species; hence, it would be useful to investigate a larger range of germplasm to better understand the level of genetic diversity.

Other traits used for assessing waterlogging tolerance in pulses include plant biomass, stomatal conductance, leaf necrosis, nitrogen content, chlorophyll fluorescence, chlorophyll content and the duration of survival when waterlogged at flowering (Malik et al. 2015; Stoddard et al. 2006). Boron accumulation visualised as brown leaf spots have also been used to screen field pea for waterlogging tolerance (Malik et al. 2015; Stoddard et al. 2006). It would seem that the presence of aerenchyma is a key trait for waterlogging tolerance and identification of genetic diversity for this trait in pulses would be helpful in extending their production into the southern high rainfall region.

Heat

Temperature extremes have always been a feature of temperate crop production in Australia, but these are expected to occur more frequently due to climate change (Jarvis et al. 2010). Crops are likely to experience chronic heat stress as both average day and night temperatures increase. There is also likely to be an increase in acute stress as heat waves become more intense in peak temperature and duration. The heat the plant experiences can differ from the air temperature due to transpirational cooling, but this is reliant on soil water availability. Excess heat affects plant morphology, physiology, reproduction, and productivity. It inhibits seed germination, reduces photosynthetic rate, alters dry matter partitioning, reduces vegetative growth, increases the transpirational loss of water, alters phenology, reduces seed quality, and lowers grain yield (Kaushal et al. 2016; Nadeem et al. 2018). Photosynthetic machinery is the most thermo-sensitive part of plant function, and high temperatures can severely damage the chloroplast, stroma and thylakoids (Kaushal et al. 2016). Hence, chlorophyll fluorescence is a useful method to assess the extent of heat damage to photosynthesis (Maxwell and Johnson 2000).

High-temperature stress in pulses has been shown to increase flower abortion, cause pollen and ovule infertility, impair fertilization, reduce grain filling and result in smaller seed sizes and lower seed yields (Barlow et al. 2015; Delahunty et al. 2018; Sita et al. 2017). Documented heat stress thresholds for pulses cultivated in Australia range from 25 °C for faba bean and field pea to 30 °C for chickpea and lentil (Sita et al. 2017). Heat avoidance mechanisms identified for Australian rain-fed systems in crops such as wheat includes early and deep sowing to avoid heat stress periods and to allow access to subsoil moisture to overcome heat stress (Hunt et al. 2018). Other morphological traits that pertain to heat tolerance and avoidance in cereals include glaucousness plants with, erect canopies, rolled leaves to reduce surface area exposure and transpiration accompanied by management practices that ensure water is available for grain set and filling (Hunt et al. 2018). It would be worth investigating genetic variability for these traits in pulses alongside the variation in intrinsic heat tolerance.

Heat is often accompanied by drought. Drought-tolerant and heat-tolerant lentil genotypes exposed to heat stress alone (temperatures > 30/20 °C (day/night), increased rubisco activity by 22–32% over control plants (Sehgal et al. 2017). Whilst, under drought stress at 50% of field capacity, rubisco activity was reduced in both tolerant and sensitive genotypes, but more so in the sensitive genotypes (37–52%). A combination of heat and drought stress reduced rubisco activity by 45–85% in all genotypes. The photosynthetic rate decreased significantly more under drought (33–57%) than under heat stress (13–43%) when compared to control plants (Sehgal et al. 2017). Stomatal conductance increased across all genotypes under heat stress and decreased under drought and in the combination of the two stresses. The increase in rubisco activity and stomatal conductance has been linked to plants regulating internal temperature for continued growth and survival. Under drought conditions, plants limit water loss through reduced stomatal conductance and subsequently limit rubisco activity and photosynthesis. Regulation of internal temperature under high ambient temperature is another mechanism of heat tolerance and has been has been indirectly selected for in lentils where cooler canopy temperatures were observed in the presence of ~30 °C of ambient temperature (Silva-Perez et al.

2022). Alongside selection for cooler canopies, lower $CO_2$ assimilation rate and stomatal conductance was also observed in recently released lentil genotypes.

