



## Review

# Faba bean breeding for drought-affected environments: A physiological and agronomic perspective

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## ABSTRACT

The faba bean (*Vicia faba* L.) crop often experiences drought during its growth and development such that soil moisture deficits constrain its production. As droughts are predicted to increase in both frequency and intensity due to climate change, a better understanding of drought response patterns and associated traits is essential for obtaining yield stability in water-limited environments. This review deals with adaptation mechanisms associated with drought avoidance, escape and tolerance, with an emphasis on physiological traits such as stomatal conductance, carbon isotope discrimination and leaf temperature. Leaf temperature is considered an effective surrogate measure for other measures of stomatal characteristics. Drought tolerance through osmotic adjustment has not yet been demonstrated in faba bean although it is found in many other legumes including chickpea and pea. Deeper root growth, leading to uptake of otherwise unavailable water, helps the plant to avoid drought by delaying dehydration, but genetic variation and heritability of the trait are essentially unknown for faba bean. Crop management strategies, such as early planting, and appropriate phenology, are particularly important for drought escape in regions where terminal drought is common. Disease resistance is especially important in drought-prone areas to reduce the need for expensive control measures when yields are uncertain. The relevance of soil fertility status and nutrient availability are also covered. Drought escape and ascochyta blight resistance are important breeding objectives for terminal drought regions. Some form of drought resistance is necessary for the transient droughts experienced in most regions, and drought avoidance can be screened by a combination of leaf temperature or other rapid test of stomatal characteristics followed by carbon isotope discrimination in the most valuable materials. No single trait is adequate to improve yield in drought-prone environments, rather, a combination of characteristics is needed.

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## 1. Introduction

Drought, an interval of water deficit leading to a significant reduction in yield, is widely considered to be the most important environmental constraint to crop productivity (Fischer and Turner, 1978; Borlaug and Dowsell, 2005); and faba bean (*Vicia faba* L.) is reputed to be more sensitive to water deficits than some other grain legumes (McDonald and Paulsen, 1997; Amede and Schubert, 2003). In many production regions in the Mediterranean basin (Sau and Mínguez, 2000), Western and Central Europe (Link et al., 1999) and Australia (Loss et al., 1997; Siddique et al., 2001), the crop is seldom if ever irrigated and generally relies on stored soil moisture and current rainfall for its growth and development. Temporary water deficit may occur at almost any stage of growth wherever faba bean is grown, and in many areas, especially Mediterranean-type climates, terminal drought occurs during reproductive development (Wery et al., 1994; Siddique et al., 1999; Ricciardi et al., 2001). Variation in the amount and distribution of rainfall is generally considered the major reason for variability in seed yield of faba bean (Bond et al., 1994; Manschadi et al., 1998a; Abdelmula et al., 1999; Siddique et al., 2001).

Models predict that climate change attributed to the emission of greenhouse gases will probably increase the frequency and intensity of droughts (Oldfield, 2005; Rosenzweig and Colls, 2005). A better understanding of the effects of both transient and terminal types of drought on plants is vital for breeding efforts in agriculture under this predicted climate change. Furthermore, characterization of drought patterns in major growing regions is an important step in designing strategies for improving crop drought responses (Subbarao et al., 1995). The key to drought “resistance” for plant breeders and crop physiologists is tailoring the phenology and physiology of a crop to its environment in order to manage water economy (Passioura, 2007). The yield ( $Y$ ) of a crop may be modelled by a generalized equation,  $Y = Q \times I \times \varepsilon \times HI$  (Hay and Porter, 2006) where  $Q$  is the received input (in this case, water),  $I$  is the fraction of that input that is intercepted or absorbed by the crop,  $\varepsilon$  is the efficiency (water use efficiency at the crop level (WUE) or transpiration efficiency at the leaf level (TE)) and  $HI$  is the harvest index. For water-limited crops, therefore,  $Q \times I$  is the total amount of water transpired. Losses by runoff and deep drainage below the root zone are considered minimal in crops such as faba bean grown in low-rainfall Mediterranean environments or on residual soil water, but soil evaporation can be high. Thus to maximize yields in water-limited environments, agronomic practices to minimize water loss by soil evaporation and maximize crop transpiration, WUE and  $HI$  are required (Passioura, 1977).

