Chapter 16
Physiology of the Yield Under Drought: Lessons from Studies with Lupin

Jairo A. Palta, Jens D. Berger and Helen Bramley

Abstract The ‘Old World’ lupin species are unique among grain legume crops in their strong specific adaption to acid sandy soils, and in their extremely recent domestication history. Our understanding of lupin responses to drought is limited; based on studies with elite cultivars, representing only a small fraction of the genetic diversity resident in the species, and subjected to strong selection for early phenology throughout their domesticated history, facilitating drought escape. Lupins appear to have a mix of competitive and conservative water use strategies, with profligate water use and high rates of photosynthesis when water is freely available; coupled with high sensitivity to water deficits, whereby stomatal conductance is reduced, phytohormone concentrations and metabolism modified, well before changes in leaf water potential occur. With high root-shoot ratios and high hydraulic conductance, lupin roots are highly efficient at taking up and transporting water. However, the predominantly apoplastic flow in lupins cannot be regulated as flexibly as the symplastic water transport that is so important in cereals. Low rates of remobilization of pre-anthesis stored C in lupin forces the crop to rely almost completely on current photosynthesis, which exacerbates the effects of terminal drought, given that the species respond by reducing leaf area through abscission. Because of the past narrow focus on domesticated material it is not currently possible to put these observations in an ecophysiological context, to answer which

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J. A. Palta (✉) · J. D. Berger
CSIRO, Plant Industry, Private Bag No. 5, Wembley, WA 6913, Australia
e-mail: jairo.palta@csiro.au

J. D. Berger
Faculty of Natural and Agricultural Sciences, School of Plant Biology, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia

H. Bramley
The UWA Institute of Agriculture (M082), The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia

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of these attributes are characteristic of lupins as a species, and which can be expected to vary in response to environmental selection pressure. To advance our understanding of the species we advocate the study of wild germplasm specifically-adapted to habitats that impose contrasting drought stress, to address both the narrowness and short evolutionary history of the domesticated material, by highlighting responses to millennia of natural selection. By identifying the pros and cons of adaptive traits in an ecophysiological context our capacity to improve elite material will be considerably advanced.

16.1 Introduction

This review focuses on the agriculturally most important Old World lupin species, *L. angustifolius* (narrow-leafed lupin), *L. albus* (white lupin), and *L. luteus*, (yellow lupin), which are of wider scientific interest, and arguably have considerable untapped potential, due to their strong specific adaptation to acid, sandy soils; and their very short history as domesticated crop. Accordingly, the lupins are still minor grain legume crops, with a combined average global production ~1 million t year^{-1}, 3 times smaller than lentil or pigeon pea, and 205 times smaller than soybean (FAO 2010). Despite their relatively minor global role, lupins are the principal grain legume option for acid sandy soils, and therefore Australia dominates world production (FAO 2010), largely due to the Western Australian (WA) contribution (ABARE 2010), reflecting the prevalence of suitable soils in that region.

Australian genotype by environment interaction (G × E) studies confirm that terminal drought is a consistent yield constraint of lupin in both the Mediterranean climates of Western Australia and summer-rainfall dominant eastern Australia (Berger et al. 2012a), leading to 8–16 fold reductions in grain yield. These data are confirmed by studies with controlled water regime treatments contrasting productivity under rainfed, well-watered, and rainout shelter conditions (Palta and Plaut 1999; Palta et al. 2004, 2007), and demonstrate that the lupin species are more sensitive to drought than cereals such as wheat (Henson et al. 1989a; Palta et al. 2008) and grain legumes such as chickpea and lentil Leport et al. (1998). Why is this so? This chapter explores the reasons underlying lupin sensitivity to drought by reviewing the origins, natural, and domestication history of the crop and its principal adaptive strategies. We highlight the relatively sparse literature that focuses on lupin responses to terminal drought using field and controlled environment experiments, and suggest new avenues to better understand the species and their potential in dryland agriculture.

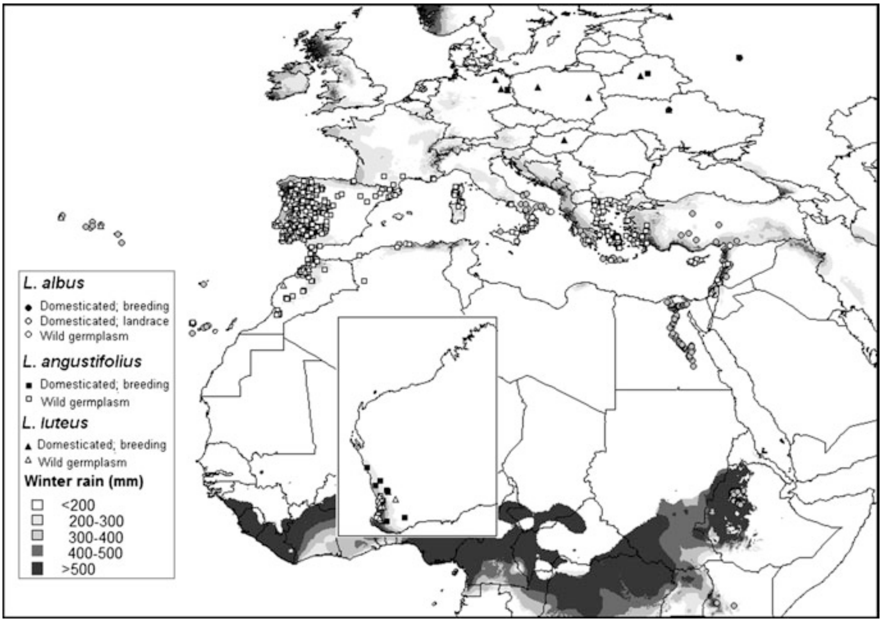

Fig. 16.1 Origins of the agriculturally significant 'Old World' lupin species (*L. albus*, *L. angustifolius, L. luteus)* as defined by collection sites sampled by the Australian Lupin Collection (DAFWA), categorized by domestication status. The inset shows Western Australia, world's dominant lupin production region (ABARE 2010), where wild germplasm represents naturalized environmental weed populations, and domesticated material are cultivars developed at various locations

