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Vincent Vadez, Jens D. Berger, Tom Warkentin, Senthold Asseng, Pasala Ratnakumar, K. Poorna Chandra Rao, Pooran M. Gaur, Nathalie Munier-

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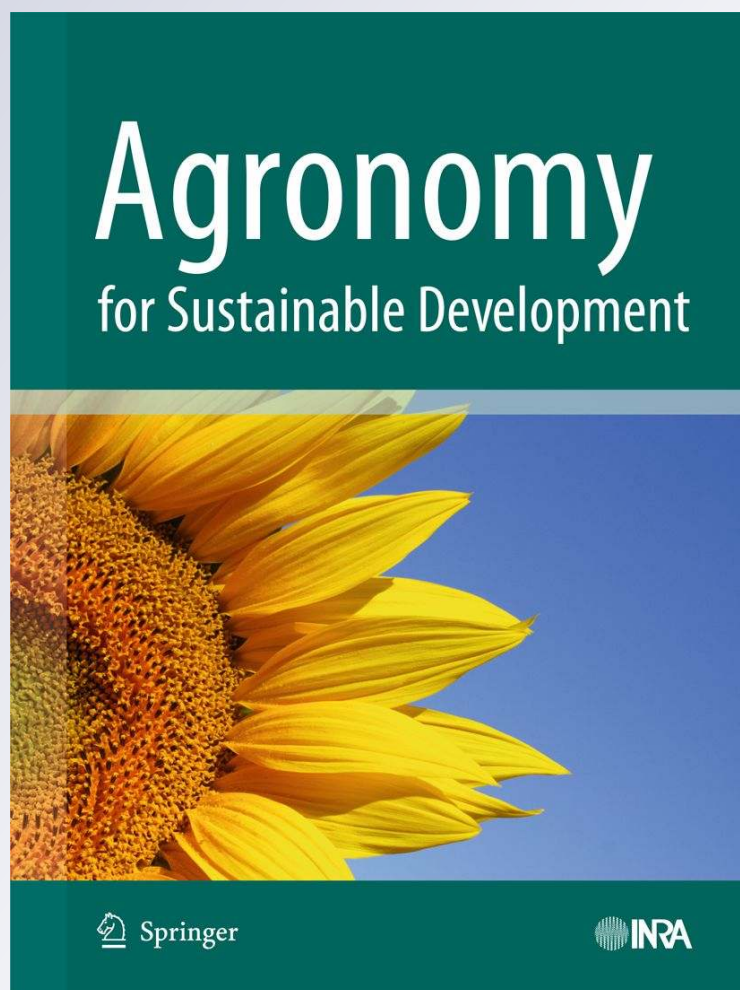
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Adaptation of grain legumes to climate change: a review

Vincent Vadez · Jens D. Berger · Tom Warkentin · Senthold Asseng ·
Pasala Ratnakumar · K. Poorna Chandra Rao · Pooran M. Gaur ·
Nathalie Munier-Jolain · Annabelle Larmure · Anne-Sophie Voisin · Hari C. Sharma ·
Suresh Pande · Mamta Sharma · Lakshman Krishnamurthy ·
Mainassara Abdou Zaman

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Abstract Humanity is heading toward the major challenge of having to increase food production by about 50% by 2050 to cater for an additional three billion inhabitants, in a context of arable land shrinking and degradation, nutrient deficiencies, increased water scarcity, and uncertainty due to predicted climatic changes. Already today, water scarcity is probably the most important challenge, and the consensual prediction of a 2–4°C degree increase in temperature over the next 100 years will add new complexity to drought research and legume crop management. This will be especially true in the semi-arid tropic areas, where the evaporative demand is high and where the increased temperature may further strain plant–water relations. Hence, research on how plants manage water use, in

particular, on leaf/root resistance to water flow will be increasingly important. Temperature increase will variably accelerate the onset of flowering by increasing thermal time accumulation in our varieties, depending on their relative responses to day length, ambient, and vernalizing temperature, while reducing the length of the growing period by increasing evapotranspiration. While the timeframe for these changes (>10–20 years) may be well in the realm of plant adaptation within breeding programs, there is a need for today's breeding to understand the key mechanisms underlying crop phenology at a genotype level to better balance crop duration with available soil water and maximize light capture. This will then be used to re-fit phenology to new growing seasons under climate change conditions. The low water use efficiency, i.e., the amount of biomass or grain produced per unit of water used, under high vapor pressure deficit, although partly offset by an increased atmospheric CO₂ concentration, would also require the search of germplasm capable of maintaining high water use efficiency under such conditions. Recent research has shown an interdependence of C and N nutrition in the N performance of legumes, a balance that may be altered under climate change. Ecophysiological models will be crucial in identifying genotypes adapted to these new growing conditions. An increased frequency of heat waves, which already happen today, will require the development of varieties capable of setting and filling seeds at high temperature. Finally, increases in temperature and CO₂ will affect the geographical distribution of pests, diseases, and weeds, presenting new challenges to crop management and breeding programs.