Different crop species show variable susceptibility to water deficit at different stages from emergence to maturity. Drought

stress is affected by climatic, edaphic and agronomic factors, and varies in timing, duration, and intensity (Serraj et al., 2003). Crop plants have various adaptive mechanisms to cope with drought stress, but the responses are complex, and adaptation is attributable to a plant's ability to exercise one of these mechanisms (Hall et al., 1979). The components of response to water deficit have been classified as escape, avoidance or postponement, and tolerance (Levitt, 1980; Ludlow and Muchow, 1990). In those regions where the growing season is short and terminal drought stress predominates, drought can be escaped by earliness, matching phenological development with periods of soil moisture availability (Turner et al., 2001). Dehydration avoidance is related to the maintenance of high tissue water potential and consists of mechanisms that reduce water loss while maintaining water uptake. Reduction of water loss generally depends on stomatal control of transpiration while increased water uptake depends on a deep and prolific root system. Dehydration tolerance refers to the ability of the plants to withstand low tissue water potential (Turner et al., 2001), and the ability to recover is an important component of this. The components of drought resistance and the physiological factors that contribute to them are listed in Table 1. In order to define the criteria needed to develop cultivars suitable for drought-prone areas, it is first necessary to identify the traits associated with drought response and to explore how they are expressed in this species.

## 2. Screening techniques

Progress in the development of drought-tolerant faba bean cultivars has been slow, mainly due to large seasonal variations in the intensity of drought stress, the timing of its arrival and a lack of efficient screening techniques (Turner et al., 2001; Stoddard et al., 2006). Rain-exclusion shelters allow control of the timing and intensity of the drought stress (Link et al., 1999) but building a system large enough for large-scale screening can be very expensive. Nevertheless, it is possible to develop specific screening techniques under controlled conditions by applying knowledge from other field crops and validating it in the target crop (Wery et al., 1994). Screening under controlled conditions allows responses to be evaluated rapidly and uniformly (Grzesiak et al., 1996) and the method should be non-destructive, accurate and able to handle many samples (Wery et al., 1994).

The use of secondary plant characteristics related to enhanced production in water-limited environments has often been suggested to complement phenotypic selection (Lafitte et al., 2003). In this regard, analysis of physiological responses to water deficit can identify sources of TE and water interception, and furthermore provide efficient tools for use by breeders (Jackson et al., 1996; Richards, 2006). Cultivars that show stability of

**Table 1**  
Traits measured in drought-resistance experiments and their value in determining the different mechanisms of drought response.

Trait	Drought resistance mechanism evaluated	Labour time costs	Capital and consumable costs	Genetic variability	Quality of information
Shoot dry matter, water use, transpiration efficiency	Avoidance (stomata)	High	Medium	Medium	Medium
Relative water content	Avoidance (stomata)	High	Low	Medium	Medium
Stomatal conductance	Avoidance (stomata)	High	Low	High	High
Leaf temperature	Avoidance (stomata)	Low	Low	Low	High
Carbon isotope discrimination	Avoidance (stomata)	Low	High	Low	Very high
Leaf cuticle characteristics	Avoidance (morphology)	Medium	Low	Unknown	Unknown
Root length	Avoidance (roots)	High	Low	Low	High
Root dry matter	Avoidance (roots)	High	Low	Medium	Medium
Osmotic potential	Tolerance	Medium	Low	Medium	High
Oxidative response	Tolerance	Medium	Medium	Unknown	Unknown
Specific leaf area	Escape	Low	Low	Low	Medium
Earliness	Escape	Low <sup>a</sup>	Medium	High	High