As heat (and frost) tends to occur more frequently during drought events in Australia, most of the traits listed in the drought section can be used to improve adaptation of pulses to heat stress, such as reduced canopy temperature and avoidance mechanisms such as early flowering and maturity. However, in circumstances where there is adequate water during heat stress, adaptive mechanisms for heat may differ with a greater focus on tolerance to flower and pod abortion arising from heat stress. Indeterminacy may also help by allowing aborted floral organs to be replaced when temperatures return to a normal growth range.

Cooler canopies during drought have been linked with deeper roots that can access subsoil moisture, reducing water and heat stress on the plant, and resulting in significant yield increases (Lopes and Reynolds 2010). Giri (2013) examined tomato plants grown under heat stress and observed reductions in shoot mass to be less than the reduction in root mass. Root respiration, protein concentration and membrane integrity were also severely affected. Studies on root response to heat have often been conducted in detached roots or by applying heat to only roots, which is non representative of plants growing in the field. However, heat application studies ($\geq 35/30$ ºC) have shown roots to be more sensitive than shoots to heat stress (Giri 2013; Heckathorn et al. 2013) and under extreme heat or open canopies, the top soil can be exposed and roots can experience heat stress. All regions can experience heat stress, hence, one of the traits that could help avoid heat stress is deep roots to access cooler soil layers where moisture is present, while transportation of water to the canopy keeps the heat-exposed roots cool as well. In southern low rainfall and subtropical northern regions, where water is not available at depth options for heat tolerance is limited. Avoidance by early sowing or breeding for increased intrinsic heat tolerance that can support a prolific shallow root architecture that could potentially aid in plant survival to some degree, provided it is able to maintain activity in low order lateral roots as higher order roots lose function and senesce (Hunt et al. 2018; Xu and Huang 2001; Tiwari et. 2022).

Cold and frost

Pulses in the temperate regions of Australia are sown in autumn and growth is over winter with average daily temperatures ranging from 10 to 15 °C, followed by rapid growth and flowering in spring where temperatures range from 25 to 30 ° (Siddique 1999). Crops often experience chronic cold i.e., daily maximum air temperatures less than 15 °C over extended periods during winter, or episodic cold events such as frost (air temperature $\leq$ 0–2 °C) (Grains Research and Development Corporation 2017). Whilst chronic cold slows plant growth, plants usually recover when temperatures increase. However, frost events are more detrimental, and the severity of the damage depends on the timing of the frost in relation to phenology and the duration of low temperatures. In both shoots and roots, plant cells expand and shrink as ice crystals form and melt, damaging cell membranes and resulting in severe cellular dehydration, intensified by ice nucleation, and increased cellular osmolarity (Ambroise et al. 2019; Thomashow 2001; Xin and Browse 2000). Both chilling and freezing stress can alter photosynthesis, stomatal conductance and assimilation of $CO_2$ (Hussain et al. 2018; Van Heerden et al. 2003).

All the temperate pulses are susceptible to frost during the reproductive growth stage as freezing reduces pollen viability (Barlow et al. 2015; Maqbool et al. 2010). In chickpea, mean daily temperatures of less than 15 °C reduced pollen viability, delayed flowering and podding, and reduced seed yield (Clarke and Siddique 2004; Singh 1997). In field pea and lupin, flowering requires a minimum of 7–10 °C: at lower temperatures plants delay flowering, drop flowers, abort set pods or stop grain development. Frost during pod filling can affect grain quality due to damaged seed coat and kernels (Murray et al. 1988). Field pea can also suffer complete plant death due to early season severe frosts that damage leaf tissue and facilitate the entry of *Pseudomonas syringae* pathovars that cause bacterial blight (Hollaway et al. 2007). Faba bean can tolerate temperatures below 10 °C but not extreme frost events and lentil has been shown to be able to tolerate temperatures as low as -2 to -3 °C during the vegetative growth stage (GCite Referencerains Research and Development Corporation 2018b; Murray et al. 1988). In lentil, frost events result in the discolouration and fine wrinkling of seed coats that

adhere strongly to the kernel (Maqbool et al. 2010; Yeatman et al. 2008, 2009). Apart from reduced pollen viability, frost can injure plants, causing necrosis on leaves, delay plant growth, induce wilting and susceptibility to pathogens and diseases (Grey 2014; Hussain et al. 2018). The presence of antifreeze proteins, fructans, dehydrins, polyamides, heat shock proteins, antioxidants and sugar alcohols have been highlighted as compounds that can mediate and reduce the cell damage caused by intra and extracellular ice crystal formation (Ambroise et al. 2019).