V. Vadez (✉) · P. Ratnakumar · P. M. Gaur · H. C. Sharma ·
S. Pande · M. Sharma · L. Krishnamurthy · M. A. Zaman
ICRISAT,
Patancheru 502324, Andhra Pradesh, India
e-mail: v.vadez@cgiar.org

J. D. Berger · S. Asseng
CSIRO Plant Industry,
Private Bag 5, PO,
Wembley, WA 6913, Australia

T. Warkentin
Department of Plant Sciences, Crop Development Centre,
University of Saskatchewan,
Saskatoon, SK, Canada

K. P. C. Rao
ICRISAT-Nairobi,
PO Box 39063, Nairobi, Kenya

N. Munier-Jolain · A. Larmure · A.-S. Voisin
INRA, Agro-Sup Dijon, UMR102,
Genetics and Ecophysiology of Grain Legumes,
BP 86510, 21065 Dijon, Cedex, France

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1 Introduction

Alongside the recent crisis in the price of major food staples, climate change has become a major concern to agricultural development (Tubiello et al. 2008; Fedoroff et al. 2010). Humanity is facing a major challenge in producing enough food for an additional three billion people, i.e., about 50% more, within the next 50 years in conditions that are increasingly adverse: (1) arable lands are shrinking and becoming degraded; (2) food habits are

becoming more “calorie-intensive” (shift from plant to animal food); (3) water and nutrients are becoming scarce, (4) climate is changing and is becoming hostile to food production, especially in the areas where most of the extra food production is needed, such as the semi-arid tropics (Cooper et al. 2009). Since climate change is only one of many drivers affecting future food production, this review concentrates on current food production issues, in particular, legume crops, with a particular focus on drought and how these issues relate to the forecasted changes in climate.

Among the changes expected in the new climate, all prediction models consensually forecast a 2–4°C increase in temperature over the next century (Tadross et al. 2007). In addition, atmospheric CO₂ concentration has been increasing at a rate of about 1 ppm/year over the last 50 years and will increase at higher rates in the future. By contrast, there is no agreement in relation to precipitation, with predictions ranging from 10–20% increase or decrease, depending on region. The variability of climatic events within years is also expected to increase, and crops will face extreme events such as more frequent heat stress, and these heat waves are already happening. However, the prediction of such events is difficult, and dealing with current climate variability is at least equally important. Therefore, in view of these predictions, this review focuses on current research challenges that have also relevance for climate change scenarios, with a view at the most likely predictions, i.e., an increase of 2–4°C in the mean temperature associated with an increase frequency of heat stress events, an increase in atmospheric CO₂ concentration, and a likely increase in climate variability.

While certain regions of the globe will be favored by climate change, by bringing areas under production that were traditionally too cold, the regions that will suffer the most from climate changes are those where cropping conditions are already under environmental pressure, in particular, from the point of view of water. Resilience of crop yield under already harsh conditions, like the semi-arid tropics that are home to 600 million people and to the deepest pockets of poverty, is a problem that must be dealt with today and would receive specific attention here. Drought is indeed currently the most widespread and yield-limiting abiotic stress in many crops, in particular, in legumes. Therefore, a great deal of work on crop adaptation to climate change is first a matter of adapting crops to water limitation. Climate change will simply add another layer of complexity to the problem of drought. Therefore, improving the tolerance of crops to water deficit is a must if agricultural production is to keep up with the expected demographic increases in future climatic scenarios.

Given the complexity of drought, methods are needed to assess how different traits interact, and interact with the environment, to eventually contribute to enhancing genotype's performance to water limitation, rather than looking

at specific traits independently from other interacting traits. For instance, drought research in chickpea has so far focused only on the measurement of root morphology at a given point in time, paying no attention to other possible traits, for instance, water-saving traits, possibly contributing to its adaptation. So, new methods are needed where it is possible to measure dynamically (*in vivo*) how such different traits interact and contribute to crop adaptation. An example will be given of ongoing effort in this direction at ICRISAT. In this effort, crop simulation models will then play a critical role in helping disentangle the complexities at stake.