<sup>a</sup> This trait requires years of testing in multi-environment trials so the practical time consumption is very high.

performance under unfavourable environments maintain physiological components of tolerance to environmental stresses (Blum, 1984). Direct measurement of physiological processes involved in drought response is useful when a large number of genotypes can be measured (Wery et al., 1994). Various physiological attributes of the faba bean plant, such as water use (Amede et al., 1999), water potential (Karamanos and Papatheohari, 1999), stomatal characteristics (Ricciardi, 1989; Bond et al., 1994), leaf temperature, and carbon isotope discrimination ( $\Delta^{13}\text{C}$ ) (Khan et al., 2007) may be useful in developing selection techniques for drought escape, avoidance or tolerance. Although these measurements have a sound physiological basis, few can be integrated into a breeding program, as the rest require complex or time-consuming protocols (Karamanos and Papatheohari, 1999; Monneveux and Ribaut, 2006).

### 3. Drought avoidance

#### 3.1. Controlling water loss through the leaf surface

Stomatal closure is a drought avoidance mechanism and is one of the first steps in a plant's adaptation to water deficit, allowing the water status to be maintained. Stomatal conductance is determined by the combination of stomatal density, size and opening. While stomatal size and density are evaluated by microscopy of leaf surfaces (Grzesiak et al., 1997a), and the average size of stomatal opening is hard to measure since it responds rapidly to the environment, stomatal conductance is efficiently measured with a porometer. Stomatal size and density vary widely in faba bean (Tanzarella et al., 1984; Grzesiak et al., 1997b). Ricciardi (1989) found that accessions with higher stomatal density had lower seed yields and less resistance to water deficit, while low stomatal density was associated with better adaptation to stress conditions. Nerkar et al. (1981) found that stomatal conductance was by far the most important of several traits (such as relative water content and WUE) determining water use in five faba bean accessions. Amede et al. (1999) observed significantly higher water use in cv. Adriewaalse than in line L-7, which avoided drought by means of low transpiration rates. Khan et al. (2007) reported twofold variation in stomatal conductance among eight faba bean inbred lines; ILB938/2 and Mélodie exhibited low stomatal conductance combined with high transpiration efficiency (TE), whereas lines 332/2/91/015/1 and Victor/2 had the opposite combination. Appropriate stomatal behaviour may be useful for improving drought response in faba beans by reducing water loss and increasing TE (Darwish and Fahmy, 1997), and efficient measurement of stomatal conductance would increase the reliability of assessing cultivar performance under drought (Soja et al., 1988).

Carbon isotope discrimination has been proposed as an indirect selection index for TE in several  $\text{C}_3$  species under water-limited environments (Condon et al., 2004). The carbon in atmospheric  $\text{CO}_2$  occurs as two stable isotopic forms: 99% is  $^{12}\text{C}$  and 1%  $^{13}\text{C}$ . The  $^{13}\text{C}$  content of plant material is described in two ways, carbon isotope composition ( $\delta^{13}\text{C}$ ) and carbon isotope discrimination ( $\Delta^{13}\text{C}$ ).  $\Delta^{13}\text{C}$  is a measure of the  $^{13}\text{C}/^{12}\text{C}$  ratio in the plant material relative to the value of the same ratio in the air that the plant consumed (Farquhar and Richards, 1984), and plant material contains fractionally less  $^{13}\text{C}$  and more  $^{12}\text{C}$  than the atmosphere (Condon et al., 2006). In  $\text{C}_3$  plant species, the variation in  $\Delta^{13}\text{C}$  can result from variation in stomatal conductance and photosynthetic capacity, which is large enough to generate substantial differences in TE (Condon et al., 2006).