Cold and frost events frequently occur in the southern low and high rainfall regions and genetic tolerance through the presence of antifreeze metabolic compounds would aid in this regard. A proposed screening method for robust genetic tolerance to cold extremes could be through a range of early sowing times such that any given genotype would likely experience a naturally occurring frost event during critical time periods such as flowering (Maqbool et al. 2010; Frederiks et al. 2012). Lines could then be assessed in comparison to a susceptible check after it has suffered extensive cold damage (Singh et al. 1989). In addition, potassium applied to susceptible wheat has been shown to maintain physiological functions such as cell osmoregulation, plant photosynthesis and antioxidant systems (Ma et al. 2019). Similar to heat stress, the photosynthetic machinery in plants damaged by cold or freezing temperatures can be assessed by chlorophyll fluorescence and tracked using thermography (Livingston et al. 2018). In wheat, hyperspectral reflectance and fluorescence have been used to assess frost damage, (Fitzgerald et al. 2019; Perry et al. 2017), but progress on improving tolerance has been slow.

## Soil constraints

The major soil constraints currently affecting pulse cultivation regions of Australia are detailed below. The impact of these constraints is examined in relation to plant growth, reproduction, and corresponding plant traits, that have shown some degree of adaptation and how it supports the proposed physiological framework. Table 3 provides a summary of the major pulse cultivation soil constraints encountered in Australia and traits that have been suggested for adaptation.

### Soil pH

The above-mentioned soils in combination with rainfall and pH give rise to diverse and varying degrees of constraints. Supplementary Fig. 2 outlines the pH of soils across Australia. This shows that the south-central cropping region is dominated by alkaline soils, while the western and eastern regions are generally more acidic. However, as with soil types, pH can also be quite heterogeneous within a given region.

Chickpea, field pea and lentil prefer neutral to alkaline soils and struggle to grow on acid soils whereas lupins, with their proteoid roots, prefers acid soils, and faba bean can grow on both mildly acid and alkaline soils (Drew et al. 2012; Richards and Gaynor 2016). Neutral-acid pH topsoils are common across the cropping areas. Some of the high rainfall areas in Victoria and NSW have very low soil pH in the topsoil (Agriculture Victoria 2019b) which inhibits the plant available forms of essential nutrients such as phosphorus, potassium, magnesium, calcium, and molybdenum, whilst creating high concentrations of toxic ions such as aluminium ($Al^{3+}$) (Brennan et al. 2004; Lake 2000). In low rainfall areas, strongly alkaline soils are common and are often associated with high soluble forms of boron (B) which can be toxic to plants in high concentrations.

Despite the aforementioned pH preferences, pulses have been grown successfully at a pH of 5–6 in south-eastern Australia in medium and high rainfall zones (Burns et al. 2017) as often the subsoils are alkaline even when topsoils are acidic. At a pH of < 5, soil acidity severely affects nodulation leading to inefficient $N_2$ fixation, which results in poor plant vigour, root architecture and growth (Burns et al. 2017; Marschner 1991; Tang et al. 2001). The soil environment plays a crucial role in pulse productivity. Chemical properties such as low pH also affect rhizobia growth and survival, nodulation, nitrogen fixation and general growth of pulses (Robson 1988).

### Boron toxicity

A major soil constraint in low and medium rainfall areas of south-eastern Australia is boron toxicity (Adcock et al. 2007). Boron toxicity can arise in plants when internal boron concentration reach 1–5 mM (solution boron) from exposure to soil with high boron and is less readily ameliorated

than boron deficiency in the soil (Reid et al. 2004). Boron becomes toxic to plants when boron formed complexes (boron binding with ATP, $NAD^+$, other enzymes or incorporation of 14 C-glycine into protein) accumulate to an extent that creates a negative impact on the plant.