16.2 Lupin Background: Origins, Natural, and Domestication History

The Old World lupin species originate from the Mediterranean basin, where they tend to act as early succession colonizers in neutral-acid, sandy soils of coastal regions (Fig. 16.1) (Cowling et al. 1998a). *L. albus* is somewhat of an exception, also found in inland areas of Turkey and East Africa (Fig. 16.1), including neutral to alkaline clay loams in the Nile Valley and elsewhere (Cowling et al. 1998a). While water-holding capacities of sandy soils are low compared to finer-textured loams and clays, plant available water is relatively high because of low crop water use. As a result, rainfall is readily available, even in dry sandy soils, but can also be quickly lost due to drainage. There are strong west coastal winter rainfall gradients along the Mediterranean basin lupin distribution, particularly in Iberia, the Balkans and Eastern Mediterranean (Fig. 16.1); overlaid with decreasing rainfall, and increasing temperature latitudinal gradients over much of the area. Although there is little published data within and between species, the Old World lupins appear to be typical Mediterranean winter annuals, using appropriate phenology to avoid the key stresses of early season low temperatures and subsequent

Table 16.1 Influence of geography on phenology in old world lupin species

Species	Origin	Reference
Early flowering		
L. albus	Northern Africa: Nile valley (Egypt, Sudan), Ethiopia, Morocco	Christiansen et al. (2000), and Noffsinger and van Santen (2005)
L. albus	Eastern Mediterranean: Anatolian plateau & coastal zones, Israel	Huyghe (1997), and Noffsinger and van Santen (2005)
L. albus	Western Mediterranean: SE Iberia	Simpson (1986), and Huyghe (1997)
L. angustifolius	Eastern Mediterranean: Palestine, S Greece	Troll (1940), and Clements and Cowling (1994)
L. luteus	Western Mediterranean: NW Iberia	Berger et al. (2008)
Late flowering		
L. albus	Western Mediterranean: NW Iberia	(Simpson, 1986; Huyghe, 1997)
L. angustifolius	Eastern Mediterranean: N Greece	Clements and Cowling (1994)
L. luteus	Western Mediterranean: S Iberia	Berger et al. (2008)
L. luteus	Eastern Mediterranean: Israel	Berger et al. (2008)
L. luteus	Northern Africa: Morocco	Berger et al. (2008)

terminal drought. Thus germplasm from terminally drought-prone southern Mediterranean habitats tends to flower and mature early, compared to material collected from cooler, wetter northern regions (Table 16.1), an adaptive strategy that trades off drought escape against biomass production and reproductive potential (Grime 1979).

Lupins are indeterminate, with maximum growth rates occurring after flowering, such that >80 % of carbon accumulation may take place post-anthesis (Pate et al. 1980). Despite their indeterminate nature, lupin architecture comprises an acropetal series of determinate shoots, starting with the main stem, followed by the primary lateral branches which form synchronously with main stem anthesis, and so on up the branch orders, depending on season length (Farrington and Pate 1981; Munier-Jolain et al. 1996). In the first 5 weeks after main stem flowering the stem and roots represent the principal C sink, where after pods and seeds become increasingly dominant (Pate et al. 1980). However, because there is considerable overlap in the development of reproductive and vegetative sinks within and between sequential branch orders, there is competition for C, and the probability of fruit-set decreases acropetally; increasing when earlier set basal pods on the same branch order, or subtending lateral branches are removed (Pate et al. 1980; Farrington and Pate 1981; Pate and Farrington 1981). The growing season is terminated by water stress, associated with leaf drop and the attendant decline in photosynthesis, and increase in respiration (Pate et al. 1980). This is important because lupin is heavily dependent on current photosynthesis; only <3 % of pre-anthesis C is transferred to seeds, where it contributes to the protein fraction (Pate et al. 1980). As a result lupin is very sensitive to environmental factors that reduce photosynthesis, especially if this is associated with terminal leaf drop, and cannot be recovered. Accordingly, in Mediterranean climates early planting allows more time for the development of higher order branches and pod fill within branch orders prior to the onset of terminal drought (Perry 1975).

All the Old World lupin crops species are recent to very recent domesticates; largely sharing a tortuous evolutionary path as crops, characterized by populations of small effective size, isolated in both space and time, subject to strong bottlenecks and selection pressures, as outlined below. *L. albus* is by far the oldest, with Bronze Age remains identified in a number of Aegean locations, and more recent Roman sites throughout Egypt (Zohary and Hopf 2000), and is the only member of the group that could be considered to be a traditional Mediterranean pulse crop. *L. albus* became a temperate crop in the eighteenth century, after Frederick the Great of Prussia took a personal interest in introducing it to the acid sandy soils of his homeland, but these efforts failed because of the inability of the crop to mature in a timely manner (Hondelmann 1984). Subsequently *L. luteus* was successfully introduced as a green manure crop, and became widespread in the north German lowlands from the mid nineteenth century, whereupon *L. angustifolius* was also taken up (Hondelmann 1984). Systematic plant breeding began in Germany and Poland in the early 1900s; rapid early growth and early maturity remaining key breeding priorities, as attested by cultivar names such as Pflugs Allerfrüheste (plough's earliest), a narrow-leafed lupin variety released in 1920. In the 1920–1930s, advances in analytical chemistry facilitated the search for alkaloid-free 'sweet lupins' independently in Germany and Russia, and the crops passed through a series of bottlenecks as many 100,000 of single plants were screened (Hondelmann 1984). This process was repeated during the search for permeable 'soft' seeds and non-shattering pods (Sengbusch and Zimmermann 1937). After the World War II the acid sandy regions of Central Europe became part of the Eastern Bloc, and therefore western interest in lupin breeding declined. In the 1950–1970s Gladstones in Western Australia fully domesticated the narrow-leafed lupin using European material, stabilizing pod shattering, introducing white flower and seeds as unlinked markers of domestication, and made the crop far earlier in warm environments by modifying the vernalization response (Gladstones 1970, 1994; Cowling et al. 1998b). Subsequently, the narrow-leafed lupin has become an important component of Australian acid sandy soil cropping systems, which are particularly prevalent in WA; production peaking at almost 2 million t in 1999, representing 93.5 % of the world total (FAO 2010).