The use of  $\Delta^{13}\text{C}$  to evaluate TE has been well established in cereals and more recently extended to legumes (lucerne (*Medicago sativa* L.), Johnson and Tieszen, 1994; common bean (*Phaseolus*

*vulgaris* L.), Zacharisen et al., 1999; soybean (*Glycine max* (L.) Merr.), Clay et al., 2003; chickpea (*Cicer arietinum* L.), Khan et al., 2004). Genetic variation for  $\Delta^{13}\text{C}$  also exists in faba bean (Khan et al., 2007); the youngest fully expanded leaf of six-week-old plants of drought-avoiding accession ILB 938/2 and cv. Mélodie had significantly lower values of  $\Delta^{13}\text{C}$  than those of the drought-sensitive inbred line Aurora/1 at adequate moisture supply.  $\Delta^{13}\text{C}$  was negatively correlated with TE in these controlled-environment experiments (Khan et al., 2007), and these measures of drought avoidance were correlated with yield maintenance as shown in earlier experiments using rain-exclusion shelters (Link et al., 1999), but it has not yet been confirmed that  $\Delta^{13}\text{C}$  can be used to predict grain yield in field experiments in this species.  $\Delta^{13}\text{C}$  is the "gold standard" against which other methods are compared, but it is expensive, so it is best kept as a final test for a few tens of lines after the thousands have been screened by more economical methods such as leaf temperature, discussed below. It is not yet reported that any faba bean breeding program is using selection for high TE.

Leaf temperature, or its depression below atmospheric temperature, is a potential indicator of plant water deficit. Stomatal closure resulting from plant water deficit leads to decreased transpirational cooling and consequently increased leaf temperature, relative to well watered plants (Kramer and Boyer, 1995; O'Neill et al., 2006). Even when stomata are fully closed, there is some transpiration, termed residual transpiration (Clarke and Richards, 1988), and field pea (*Pisum sativum* L.) cultivars with a high stomatal density showed high residual transpiration rates and cool canopies (Sánchez et al., 2001).

Assessing canopy temperature with an infrared thermometer is a rapid technique giving instant measurements (Fischer et al., 1998). Since leaf temperature is a function of stomatal conductance, differences in canopy temperature between genotypes are associated with differences in the carbon exchange rate of the canopy (Reynolds et al., 1994). Wheat (*Triticum aestivum* L. emend. Thell.) canopy temperature decreased as stomatal conductance increased (Fischer et al., 1998). Amani et al. (1996) found the difference between leaf and air temperatures (canopy temperature depression, CTD) to be linearly related to stomatal conductance in spring wheat, suggesting that leaf temperature or its difference from air temperature may serve as a rapid surrogate measurement for stomatal conductance.

Leaf temperature in faba bean accessions was shown to be positively correlated with TE and negatively with stomatal conductance and  $\Delta^{13}\text{C}$  (Khan et al., 2007), even when water supply was adequate. Faba bean leaf temperature can be measured easily and economically with a simple handheld non-contact infrared thermometer. Its assessment is non-destructive and large numbers of accessions can be evaluated at the vegetative stage. Opportunities exist for increasing the efficiency of canopy temperature measurements, enhancing preliminary selection for efficient water use characteristics under controlled or uniform conditions.

Since TE and WUE are ratios of dry matter produced per unit water consumed, they are affected by both numerator and denominator. Using either as a single selection criterion is therefore as likely to select material with low productivity as that with high productivity (Blum, 2009). Faba bean line ILB938/2 is an example of the former, being relatively low in yield (Link et al., 1999) while cv. Mélodie is an example of the latter, being a high yielding, modern cultivar. For future research, there is a need that these traits should be assessed across a wider range of faba bean germplasm.