The increase in temperature will also influence the rate of crop development as the accumulation of thermal time increases. These changes will produce variable effects in crops depending on the relative importance of day length, ambient, and vernalizing temperature on phenology. Therefore, a new balance between duration of the crops and the available cropping season, based on an understanding of the key phenological mechanisms will be needed. While the timeline for these changes (>10–20 years) may well be in the realm of plant adaptation in the shorter time frame (<10 years) of breeding programs, there is a need today to understand key mechanisms underlying crop phenology at a genotype level to better balance crop duration with available soil water and maximize light capture. Climatic changes due to temperature, water availability variation, and increase in CO₂ will also affect the carbon–nitrogen balance in the plants and eventually how seeds set and grow. Although it is impossible to predict how extreme climatic events within years will occur, heat waves are already becoming more frequent, and this trend can be expected to strengthen as the temperature gradually increases (Battisti and Naylor 2009). As a result, high-temperature-tolerant crops will be needed.

Changes in temperature and relative humidity are likely have a profound effect on geographical distribution and incidence of insect pests and diseases, presenting new challenges for breeding programs. Climate change will affect the physiology and then the equilibrium of the host–pathogen interactions and then the rate of development of pathogens, resulting in either increased epidemic outbreaks, new pathogens emerging as threats, or less known pathogens causing severe yield losses. Climate change will not only affect the individual plant species and plant communities, but will also influence the interaction of crop plants with insect pests. Temperature increases associated with climatic changes could result in a geographical expansion of pests, a change in aestivation/hibernation, changes in population growth rates, loss of resistance in cultivars containing temperature-sensitive genes, changes in crop-pest synchrony, changes in natural enemy–insect–host interactions, and changes in the diversity of natural enemy complex. Monitoring current prevalence, incidence and

abundance of insect pests and diseases, and the biological control agents, may provide some of the first indications of a biological response to climate change.

2 Control of plant water losses

2.1 Drivers of plant water use and what may change with climate change

It is well known that the water moves along the soil–plant–atmosphere continuum along gradients of water pressure. Under fully irrigated conditions, transpiration is driven by radiation and by the evaporative demand. Evidence in groundnut (Ratnakumar et al. 2009), pearl millet (Kholová et al. 2010a, 2010b), and wheat (Fischer 1979) indicate that lower vegetative rates of water use leave more water available for grain filling. High vapor pressure deficit conditions imposes high plant–atmosphere pressure gradients and drives water out of the leaves at a faster rate, leading to more rapid depletion of the soil moisture, especially when water is available and when plants have no “incentive” to limit water losses. So, understanding/identifying possible control of these losses is important, especially for areas where the vapor pressure deficit is high.

Many models have been used to predict changes in climate, and all agree that temperature will increase from 2°C to 4°C over the next 100 years, with only the magnitude of the temperature increase varying across models (Christensen et al. 2007). While temperature is expected to increase, models also point to increasing humidity (Peterson et al. 1995; Liu and Zeng 2004), which is also reported as the “pan evaporation paradox”. Reports show indeed that the pan evaporation decreased over time in most of 40 Australian sites spread all over the country, and the decrease in pan evaporation was driven by decreased solar radiation and additionally by reduced wind speed (Roderick et al. 2007). Surprisingly, there has been little attempt to assess whether the vapor pressure deficit had changed in past recent climate. Szilagyi and colleagues (2001) have reported no statistical change in VPD in the USA for the period 1948 to 1996. While this appears contradictory with the increase in temperature and the reported increases in evapotranspiration (Szilagyi et al. 2001; Golubev et al. 2001), the paradox could be reconciled by the fact that dew point temperatures have increased (Gaffen and Ross 1999; Robinson 2000). This is indeed further explained in Roderick and Farquhar (2002), building on previous report that while temperature has been increasing by about 0.15°C decade^{−1} in the past 50 years (Folland et al. 2001), the minimum temperature has increased substantially more than maximum temperature, i.e., over 0.20°C decade^{−1}. A more recent review of pan evaporation data indicates, in fact, that vapor pressure deficit,

wind speed, and solar radiation are major players in explaining the reported decreases in pan evaporation (Fu et al. 2009), but the trends are specific to different regions, in particular, whether the regions are water-limited or not. So, it is not clear whether the expected increases in temperature will be accompanied with a similar increase in vapor pressure deficit, as it may be location-specific, and also because there is still debate on the method to accurately measure pan evaporation (Szilagyi and Jozsa 2008).