16.3 Implications for the Crop

The domestication histories outlined above have had important ramifications for the Old World lupin crops; severely limiting their genetic diversity and selecting very strongly on early phenology. The best evidence for a narrow genetic base exists in narrow-leafed lupin, where Australian and European cultivars and breeding material form a single tight cluster in an ocean of wild germplasm of far greater diversity (Berger et al. 2012a). White lupin genotyping has been far more superficial (Raman et al. 2008), ($n = 94$ genotypes, compared to 1,343), but shows similar trends with breeding lines and landraces clustering separately. Given that all published research into lupin responses to terminal drought is based on domesticated material, this implies that our current knowledge is based on a very limited sample, which may not be representative of the species as a whole.

Strong selection for early phenology throughout its crop development history has led to highly temperature responsive, early flowering in narrow-leafed lupin (Berger et al. 2012b), equivalent to that of chickpea specifically-adapted to South India, an environment more than twice as warm during the vegetative phase as the northern WA grainbelt (Berger et al. 2011). This temperature responsive phenology facilitates drought escape in the northern WA grainbelt, the world's principal lupin production area, as demonstrated by the contrast of modern vernalization-unresponsive (VU) cultivars with their older, highly vernalization responsive (VR) counterparts (Berger et al. 2012a). Under these conditions, VU types flowered at 76–79 days, compared to 107–114 days among VR types; leading to 2.5-fold yield advantage in the favor of the former. Both phenology and yield differences between VR and VU types disappeared in terminally drought-stressing environments with sufficiently cold vegetative phases to induce a vernalization response (typical of eastern Australia); yields were consistently low in both groups. These results suggest that the principal breeding response to terminal drought has been to modify phenology, first by removing the vernalization response (Gladstones 1994), and then by selecting for higher temperature responsiveness (Berger et al. 2012a, b). This is confirmed by controlled experiments exposing Australian lupin cultivars to water deficit; where yield has been linked with other escape characteristics, such as rapid seed growth, pod fill, and the associated capacity to set and retain pods under stress (Palta et al. 2003, 2004, 2007).

16.4 An Unusual Mix of Water Use Strategies

In an ecophysiological context, narrow-leafed lupin appears to have a curious mix of conservative and competitive water use strategies. It is considered to be a profligate water user when water is freely available, a competitive strategy that facilitates water capture before it is lost to drainage, or is taken up by neighboring plants (Turner and Henson 1989). However, higher water use in comparison to other crops such as wheat or other cool-season grain legumes depends on timing within the season, particularly after flowering (Farrington et al. 1992; Siddique et al. 2001), with total water use generally being similar for the entire season (Hamblin and Tennant 1987; Gallardo et al. 1996; Eastham and Gregory 2000; Siddique et al. 2001). Conversely, narrow-leafed lupin is very sensitive to drying soils, reducing stomatal conductance well before changes in leaf water potential (Turner and Henson 1989); a strategy that is likely to conserve water when soil water content is relatively low, and drainage unlikely to be an issue. It may be that this mix of water use strategies is the ideal adaptation of lupin to sandy soils. Deep sandy soils have with limited water-holding capacity allowing lupin crops to profligate when there is a high risk of losing water to drainage, and to be conservative when there is not. This is speculative because it is not possible to put these trends into an ecophysiological context, because we simply do not know about the range of water use strategies in the species as a whole, because material specifically-adapted to contrasting environments has not been studied. However, these strategies contrast with cereal crops such as wheat (Henson et al. 1989a) that are more tolerant to terminal drought under the same field conditions, so we will examine these differences more closely in the following section.

16.5 Maintenance of Leaf Water Status

Perhaps the most studied aspect of lupin water relations is the regulation of their stomatal conductance. Stomates of narrow-leafed, yellow, blue, and white lupin behave similarly (Henson and Turner 1991; Correia and Pereira 1994) and are particularly sensitive to changes in the soil water content, rapidly closing when the soil starts to dry (Henson et al. 1989a; Jensen et al. 1989; Correia and Pereira 1994). In pot studies, stomatal closure occurred with partial soil drying (Jensen et al. 1989), associated with small increases in matric potential in the top half of the pots (Henson et al. 1989a). Stomatal conductance, root water uptake, and the fraction of roots in wet soil has been shown to decline linearly with soil water content (Jensen et al. 1989). Stomatal closure with partial soil drying was confirmed for narrow-leafed lupin in the field (Jensen et al. 1998), which appeared to be more related to soil water potential than relative soil water content or the fraction of roots in wet soil (Jensen et al. 1998).

Stomatal closure prevents leaf dehydration under moderate soil water deficit, allowing lupin leaves to maintain high relative water contents and constant water potential (Henson et al. 1989a; Jensen et al. 1989; Correia and Pereira 1995; Rodrigues et al. 1995). However, ongoing severe water deficit causes leaf water status to decline (Henson et al. 1989a). This is in contrast to wheat leaves that tend to have higher bulk turgor (Henson et al. 1989a), lower levels of stomatal conductance (Henson et al. 1990), and more negative leaf water potentials under adequate water conditions. Leaf water potential of wheat is also more closely coupled to soil water content decreasing as the soil dries, reflecting its much lower threshold leaf water potential for stomatal closure (Henson et al. 1989a). The behavior of wheat leaves may however, be dependent on growing conditions and genotypes, as inhibition of stomatal conductance before any decrease in leaf water potential has also been reported (Ali et al. 1999).

The closure of lupin stomata under soil water deficit is associated with increased leaf xylem concentrations of the phytohormone abscisic acid (ABA) (Henson et al. 1989b; Correia and Pereira 1994). ABA was closely negatively related to bulk turgor in wheat leaves, but not in blue lupin leaves, although ABA progressively increased with soil drying in both species (Henson et al. 1989b). There is clear evidence that ABA mediates stomatal conductance in lupin. Feeding detached leaves from well-watered blue, white, or yellow lupin plants with ABA concentrations similar to those found under drought resulted in similar reductions in stomatal conductance as those of attached leaves under drought (Henson et al. 1989b; Henson and Turner 1991; Correia and Pereira 1995). As with wheat leaves, lupin abaxial stomata are more sensitive to drought and ABA (Henson et al. 1989a; Correia and Pereira 1995) and the sensitivity of stomatal conductance to ABA depends on the severity of drought (Correia and Pereira 1995). The origin of the ABA is unclear. A study with saline-stressed white lupin suggests that ABA may be synthesized in roots and transported to shoots, or originates in the shoot and is translocated to roots via phloem where it is re-circulated back to the shoot (Wolf et al. 1990). Other phytohormones and metabolic adjustments have also been implicated in lupins response to soil water deficit before changes in leaf water status (Pinheiro et al. 2011). For example, a 12 % decrease in the soil water content did not affect the water status of white lupin, but caused changes in the phytohormones IAA and cytokinins. IAA increased in leaves, but decreased in roots, while the cytokinin activity was reduced in both roots and shoots (Pinheiro et al. 2011). Metabolic changes also occurred in response to soil water deficit before changes in plant water status, as indicated by changes in carbohydrate (starch and sugars) concentrations in different plant organs. Pinheiro et al. (2011) suggested that these early metabolic changes may be part of a mechanism that triggers adjustments to longer term soil water deficit.