Boron toxicity limits root development and elongation with root tips being sensitive to boron toxicity. Young root tissues are affected more by boron toxicity than mature tissue (Nable et al. 1997) due to the impact of boron on cell wall formation and metabolite function. In mature tissues where cell growth has ceased, boron toxicity has less of an effect. Boron tolerant lentil plants show better growth of both shoots and roots with less necrosis and chlorosis. In Australia, boron tolerant genotypes have been developed in wheat and barley using genetic improvements (Schnurbusch et al. 2010), and in pulses, tolerant lines have been identified in field pea (Bagheri et al. 1992) and lentil (Hobson et al. 2006). High boron soil are often alkaline, sodic or saline, thus, selection for boron tolerance needs to be stacked with tolerance to other soil constraints for feasible yield benefit (Nuttall et al. 2005).

Hobson et al. (2006) examined 310 lentil genotypes for boron tolerance and observed that high boron levels resulted in chlorosis and necrosis in leaves and tips, reduced root biomass, root:shoot ratio, plant height, number of nodes, branch number on the main stem, green leaf area, number of pods per pot, seeds per pod, harvest index and seed yield. Whilst lentil were generally very susceptible to boron toxicity, lines from Afghanistan and Ethiopia performed better (Hobson et al. 2006). Tolerant genotypes resisted plant internal boron toxicity of 18.20 mg $kg^{-1}$ in comparison to intolerant lines where yield was significantly affected at concentrations of 1.55 mg $kg^{-1}$ of boron.

## Aluminium toxicity

Aluminium (Al) toxicity is the most common constraint in acid soils and is similar to boron toxicity as it affects root growth *via* the root tip, where it suppresses cell division and roots become stunted and brittle (Panda et al. 2009). Various ionic forms of aluminium exist naturally in the soil and of these, $Al^{3+}$ which is released to the soil at pH ($CaCL_2$) lower than pH 5, is the most phytotoxic (Panda et al. 2009). At pH 6.3 and higher aluminate $[Al(OH)_4^-]$ is the major

toxic ion; it has been found in Australian subsoils with a pH of 9 and above inducing a phytotoxic effect on wheat (Ma et al. 2003).

Improved aluminium tolerance can be achieved through either exclusion and/or compartmentalisation of Al ions. The Al exclusion was conferred by the active extrusion of organic acids that chelate Al in several crops including soybean, common bean and some cereals (Rao et al. 2016). A comparison between dicots and monocots using faba bean and maize plants demonstrated that in maize, toxic levels of Al in the stele accumulated faster than they did in faba bean. The higher levels of pectin present in the faba bean cell wall increased the potential Al binding sites, thus, slowing down the radial flow of Al to stele (Marienfeld et al. 2000). Yu et al. (2009) observed that the presence of border cells that had high pectin in their cell walls at the root tip of field pea improved tolerance to Al toxicity when exposed to $AlCl_3$ concentration of 4 mmol $l^{-1}$ in the mist culture solution. Kulkarni et al. (2021) examined lentil accessions and found that application of toxic levels of Al reduced root length by 32% compared to the control; the study also found that highly tolerant lines had 14% higher root growth rate than the known tolerant line. Although there is a reasonable understanding of the impact of Al toxicity on several crop species, there is a lack of knowledge on the impact of Al toxicity on pulses and pulse roots. To address aluminium toxicity in pulses a multifaceted approached is required that encompasses research on formation and function of nodulation under Al toxicity, Al tolerant rhizobia, root architecture and response, and intrinsic plat tolerance genetic gain through variation in pulse germplasm (De Carvalho et al. 1982).

## Salinity

Soils are considered saline when electrical conductivity (EC) is 1.5 S/m or higher in 1:5 soil: water, resulting from either dryland or transient salinity (Rengasamy 2010). Dryland salinity results from a rising water table from which salts migrate up the profile by capillary action and is a major production constraint of southern Australia (Lambers 2003). It can also be associated with and exacerbated by water logging (Barrett-Lennard and Shabala 2013). Transient salinity typically occurs in sodic soils where water percolation is restricted, evaporation and transpiration

are high and rainfall is low, resulting in salt accumulation in the root zone (Rengasamy 2002). High transient and dryland salinity impose both ionic and osmotic stress; it can indirectly affect plant growth *via* increased osmotic effect (on water uptake) or *via* inducing toxicity in cells. Whereas a lot of the focus has been on Na, a range of other elements e.g. K and Cl can induce 'salinity effects' (Shrivastava and Kumar 2015).