The waxes on plant cuticles form a protective cover against biotic and abiotic stresses including drought (Jenks and Ashworth, 1999). Drought stress enhanced the deposition of cuticular waxes

and subsequently improved drought avoidance in transgenic alfalfa (Zhang et al., 2005). Similarly, soybean plants exposed to drought produced greater amounts of cuticular wax, with variation between genotypes, but it was not correlated with seed yield (Kim et al., 2007). In pea, however, an increase in cuticular wax content did not reduce transpiration rate (Sánchez et al., 2001) and abundant wax is not always correlated with drought tolerance (Ristic and Jenks, 2002). Variation in the abundance of waxes, and their synthesis in response to drought stress, have not yet been documented in faba bean.

### 3.2. Maximizing water uptake through root characteristics

Dehydration may be postponed by appropriate root characteristics. The first of these is rooting depth, as deeper roots can continue to extract water from deep in the soil profile when shallow roots have already exhausted the water available to them. Faba bean is sometimes considered to be relatively shallow rooted, with maximum rooting depth of 50–90 cm, depending on soil type (Manschadi et al., 1998b). Extensive variation in rooting depth exists in faba bean germplasm; for example, rooting depth of eight accessions at 35 d after sowing ranged from 32 to 45 cm (SED 1.1 cm; Khan et al., unpublished data, EU-Faba project).

Rooting depth has been shown to be an important contributor to drought avoidance in many species, ranging from coffee (*Coffea canephora* Pierre), a woody perennial (Pinheiro et al., 2005) to sorghum (*Sorghum bicolor* (L.) Moench), an annual C<sub>4</sub> grass where rooting depth was the variate that provided the greatest single contribution to yield in models of growth in water-limited environment (Sinclair and Muchow, 2001). In two crosses of chickpea, an extra 10 cm in the average 1 m rooting depth was available and was determined by dominance gene action more than by additive gene action (Kashiwagi et al., 2008). In the same experiment, the proportion of roots deeper than 60 cm was also widely variable and was controlled by additive gene action and additive × additive epistasis. Where the crop is grown on fine textured soils with little deeply stored soil water, deep rooting may have little advantage (Loss and Siddique, 1994).

Shallow roots also have a role in nutrient uptake and gathering of water from brief showers. A dimorphic root system, with deep roots for water uptake and shallow roots for nutrient scavenging, was selected in common bean by growing plants in a stratified soil, with phosphorus in the upper layer and water in the lower layer (Ho et al., 2005).

Other measures of rooting include rooting volume, root mass, root length and root length density. Root mass is probably the easiest to measure and in chickpea was strongly correlated to shoot mass, representing 30–34% of total dry matter in a twofold range of overall plant size (Kashiwagi et al., 2008). This narrow range was statistically significant and was largely determined by additive gene action and additive × additive epistasis, indicating relative ease of breeding progress. There is a risk associated with increased root mass, that a high allocation of photosynthate to root development reduces overall growth rate or grain production by favouring heterotrophic root tissues over photosynthetic tissues (Bruce et al., 2002), but this risk is balanced by variation in the efficiency of water uptake (Nielsen et al., 2001). Total lateral root length, number and mass were all greater in drought-resistant faba bean cv. Gobo than in susceptible cv. Victor, and the differences between the cultivars was greater in drought (induced by the use of mannitol as an osmoticum in the soil solution) than in control conditions, although tap root length was not significantly affected (Grzesiak et al., 1997b). There is scope for greater investigation of variation in rooting traits in faba bean, in order to identify parent material that can contribute to breeding progress for dehydration avoidance.