Many species adapted to, or more tolerant to drought, maintain turgor by accumulating solutes in their tissues and increasing tissue elasticity. These features, particularly osmotic adjustment, have been selected for in breeding programs of many important crop species (Blum 2005). The capacity for osmotic adjustment appears to be limited in lupin species (Table 16.2), but could be dependent on growing conditions, stage of plant development when the plant experiences drought and severity of the drought (Table 16.2). Both blue and narrow-leafed lupin show some capacity to reduce their bulk leaf elastic modulus under soil water deficit, which combined with small osmotic adjustment maintained leaf turgor under lower relative water contents (Jensen and Henson 1990). But this is from a single pot study and no measurements appear to have been made under field conditions.

16.6 Root Hydraulic Properties that Favor Rapid Water Uptake Under Water Sufficient Conditions but with Little Capacity to Adjust Rapidly and Reversibly to Prevailing Conditions

Narrow-leafed and yellow lupin roots are highly efficient at taking up and transporting water, which is facilitated in-part by absorption of water along the root length and the abundance of large xylem vessels, respectively (Hamza and Aylmore 1992a; Bramley et al. 2009). They behave like large leaky conduits. In

Table 16.2 Osmotic adjustment in lupin leaves and roots in response to drought

Species	Environment	Timing of drought (DAS)	Degree of osmotic adjustment (MPa)		Reference
			Leaf	Root	
L. albus	Glasshouse, commercial potting mix filled pots	60	0.35		Correia and Pereira, (1995)
L. albus (3 genotypes)	Outdoors, large containers filled with sandy soil—outdoors	Flowering	0		Rodrigues et al. (1995)
L. consentinii	Glasshouse, 1 m soil (coarse field sand) columns	56	Osmotic potential decreased 1 MPa		Gallardo et al. (1994)
L. consentinii	Glasshouse, coarse sand-filled containers—severe drought	27–65	0.3		Jensen and Henson (1990)
L. angustifolius			0.4		
L. consentinii	Growth cabinet, small sand-filled pots	14	0.2		Kuang et al. (1990)
L. angustifolius (5 genotypes)	Field—coarse sandy loam overlying clay loam	107	0		Palta et al. (2007)
L. luteus					
L. angustifolius (2 genotypes)	Glasshouse, sandy/loam filled pots	45	0		Turner et al. (1987)
L. consentinii			0.2		
L. pilosus	Glasshouse, sandy/loam filled pots	40	0.4–0.5		Turner et al. (1987)
L. atlanticus			0.4–0.5		
L. luteus (2 genotypes)			0.2		
L. angustifolius			0.1		
L. angustifolius	Field—deep loamy sand (rainfed v irrigated)	76	0.2–0.3	0.4	Turner et al. (1987)

comparison, cereal roots confine their water absorption to a small region behind root tips (Bramley et al. 2009), but may have the ability to vary which region is involved in water uptake in response to abiotic stress (Bramley et al. 2010). In the field, wheat has several-fold greater root length densities than narrow-leafed lupin (Hamblin and Tennant 1987; Gallardo et al. 1996; Gregory and Eastham 1996), but water uptake per unit root length 2–5-fold lower (Hamblin and Tennant 1987; Gallardo et al. 1996). Despite these differences in root length, as result of larger diameters (Hamblin and Tennant 1987; Bramley et al. 2009) and higher root dry weights (Gregory and Eastham 1996), narrow-leafed lupins invest a greater proportion of their total biomass in the root system (Gregory and Eastham 1996).

So why is specific root water uptake greater in narrow-leafed lupin than wheat when water is not limiting? Lower leaf water potentials in wheat compared with lupin under the same transpirational demands, and soil water contents (Henson et al. 1989a), imply a greater resistance to water transport from roots to shoots in wheat. Measurements on young seedlings (Bramley et al. 2009) and estimations from flowering plants in the field (Gallardo et al. 1996) confirm this supposition. Although the hydraulic resistance of lupin roots is linearly related to xylem development and hence, decreasing axial (longitudinal) resistance with increasing distance from the root tip, the radial resistance is also lower than wheat despite their 2–3-fold larger diameter (Bramley et al. 2009). The transport of water from the root surface to the vasculature is usually the most limiting aspect of root hydraulic resistance (Steudle and Peterson 1998). Water traveling along the radial flow path has to navigate a series of concentric cell layers that are obstacles to water flow in the form of cell membranes and cell walls of varying composition impregnated with hydrophobic barriers such as suberin. In comparison to wheat, water flow through the apoplast is not as obstructed in lupin roots because they do not develop an exodermis (Hartung et al., 2002; Bramley et al. 2009), and suberization and secondary thickening of their endodermis occurs much further from the root tip (Bramley et al. 2009). The absence of these barriers may be the reason that water flow through narrow-leafed and yellow lupin roots preferentially occurs via the apoplast, whereas water crosses membranes in wheat roots with regulation most likely being controlled by aquaporins in the endodermis (Bramley et al. 2009, 2010). Aquaporins are membrane-intrinsic, water-conducting proteins, whose production and pore-gating (opening and closing) can rapidly and reversibly control the rate of water flow across cells, tissues, and organs (Tyerman et al. 2002; Bramley et al. 2007a). Without this facility, changes in root hydraulic resistance are constrained to slow and irreversible growth-related processes. In summary, while high hydraulic conductance facilitates rapid and efficient water flow in and out of lupin roots, the control of these fluxes much weaker and less flexible than in wheat.

The implications of these contrasting root hydraulic properties and water transport strategies may be linked to the strategies of controlling water loss at the shoot level. With aquaporin-regulated water transport, wheat roots can diurnally alter their root hydraulic conductance (reciprocal of resistance) to match transpiration demands (Carvajal et al. 1996) and minimize drop in leaf water potential, whereas this feature has not been observed for lupin species (Passioura and Munns 1984; Hamza and Aylmore 1992b). Lupins apparently rely on controlling leaf hydration by controlling the driving force for water flow through stomatal regulation.