Pulses are generally more sensitive to salinity than most other crops and yields can be significantly affected. For example, the growth rate of white lupin has been shown to decrease rapidly when exposed to salinity (Jeschke 1984; Munns et al. 2002). The impact of salinity appears to increase with root order (Rewald et al. 2012) and impacts hormone signals especially those associated with auxin production and transport to the roots, thereby reducing the emergence of lateral roots and inducing agravitropism (Galvan-Ampudia and Testerink 2011; Sun et al. 2008). In *Arabidopsis*, under high salinity conditions, elongation of the taproot, rooting depth and lateral root initiation is deterred (Galvan-Ampudia and Testerink 2011).

Five main mechanisms which plants utilise to increase salt tolerance are (1) selectively excluding $Na^+$ and $Cl^-$ by roots; (2) preferential loading of $K^+$ rather than $Na^+$ in the xylem; (3) removal of salt from the xylem in the upper part of the roots, stem petiole or leaf sheaths; (4) reduced translocation of $Na^+$ or $Cl^-$ in the phloem; (5) excretion of salt (only in halophytes). Therefore, selection for salt-tolerant wheat has been achieved by identifying low $Na^+$ uptake and high $K^+/Na^+$ discrimination (Munns et al. 2000). There is a significant change in osmotic potential when plants are exposed to high concentrations of NaCl. Using X-rays microanalysis, exclusion of $Na^+$ and $Cl^-$ ions have been observed in roots. In addition to X-ray microanalysis, measuring transpiration efficiency in shoots has also been used to identify salt tolerance in plants (Munns et al. 2020).

In summary of the physiochemical constraints discussed in "Soil pH" to "Salinity" sections, there is good evidence that genetic variation for tolerance to the soil constraints of boron, aluminium and salt exists in a range of crops. In some cases, such as boron tolerance, superior germplasm has been identified in pulses and it is likely that tolerances to other constraints can similarly be found. Deployment of these tolerances will facilitate improved yield production per se, as well as providing options to redefine a broader ideotype. For example, a variety tolerant to a certain soil constraint will likely be able to develop an improved root system and access more soil water. This could then facilitate changes in optimal phenological traits such that the crop can optimise production in light of greater access to water.

Soil physical constraints

Soil strength is the ability of a given soil mass to resist applied force and is critical in plant anchorage needed for growth; however, soils with high soil strength can impede root growth. Soil strength is determined by its particle composition (including organic matter), water content and degree of compaction (Agriculture Victoria 2020; Unkovich et al. 2023). Clay particles in the soil influence cohesion, hence, as the soil dries out cohesion between particles increase and the interlocked particles result in greater resistance. High soil strength has a similar impact on roots as high soil bulk density in that they both impede root penetration, limiting their ability to absorb nutrients and water (Rengasamy 2002). High soil strength can result from either machinery operations (commonly referred to as 'compaction') or naturally, such as the movement of small or sandy soil particles down the profile or through the action of cementing agents and decline in organic matter.

Soil compaction/ high soil strength is common in sodic soils (Ford et al. 1993). The low porosity in soils with high soil strength can reduce leaching rates of salts, and is most severe in subsoils in the low and medium rainfall zone in the southern and western cropping regions (Agriculture Victoria 2019a). Under high pH, plant growth is hindered by the morphological changes in soil structure due to the presence of excess sodium rather than $OH^-$ ions. In Australia, soils are considered sodic if the excess sodium exchangeable sodium (% ESP) is greater than 6% and highly sodic if greater than 15% (Department of Primary Industries and Regional development 2021). High sodicity results in spontaneous dispersion of clay (expect in the presences of high salinity) and extremely low rates of hydraulic conductivity as the dispersed clay particles fill in the soil pores creating blockages resulting in decreased porosity and high soil bulk density

(Agriculture Victoria 2019a). This low porosity and high bulk density significantly hinders gas exchange, water movement, nutrient uptake, root penetration and growth (Pardo et al. 2000; Rengasamy 2002).