## 4. Drought tolerance

Osmotic adjustment is an important physiological mechanism by which plants synthesize and accumulate solutes that function as osmolytes in cells in response to water deficits (Seki et al., 2007), maintaining the structure of cellular components and protecting cellular function (Bartels and Sunkar, 2005). Water potential must fall below that due to dehydration in order to demonstrate active accumulation of solute. The accumulation of sugars, amino acids and amines lowers the osmotic potential or increases the osmotic pressure of the cells, drawing water into the cells and tissues, hence contributing to the maintenance of turgor, stomatal conductance, photosynthesis and plant growth at progressively lower leaf water potentials (Turner and Jones, 1980; Subbarao et al., 1995; Link et al., 2010). Turgor maintenance by osmotic adjustment is an important physiological adaptation for minimizing the detrimental effects of drought stress (Morgan, 1984). Peas exposed to water deficit accumulated significant amounts of soluble sugars and proline, with the former making a much greater contribution to osmotic adjustment than the latter, and wide variation among accessions was found (Sánchez et al., 1998). Amede et al. (1999) noted a decrease in osmotic potential in water-stressed inbred lines of faba bean but there was no evidence of osmotic adjustment, as solute accumulation was merely a concentration effect resulting from water loss and growth inhibition. When subjected to water deficit, chickpea (*C. arietinum* L.) cv. Ghab 3 maintained turgor, while faba bean cv. Alfred lost turgor despite having a greater decrease in osmotic potential (Amede and Schubert, 2003). Similarly, Katerji et al. (2002) reported that faba bean variety Superaquadulce did not demonstrate effective osmotic adjustment in response to moisture stress. To date, osmotic adjustment in faba bean in response to water deficit has not been found. Further experimentation using cultivars from diverse genetic backgrounds and varying drought tolerance would be valuable.

Closure of stomata during drought stress decreases CO<sub>2</sub> concentration in leaf mesophyll tissues, resulting in the accumulation of NADPH and superoxide radical (Cadenas, 1989). A component of drought tolerance is therefore an active system that protects against oxidative injury, including antioxidant enzymatic activity such as superoxide dismutase (SOD). SOD activity has been used to characterize some common bean (*P. vulgaris* L.) cultivars for drought tolerance (Zlatev et al., 2006) but corresponding experiments on faba bean have yet to be reported.

### 4.1. Recovery

The most drought-sensitive stage of development in faba bean has been shown to be the pod set and early pod filling phase; plants were able to recover after transient drought was imposed in the floral initiation phase (Xia, 1997; Mwanamwenge et al., 1999). Variation in the ability to recover from transient drought has hardly been examined in faba bean, but it has been demonstrated in soybean and attributed to genetic differences in the maintenance of leaf area, where leaves of resistant material were less likely to “fire” and abscise than those of sensitive material (Lawn and Likoswe, 2008). An extensive root system contributed further to recovery in that experiment.

## 5. Drought escape

### 5.1. Phenology and time of sowing

In regions where terminal drought is a regular occurrence, the length of the critical growing period may be minimized by selection of varieties with an appropriate phenology or by adoption

of appropriate crop management strategies. These strategies of drought escape are not as successful when transient drought occurs, with unpredictable timing, earlier in the growing season. Generally, drought affects seed yield by reducing total biomass production and therefore the plant's capacity to sustain a high yield depends on its stage of growth.

In dryland environments, crop water use or evapotranspiration is correlated with seasonal rainfall and its distribution, with greater losses in wet seasons than in dry seasons (Zhang et al., 2000). Soil evaporation is greatest during the early stages of crop growth, when canopy cover is small. Early planting and vigorous early growth help to cover the ground and thus to reduce unproductive soil evaporation (Loss and Siddique, 1997; Loss et al., 1997). Rapid ground coverage from low specific leaf area (large, thin leaves) has been shown valuable in other species (e.g., groundnut (*Arachis hypogaea* L.), Nautiyal et al., 2002; wheat, Rebetzke et al., 2004) and could prove so in faba beans as well. Good ground coverage also enhances weed suppression, maximizing the proportion of water that is used by the crop.