We can only speculate what the implications of the different water transport strategies are in response to soil water deficit because there have been no comparative studies, and indeed no measurements of root hydraulic resistance in lupins in response to drought have been undertaken. We do not know whether lupin roots become more suberized to minimize water loss from roots to dry soils, but there are indications that they do not. Hartung et al. (2002) could not induce an exodermis in narrow-leafed lupin roots when the plants were grown in a mist environment (aeroponics), which have been shown to increase suberization in other plant species (Hose et al. 2001). Without suberization reducing leakiness of the shallower roots, extraction of water at depth as the surface soils dry would become increasingly difficult, as deeper roots become hydraulically isolated, or there is release of water from the wetter to drier soil regions (hydraulic lift) through the leaky surface roots. Lupin roots also dramatically shrink when the soil dries (white lupin, Carminati et al. 2009) or under osmotic stress (narrow-leafed lupin, Hamza et al. 2007). The formation of air gaps around roots associated with root shrinkage (Carminati et al. 2009) is likely to increase the interfacial resistance to water uptake, and would explain the increasing root resistance at low values of water uptake (Jensen et al. 1989). However, lupin roots may exude mucilage to alter the properties of the rhizosphere, and maintain hydraulic connection with the soil (Carminati et al. 2010).

Despite the lack of studies on lupin roots in response to drought, circumstantial evidence indicates that root hydraulic conductance is reduced under soil water deficit. Leaf water potential of blue lupin only partially recovered after transient drought, despite soil water contents returning to control levels and transpiration remaining low (Correia and Pereira 1995). This implies that root hydraulic conductance had decreased without full recovery such that roots could not supply the shoots with sufficient water. There may be a number of reasons for this. Apart from root shrinkage and the obvious loss of hydraulic conductance with root death, embolized xylem vessels would also increase root hydraulic resistance. Lupins may rapidly close stomata in response to soil drying to minimize increasing tensions developing in the xylem and hence, avoid cavitation, as large vessels are more susceptible to cavitation (Tyree and Sperry 1989). This is particularly important in sandy soils that lose water quickly. Narrow-leafed lupins may also have lower capacity to refill embolized vessels than wheat because they have very low root pressures (Bramley et al. 2007b, 2010) and lower solute reflection coefficients (Bramley and Tyerman, “unpublished”).

All of the above speculation has been derived from observations on one or two lupin species. The morphology of lupin root systems differs between species (Clements et al. 1993) and possibly growing conditions (Doussan et al. 2006; Garrigues et al. 2006). Different lupin root system architectures (taproot v fibrous) induce different water uptake patterns (Doussan et al. 2006; Garrigues et al. 2006; Oswald et al. 2008) and are likely to have different root hydraulic properties. Moreover, as emphasized in the introduction, the old world lupin distribution comprises a wide range of rainfall and reproductive phase temperatures. More research on these aspects may identify root traits that could be selected for improving lupin tolerance to terminal drought, particularly given that grain yield is correlated with post-flowering water use (Siddique et al. 2001).

16.7 Sensitivity to Drought Spells During Pre-Anthesis

The theme of liberal water use when soil water is plentiful, combined with high sensitivity to water shortages, is reflected in lupin metabolism. Rates of leaf net photosynthesis, leaf expansion, and crop growth are high when soil water is

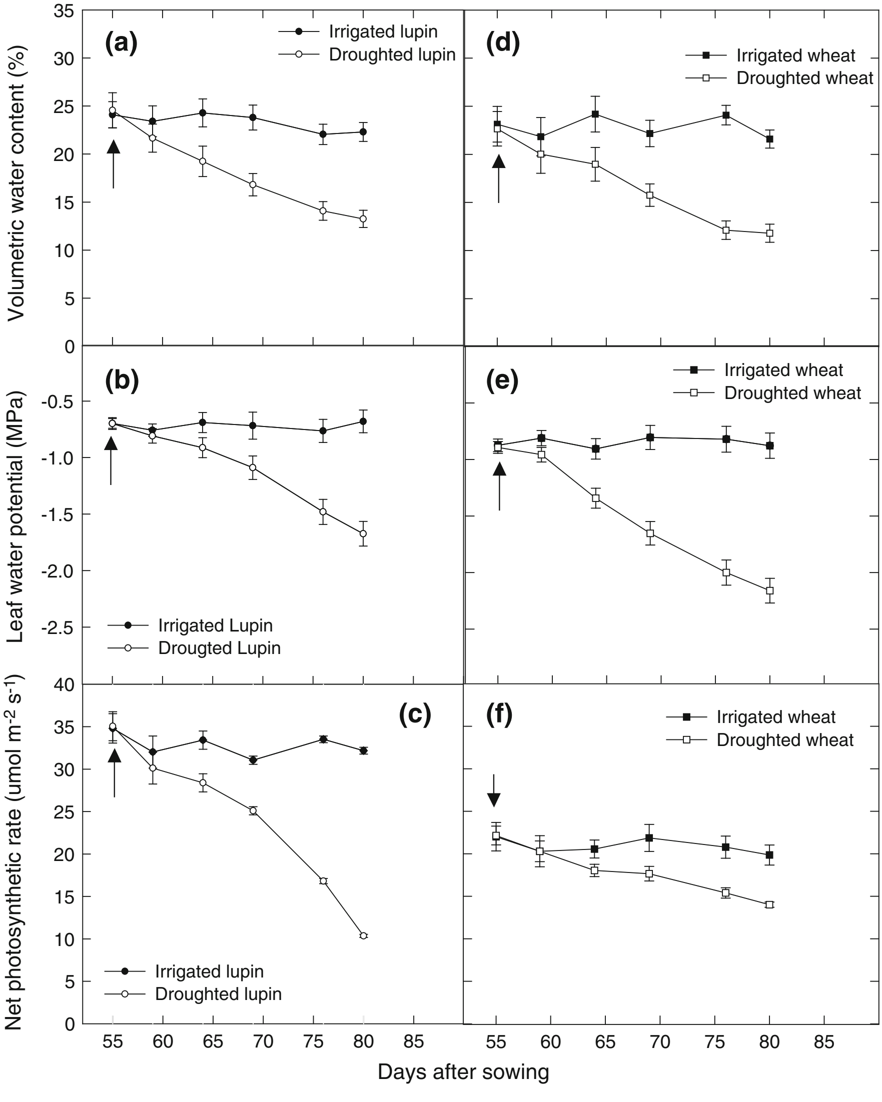

Fig. 16.2 Change with time in the volumetric soil water content, midday leaf water potential, and leaf net photosynthetic rate for narrow-leafed lupin (**a**, **b**, **c**) and spring wheat (**d**, **e**, **f**) under supplemental irrigation (*close symbols*) and under a 25 days spell of drought during pre-anthesis (*open symbols*). Drought was induced by excluding rainfall by positioning a rainout shelter over the crops for 25 days. Bars indicate ± s.e.m. for 6 replicates when larger than the symbol. The time when the drought spell was induced is indicated by the vertical arrows (Palta, “unpublished”)