Bengough et al. (2011) states that in repacked dry soils, compaction of soil particles halved the elongation rate of cotton roots at resistances greater than 0.8 MPa and of maize and peanut at $> 2$ MPa. The review also states that the occurrence of soil resistance greater than 2 MPa increased from ~10–50% as water matric potential decreased from $-10$ kPa to -200 kPa. This highlights that as soil water content decreases, root impedance increases and that soil strength in even moderately wet soils can hinder root elongation.

Dense soils can be tackled using a range of management practices (Armstrong et al. 2022) as well as plant traits such as thicker taproots, especially in the southern low rainfall region. Nuttall et al. (2008) examined crop rotation of wheat with several crop plants and observed greater root growth after a lucerne crop in the top 0.5 m compared to other crops, on alkaline sodic soils of southern Mallee Victoria, Australia. Roots of lucerne created fine 'biopores' that allowed greater root exploration by the wheat crop in the subsequent cropping cycle. The root system of narrow-leafed lupin had a similar impact on the compact sandy soils of the Western Australia wheat belt (Chen et al. 2014).

When investigating strategies for managing constraints we tend to focus on one constraint at a time. However, multiple soil constraints can affect crop production at any given time (Armstrong et al. 2022). Soil constraints can generally be managed by three basic approaches: improved tolerance, amelioration, and avoidance. Developing tolerance via identifying genetic variation and subsequent use of breeding for tolerance of particular soil constraints e.g., salinity and high boron can be complex and generally only effective for a single constraint, thus requiring pyramiding of tolerances to produce significant yield responses when many constraints are present. Amelioration of soil constraints, especially those occurring in the subsoil can involve high financial risk for grain growers and is logistically challenging when applied in a broadacre situation (Armstrong et al. 2022). Consequently, in some scenarios such as when multiple physiochemical constraints are present in the subsoil and the frequency of sufficient rainfall occurring to recharge subsoil water supplies is low, the

adoption of an 'avoidance' approach may be a more effective strategy to improve adaptation. One strategy to achieve this avoidance may be the identification of root architecture traits that encourages root proliferation in topsoils to maximise plant utilisation of available soil water and nutrients, thus avoiding the need to exploit any resources (if available) in the subsoil.

## Conclusion

Pulse cultivation in Australia is spread across a range of agroecological zones that have a combination of climate and soil constraints limiting production and profitability for farmers. This review examines three broad pulse production areas that cover these agroecological zones and proposes region specific ideotypes using a physiological framework. The three regions were the southern low rainfall, southern high rainfall and northern subtropical regions. In the southern low rainfall region, plants with early vigour, indeterminacy, dimorphic shoot growth, high water use efficiency with a combination of fine to thick, shallow and wide roots can assist adaptation to extreme temperatures, absence of subsoil moisture and soil constraints. In the southern high rainfall region, waterlogging, low light intensity and duration require the opposite with an ideotype that has late flowering and maturity, determinate growth, high chlorophyl content, open canopy, and aerenchyma filled prolific root systems. In the northern subtropical region, a combination of the previous two is more suited as the region experiences terminal drought and extreme heat but has subsoil moisture at depth. This stored subsoil moisture provides a means to avoid the effects of terminal drought and extreme heat using root traits that can access this resource. Overall, an ideotype that has high plasticity and can transform its above and below-ground architecture to match the constraint it faces without significant yield penalty is the best adaptation towards amelioration of abiotic constraints. Whilst these regions have global relevance for similar soil and climate, fine tuning to target specific crop and climate is recommended when adopting the framework.

This review examined several adaptations for specific constraints, and in doing so has highlighted the overlap of traits to particular constraints, for example, high stomatal conductance in the face of heat stress

could be associated with deep roots accessing more water. Hence, future research should consider examining plant adaptation under multiple constraints such as those that occur in these environments. Furthermore, using a biophysical modelling approach as in the study by Hammer et al. (2014) to identify the scale, intensity, and frequency of different constraints across environments would help in prioritising/selecting constraints to be addressed. However, modelling for specific regional constraints and adaptations requires precise climate, soil, and plant data.

**Declarations**

**Conflict of interest**   The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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