The pattern of water use is important in determining seed yield, with more transpiration post-anthesis considered advantageous in low-rainfall Mediterranean-type environments (Loss et al., 1997; Siddique et al., 2001). At a site with low rainfall, total water use did not differ among 10 accessions but the pattern of water use differed significantly, with the ratio of pre-flowering to post-flowering water use being approximately 1:1 for the early flowering ACC286 and 2.6:1 for the late flowering cv. Icarus (Mwanamwenge et al., 1998). Seed yield was significantly and positively correlated with time to 50% first flower. Both seed yield and harvest index were positively correlated with water use post-flowering. The time from sowing to onset of flowering among faba bean accessions varies substantially (Robertson and El-Sherbeeney, 1988; Stoddard, 1993), and development responds to both temperature and daylength (McDonald et al., 1994; Patrick and Stoddard, 2010). It is therefore possible to select cultivars that complete a substantial proportion of flowering and pod development prior to the onset of terminal drought. Large-seeded faba beans have a longer period of grain filling so the timing of flowering may be more critical for these (Agung and McDonald, 1998).

Management practices, such as adjusting the time of sowing, can influence the time of flowering and pod fill, thereby minimizing the effect of terminal drought. In Mediterranean-type climates of Australia, for example, early sowing results in greater biomass production and yield (Marcellos and Constable, 1986; Adisarwanto and Knight, 1997) and a greater proportion of water use after flowering than when sowing is delayed (Loss et al., 1997). Similarly, in cool-temperate climates, autumn-sown winter-hardy cultivars generally have established a large and deep root system when the shallower roots of much younger, spring-sown cultivars are not yet deep enough to escape the drying surface soil layer. Altered time of sowing does not always lead to the same change in onset of flowering, owing to genetic variation in earliness *per se* along with responses to temperature and daylength (Stoddard, 1993; McDonald et al., 1994; Patrick and Stoddard, 2010). Thus it is necessary to select for adaptation to early sowing during the breeding program as well as to implement early sowing in the management phase. In addition to appropriate temperature and photoperiod responses, other considerations when selecting cultivars for early sowing include frost tolerance or avoidance during flowering, level of autofertility or pod set during periods of low bee activity, susceptibility to diseases, and tolerance to herbicides as early sowing can precede weed germination so chemicals, rather than tillage, are used for weed control.

Breeding is required in order to maximize the match between the phenology of the available cultivars and the demands of the environment. Seemingly similar environments, such as true

Mediterranean and subcontinental climates, put different stresses on the crop and require different ideotypes or combinations of traits (Annicchiarico and Iannucci, 2008). Further analysis of the environments allows separation of their repeatable and non-repeatable contribution to the genotype  $\times$  environment interaction and from that, the factors associated with broad and specific adaptation that can be used in crop breeding (Basford and Cooper, 1998).

## 5.2. Disease resistance

Faba bean is susceptible to several diseases caused by fungi, including ascochyta blight (*Ascochyta fabae* Speg.), chocolate spot (*Botrytis fabae* Sard.) and rust (*Uromyces viciae-fabae* (Pers.) J. Schröt.), all of which reduce yields if not controlled. Environmental conditions favouring development differ between diseases; for example, ascochyta blight is favoured by cool, moist conditions while chocolate spot prefers warmer humid environments (Stoddard et al., 2010). Rust pustules rupture the epidermis and cuticle, so the plant can no longer control its transpiration and desiccates rapidly in a water deficit (Tissera and Ayres, 1986). Early sowing in Mediterranean-type environments can result in high biomass production, restricting air flow through the canopy and favouring disease development, while early sown crops are also more prone to attack by broomrape (Saxena et al., 1981). Management practices, such as early sowing to minimize the impact of terminal drought, may thus subject the crop to a greater risk of disease (see Stoddard et al., 2010).

In drought-prone areas where yields may be low, it is generally preferable to economize on crop inputs, so genetic resistance, rather than fungicides, should be considered the principal means of disease control when available. In Mediterranean-type environments, ascochyta blight may establish in susceptible crops early in the growing season, before the longer-term seasonal conditions are evident. Fungicides to control ascochyta blight may therefore be applied to a crop that subsequently is adversely affected by drought. On the other hand, chocolate spot is more likely to develop in humid conditions during spring in crops with high biomass, and these conditions are associated with a low risk of drought. Thus resistance to ascochyta blight is a higher priority than resistance to chocolate spot when seeking to minimize inputs to crops in drought-prone areas. Breeding of faba bean for resistance to diseases is reviewed by Sillero et al. (2010) and integrated management of pests and diseases by Stoddard et al. (2010).