adequate. Compared with spring wheat grown side-by-side on a deep sandy soil under rainfed conditions, the rates of leaf net photosynthesis and crop growth before flowering were 47–59 % and 23–33 % higher in narrow-leafed lupin, respectively (Fig. 16.2c, f; Table 16.3). When rainfall events were excluded by a movable rainout shelter the volumetric soil water content in the top 0.7 m of the soil profile decreased from 24 to 13.2 % (Fig. 16.2b) and leaf net photosynthesis and crop growth rates (CGR) in lupin decreased by 70 and 82 %, respectively (Fig. 16.2c; Table 16.3). Similar changes in the volumetric soil water content reduced wheat leaf net photosynthesis and CGRs by only 36 and 47 %, respectively (Fig. 16.2f). These differences in the reduction in leaf net photosynthesis and CGRs occurred when leaf water potential decreased from −0.7 to −1.7 MPa in narrow-leafed lupin (Fig. 16.2b) and from −0.8 to −2.1 MPa in wheat (Fig. 16.2e) and indicate the high sensitivity of narrow-leafed lupin to soil water shortages occurring before flowering.

Crop growth in lupin under pre-anthesis water shortage is reduced mainly through an adjustment in leaf area by abscission of fully expanded leaves from the mid to lower canopy, and a reduction in leaf expansion of newly formed leaves (Palta, "unpublished"). Reductions in crop growth caused by pre-anthesis drought spells may affect grain yield by reducing nitrogen fixation, limiting biomass, and the capacity to fill pods on the mainstem and develop apical branches (Pate et al. 1980). In most indeterminate grain legumes, like lupin, nitrogen accumulation at anthesis is strongly correlated with grain number per unit area (Pandey et al. 1984; Weisz et al. 1985; Muchow and Sinclair 1986) and grain number per unit area is the main determinant of grain yield (Muchow and Sinclair 1986; Dracup et al. 1998; Purcell and King 1996). Crop nitrogen accumulation in lupin depends on nitrogen fixation as up to 90 % of the accumulated nitrogen at anthesis is derived from atmospheric nitrogen fixation (Ndfa; Unkovich et al. 1994). Ndfa is more sensitive to soil water shortages than either leaf growth or leaf gas-exchange (Sinclair 1986) because Ndfa is affected by shortage of assimilates of carbon, nodule carbon metabolism and oxygen limitation (Serraj et al. 1999). A study in which rainfall was excluded for 25 days from a narrow-leafed lupin crop during its vegetative growth, showed that Ndfa was reduced from 84.2 to 28.5 % (Table 16.3) and this contributed to a 71 % reduction in total crop nitrogen (Palta, "unpublished") (Fig. 16.3).

16.8 Sensitivity to Terminal Drought

Terminal drought or "end-of-season drought" is a common feature in regions with Mediterranean-type climates, where lupin is grown as a crop. Terminal drought develops when rainfall decreases and evaporation and temperature increase in the spring, when lupin enters its reproductive stage (Reader et al. 1995; Palta et al. 2004). The sensitivity of lupin to terminal drought is the major cause of reductions in grain yield and the main deterrent for its adoption to new cropping areas (Palta et al. 2008). Compared with cereals, pulses, and some oilseed crops the grain yield of lupin is more severely affected by terminal drought. The comparison of the yield performance under terminal drought and well-watered treatments showed that while the grain yield of cereals, pulses, and some oilseed crops was reduced by

Table 16.3 Crop growth rate (CGR), nitrogen derived from the atmosphere (Ndfa) and nitrogen accumulation in narrow-leafed lupin (cv. Merrit) and spring wheat (cv. Westonia) crops under 25 d water shortage during their vegetative growth

	CGR g m^{-2} d^{-1}	CGR reduction (%)	%Ndfa	Ndfa (g m^{-2})	Total N (g m^{-2})
		Rainfed			
Narrow-leafed lupin	12.7	–	84.2	13.0	15.5
Spring wheat	8.5	–	–		7.1
		Rainfall excluded for 25 d			
Narrow-leafed lupin	2.3	82	28.5	1.3	4.4
Spring wheat	4.5	47	–	–	4.2
l.s.d (*P* = 0.05)	1.8	22	31.7	6.8	8.5

Crops were grown side-by-side on a deep sandy soil at Wongan Hills, Western Australia in 1995. Water shortage was induced by positioning over the crops movable rainout shelter to exclude rainfall. The proportion of nitrogen derived from the atmosphere (%Ndfa) was determined using the ^{15} N natural abundance method of Shearer and Kohl (1986). L.s.d (P = 0.05) is for comparison of differences between lupin and wheat and treatments. (J Palta, "unpublished")

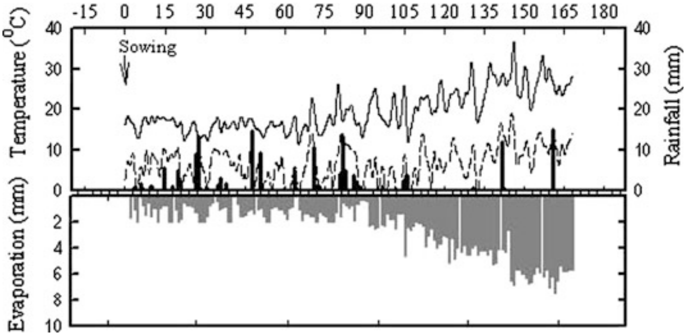

Fig. 16.3 Maximum (—) and minimum (–) air temperatures, total rainfall (*solid histogram*), and evaporation (*shaded histogram*) at Merredin, Western Australia, a region where the incidence of terminal drought is high. Adapted from Palta et al. (2004)

39.7–53.8 % the grain yield of lupin was reduced by 60–93.8 % (Table 16.4). The severe reduction in lupin grain yield under terminal drought raises important questions. What is the underlying physiology that makes it so susceptible? The sensitivity of current assimilation to water deficit and the distribution of recently photosynthesized carbon offer a framework to answer this question.

Lupin grain yield is largely reliant on current assimilation (Pate et al. 1980), and the indeterminate growth habit of the crop introduces competition between vegetative and reproductive sinks for C (Palta and Ludwig 2000). Therefore, any environmental stress that reduces the availability of carbon assimilates after anthesis will largely reduces grain yield (Palta and Ludwig 1996, 2000). A field study in which the availability of carbon assimilates in wheat, narrow-leafed lupin, and pea was reduced by intercepting 90 % of incident solar radiation after anthesis by shading, showed that while pea and wheat reduced their grain yield by 26 and 63 % respectively, lupin grain yield was reduced by 98 % (Saldaña et al. 2009). This indicates that the contribution of pre-anthesis stored assimilates was much lower in lupin than in the other crops. Pate et al. (1980) suggested that less than 3 % of pre-anthesis stored carbon is transferred to the grain, and studies in which canopies of narrow-leafed lupin were fed with $^{13}CO_2$ several times during pre-anthesis confirm that even under terminal drought, remobilization remains low (Table 16.5: 2.8–5.0 %). Compared with spring wheat, which increases pre-anthesis carbon remobilization from 7.7 to 21 % under terminal drought (Palta et al. 1994), these values are very modest, and unlikely to contribute to grain filling in lupin, even though under terminal drought the grain, as opposed to the vegetative tissue, becomes the dominant sink (Table 16.5; French and Turner 1991; Palta and Plaut 1999). ^{13}C feeding studies in narrow-leafed lupin underline the importance of current photosynthesis. C fixed in leaves during the day is either stored as starch and structural carbon compounds, or remains as water-soluble carbohydrates which are completely respired within 48 h (Palta and Ludwig, "unpublished"). This may explain why in some environments abortion of flowers and young pods (≤20 mm) occurs after 2–3 successive overcast days (≤430 μm m^{-2} s^{-1}; PAR) (Berger et al. 2008).

The second question concerns what can be done to make lupin grain yield less severely affected by terminal drought. The identification of adaptive traits in lupin germplasm for terminal drought offers a framework to answer this second question. Lupin yield under terminal drought is reduced through pod and seed abortion caused by a shortage of carbon assimilates (Palta and Ludwig 1996, 2000). As pointed out above, varietal selection has ensured early flowering in narrow-leafed lupin (Berger et al. 2012b), providing more time for podding and pod filling before the severe effects of terminal drought occurs on carbon assimilation (Palta et al. 2004). Modern narrow-leafed lupin cultivars like Belara and Quilinock escape terminal drought by flowering and podding earlier and having faster rates of seed filling than old cultivars like Merrit and Myallie (Table 16.6). However, the escape from terminal drought may not necessarily improve pod retention in lupin. The measured pod retention in the field (Palta et al. 2007) suggests it may be a potential trait conferring high yield in some cultivars like Tanjil under moderate (late) terminal drought, but not under extreme (early) terminal drought conditions, because the carbon resources generated by reduced current assimilation were only enough to fill half of the pods that were retained.

Early flowering may limit further yield improvement by constraining source size. Finishing the growing season early limits the time available for biomass accumulation, generating a tension between drought escape, and maximizing source potential. Studies by Palta and Ludwig (2000) and Saldaña et al. (2009) suggested that grain yield in narrow-leafed lupin was source—rather than sink-limited. When sink size was increased by application of cytokinin to the flowers to increase pod retention (Atkins and Pigeaire 1993; Palta and Ludwig 1996), grain yield did not increase because many pods failed to fill their seeds (Palta and Ludwig 1996). The failure to fill extra pods resulted from the inability of source to

Table 16.4 Terminal drought sensitivity of lupin crops, assessed by a comparison of droughted and well-watered treatments

Crop species	Experiment type	Region	mm per season		Grain yield (t/ha)		Yield reduction (%)	Reference
			Well-watered/ rainfall	Drought/ rainfed	Well-watered/ rainfall	Drought/ rainfed		
Narrow-leafed lupin	MET	Australia, eastern grainbelt	477.8	153.7	3.2	0.2	93.8	Berger et al. (2012b)
Narrow-leafed lupin	MET	Australia, western grainbelt	389.2	173.4	1.7	0.2	88.2	Berger et al. (2012a)
Narrow-leafed lupin	TDM	Australia, western grainbelt	494.7	306.2	3.0	1.2	60.0	Dracup et al. (1998)
Narrow-leafed lupin	YUTD	Australia, western grainbelt	217.0	160.0	1.7	0.4	76.5	Palta et al. (2004)
Spring wheat	MST	Yugoslavia, Novi Sad	352.0	138.6	7.8	4.7	39.7	Dencic et al. (2000)
Durum wheat	MET	Spain, eastern Andalusia	370.0	190.5	4.3	2.5	41.8	Garcia del Moral et al. (2003)
Chickpea	YUTD	Australia, western grainbelt	462.0	275.0	3.7	2.0	46.0	Leport et al. (1999)
Soybean (ind.)	MST	Australia, northern grainbelt	264.6	149.5	2.6	1.2	53.8	Rose et al. (1992)
Common bean	YUTD	Mexico, Durango	357.4	136.7	1.1	0.6	42.0	Acosta-Gallegos and Adams (1991)
Canola	MEY	Australia, western grainbelt	446.0	274.0	1.9	1.0	47.4	Farre et al. (2001)

MET Multi-environment G × E trial
TDM Terminal drought manipulation
YUTD Yield under terminal drought GxE trial
MST Multi-seasonal G × S trial
MEY Multi-environment yield analysis

Table 16.5 ^{13}C accumulated at the commencement of flowering, post-anthesis losses and remobilization to the seeds, pod shells, and developing apical branches