## 5.3. Tolerance to adverse soil conditions

Soils in many lower rainfall areas have poor fertility, including deficiencies in nutrients such as P, Zn, Mn, Cu and Fe and toxicities such as B and salinity, while other factors such as compaction and high soil temperature can also reduce growth and thus interact with response to drought. Nutrient deficiency is often due to the poor availability rather than the low quantity of the nutrient in the soil (Graham, 1984) and selection of efficient genotypes with higher nutrient uptake would reduce yield losses from nutrient deficiencies. Both B toxicity and salinity reduce root growth, restricting access to moisture in the subsoil (Holloway and Alston, 1992) while the osmotic effect of salinity further reduces water uptake. Breeding for nutrient efficiency, or tolerance to toxicities, should be considered an integral component of breeding for low input or drought-prone situations.

There have been limited studies on nutrient efficiency or tolerance to toxicities in faba bean, but indications can be extrapolated from other crops. Examples of nutrient efficiency in cool season pulses include Zn efficiency in chickpea (Khan et al.,

1998), B efficiency in lentil (*Lens culinaris* Medik.; Srivastava et al., 2000), and Fe efficiency in both chickpea (Saxena et al., 1990; Bejiga et al., 1996) and lentil (Erskine et al., 1993), while among Australian faba beans, the broad bean cv. Aquadulce is Fe-efficient and cv. Fiord is very inefficient (W.A. Hawthorne and J.G. Paull, unpublished data). Tolerance to B toxicity has been reported in field pea (Bagheri et al., 1994) and lentil (Yau and Erskine, 2000; Hobson et al., 2003) and observations on Australian cultivars and breeding lines indicate that faba bean is, in general, more tolerant than other pulse crops to high soil boron concentration (J.G. Paull, unpublished data). There is sufficient evidence of genetic variation in nutrient efficiency and/or tolerance to toxicities in pulses for consideration as breeding objectives for optimum plant growth in low input, drought-prone production areas.

## 6. Conclusion

Faba bean is an important source of protein for humans and a valuable feed for livestock, and is traded in international markets. However, insufficient soil water, unfavourable temperatures and several fungal diseases are important constraints in faba bean production worldwide, with drought considered the most important environmental constraint to crop productivity. Various physiological traits may be useful in screening breeding material for tolerance to drought stress. Low stomatal density is associated with water conserving attributes and consequently indicates better adaptation to drought stress conditions. Leaf temperature is a marker for both low stomatal conductance and high transpiration efficiency. Furthermore, carbon isotope discrimination shows a strong correlation with transpiration efficiency, stomatal resistance and leaf temperature. Thus economical screening of large numbers of breeding lines with leaf temperature can be followed by expensive, precision screening of a small number of lines with  $\Delta^{13}\text{C}$  combined with detailed multi-environment field trials. The value of indirect selection for components of drought response needs to be validated in field experiments.

In regions of regular terminal drought, selection of cultivars with appropriate phenology can minimize the duration of exposure to the stress. Early sowing and vigorous growth reduces soil evaporation so, by sowing earlier, the time to flowering and pod fill may lessen, thereby reducing the effect of terminal drought.

Faba beans are susceptible to a number of diseases, particularly when early sowing in Mediterranean-type environments leads to high biomass production that favours spread of fungus spores. Resistance to ascochyta blight is a high priority in order to minimize inputs to subsequently drought-affected crops. Genetic resistance rather than fungicides may be a better option to consider for disease control. Soil fertility in many lower rainfall areas is poor, so selection of nutrient efficient genotypes would reduce yield losses from nutrient deficiencies.

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