	^{13}C (mg plant^{-1})					
Treatments	Flowering	Post-flowering Losses	Remobilized			Retained
			Seeds	Pod shells	Apical branches	
Well-watered	55.6	27.6 (50)	1.6 (2.8)	0.8	3.1 (6.0)	22.5 (40)
Early terminal droughted	55.3	28.4 (51)	2.8 (5.0)	1.3	1.6 (3.0)	21.2 (38)
Late terminal droughted	55.5	27.0 (48)	2.1 (3.8)	0.9	2.2 (4.0)	23.3 (42)
l.s.d. ($P < 0.05$)	3.1	1.6	0.7	0.2	0.5	0.9

Narrow-leafed lupin canopies were fed with ^{13} CO_2 three times during pre-anthesis to label the pre-anthesis pool of carbon and the fate of ^{13} C was measured under well-watered conditions and under an early and late starting terminal drought. The values in brackets are the percentage of the ^{13} C available at the commencement of flowering. L.s.d ($P < 0.05$) is for comparison between treatments. (Palta, "unpublished")

Table 16.6 Time to flowering and podding, maximum seed growth rates (MSGR), pod retention, and seed yield of modern and old narrow-leafed cultivars grown in the field under terminal drought

Genotype	Release date	Flowering (DAS)	Podding (DAS)	MSGR (mg seed^{-1}d^{-1})	Pod retention (%)	Seed yield (t/ha)
Merrit	1991	97	105	5.4	62	1.6
Mayllie	1995	96	105	5.8	71	1.7
Kalya	1996	98	106	6.0	75	1.7
Tanjil	1997	95	105	6.2	82	2.0
Belara	1998	92	100	7.0	67	2.2
Quilinock	1999	91	99	7.6	69	2.1
l.s.d ($P = 0.05$)	–	4	2	0.7	4	0.2

L.s.d ($P = 0.05$) is for comparison among genotypes. Adapted from Palta et al. (2004), and (2007)

match sink demands (Palta and Ludwig 2000). When the availability of carbon assimilates (source) was increased by exposing plants with increased number of pods (large sink) to elevated CO_2 during pod filling, grain yield increased by 42 % (Palta and Ludwig 2000). This implies that lupin must accumulate as much biomass as the growing season will allow to meet its sink demands. Under terminal drought this is exacerbated by the importance of current photosynthesis, given the lack of C remobilization, underlining the need to screen for genetic variation for this trait. In wheat, selection for vigorous seedling growth has successfully increased biomass accumulation and yield, particularly in drier environments and seasons (Rebetzke and Richards 1999; Richards and Lukacs 2002), probably because of the capacity of that crop to remobilize earlier fixed C. Clearly lupin needs both: increased early biomass accumulation, and a greater capacity to remobilize it.

16.9 Challenges in Improving Terminal Drought Tolerance in Lupin

The challenge facing the lupin researcher identifying and evaluating traits for improving tolerance to terminal drought is to find physiological and morphological characteristics that are independent of terminal drought escape. To date this has been the primary breeding strategy for adapting the crop to dry areas (Berger et al. 2012a, b; Gladstones 1994). Further selection for even earlier flowering will be difficult, given that modern cultivars are at the upper extreme of temperature responsiveness, and will limit crop yield potential by constraining the time available for biomass accumulation by finishing the growing season early, increasing the trade-off between drought escape and maximizing source potential. Therefore, the task is to identify and evaluate traits that are associated with postponing dehydration and dehydration tolerance strategies.

Narrow-leafed lupin postpones dehydration by high stomatal sensitivity to soil water deficits (Turner and Henson 1989), as outlined previously. These can be delayed by accessing previously unavailable water through the development of deeper roots, and/or by making more efficient use of existing water resources by optimizing hydraulic conductivity. Alternatively, it may be possible to change the threshold at which stomata close, or manipulate leaf area directly, given the variation available between and within species. Finally, osmotic adjustment, the active accumulation of osmotically active solutes in plant tissues as water deficits develop so that cell turgor is maintained at low ψ_L, may improve lupin dehydration tolerance.

All these avenues for manipulating responses to water deficit are hamstrung by common constraints that are unique to the lupin species. Because of their short domesticated history we simply don't know the species' well enough to optimize adaptation to cropping systems. This problem is exacerbated because lupin cultivars are highly inbred, do not represent the genetic diversity available in the species', and have been strongly selected for drought escape. Moreover, our understanding of water use strategies and responses to water deficit in the much older, much more diverse wild germplasm pool is currently extremely rudimentary.

Despite these challenges, there is enough evidence that the search improved adaptation to soil water deficit is worthwhile. Our unpublished studies with wild germplasm exposed to terminal drought demonstrate that both yellow and narrow-leafed lupins collected from dry areas are much more conservative in water use than those from high rainfall areas. Turner and Hartung (2012) showed that isolated roots of *Lupinus* species vary significantly in their synthesis of free and conjugated ABA in response to 50 % dehydration of tips (but found no relationship with root dehydration). There is significant genetic variation in root systems of young lupin plants under controlled environment conditions (Clements et al. 1993; Chen et al. 2011), and leaflet size throughout the growing season in field plots (Buirchell, "personal communication"). Turner and Henson (1989) found significant osmotic adjustment of up to 0.2 MPa in narrow-leafed lupin grown in controlled environments, [but which was not supported by field evaluation of narrow-leafed lupin and white lupin cultivars (Rodriguez et al. 1995; Leport et al. 1998; Palta et al. 2007)].

Clearly, this short track record is a mixed one, which makes it difficult to generalize on lupin adaptive responses to water deficit. The way forward is to undertake ecophysiological studies of wild germplasm specifically-adapted to contrasting drought habitats because this addresses both the narrowness and short evolutionary history of domesticated material, and will highlight the results of millennia of natural selection. With this approach—if nature has selected for it, we will find it! Subsequently it will be important to implement a pre-breeding strategy of crossing with well-adapted elite cultivars to deliver proof of concept under real-world field conditions. This is essential, given the confounding effects of other wild traits, such as pod dehiscence, presence of alkaloids, hard-seeded ness, etc. Given the difficulty of measuring physiological traits in breeding populations this will almost certainly require some form of molecular marker tagging to ensure that the trait of interest is not lost in ongoing hybridization.

As outlined above, improving lupin adaption to water deficits represents a considerable challenge, but one which is very worthwhile, because this journey will not only increase productivity in a grain legume uniquely adapted to acid, sandy soils; it will simultaneously increase our understanding of drought adaptation in annual plants.

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