Yet, the fact is that the vapor pressure deficit is high in the semi-arid tropics, which receive a particular focus of this review. So, we used the reported 0.001% to 0.03% decreases per annum in pan evaporation by Roderick et al. (2007), to estimate possible vapor pressure deficit scenarios and their magnitude in future climate and compare to current context. Figure 1 shows that VPD is currently high in the semi-arid environments. It shows also that the vapor pressure deficit may not increase with a 3°C temperature increase and a 10% relative humidity percentage increase over the next 100 years. This is, in part, explained by temperature being in the exponential term in the calculation of vapor pressure deficit (Prenger and Ling 2000). Vapor pressure deficit would slightly increase if the increase in relative humidity was limited to 3% over the next 100 years. In any case, Fig. 1 illustrates well that, should any increase or decrease occur, the magnitude of these changes would be small in comparison to the current values, especially where these values are high. Therefore, understanding how plants regulate water losses under high vapor pressure deficit has contemporary relevance. An initial approach could therefore be to tackle the control of plant water loss under well-watered conditions. Part of this is to better understand to the

hydraulic control of water movements at the soil–root and at the leaf–atmosphere interface.

2.2 Regulation of stomatal opening

Many Mediterranean and semi-arid zone crops face terminal drought stress during the reproductive phase as a consequence of diminishing rainfall or plant available water and rising temperatures. In such cases, what is usually called “drought tolerance” could be, in part, the consequence of constitutive traits that affect how soil water is used when it is non-limiting to plant transpiration. Therefore, a key to identifying germplasm with superior adaptation to limited water is to better understand the control of leaf water losses. Recent data in pearl millet (Kholová et al. 2010a) and groundnut (Vadez et al. 2007; Bhatnagar-Mathur et al. 2007) shows that genotypes with lower rates of water use under well-watered conditions can sustain transpiration for longer periods, with important consequences on later responses to water deficit. Such type of behavior, i.e., water-sparing by the shoot in the vegetative phase when the soil is wet, should make more water available for water uptake by roots at key stages like the grain-filling period. At similar leaf area, lower leaf water conductance will reduce water losses. However, there is a trade-off here: low vegetative water use related to lower conductance would lead to reduced photosynthetic activity and growth (Farquhar and Sharkey 1982). Thus, while this water-sparing will be beneficial where crops grow on stored soil water, it can lead to lower yields where crops grow on current rainfall in a short rainy season (Turner and Nicolas 1998; Rebetzke et al. 2002; Richards et al. 2007).

2.3 Sensitivity of stomata to vapor pressure deficit to save water in the soil profile

Maintaining high photosynthetic activity when the vapor pressure deficit is high would obviously favor biomass accumulation, albeit at a high water cost, since water use efficiency is inversely related to vapor pressure deficit (see below). Therefore, genotypes capable of transpiring less at high vapor pressure deficit would save water, at the cost of a lower carbon accumulation potential. However, over the long-term, a parsimonious water-use strategy may increase mean yield if water is limited. This hypothesis is supported by modeling results in sorghum showing that imposing a maximum transpiration rate per day saves water, increases the transpiration efficiency, and leads to a yield benefit in most years (Sinclair et al. 2005). In drought-tolerant soybean there is evidence for physiological responses to water stress: at vapor pressure deficits above 2.0 kPa transpiration rates are flat or increase at relatively lower rates (Sinclair et al. 2008). This trait limits soil moisture use

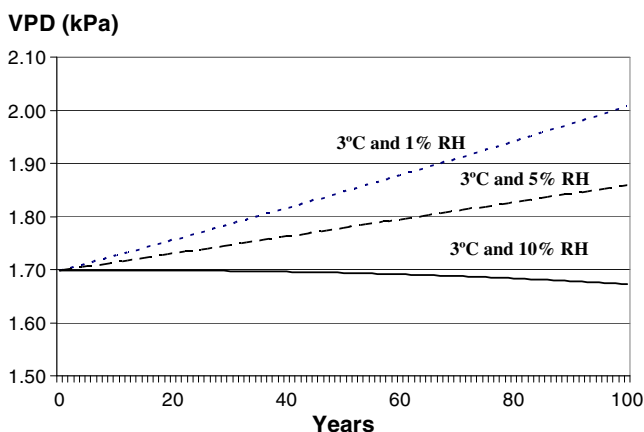


Fig. 1 Predicted vapor pressure deficit (VPD) increase over a 100-year period, starting with a baseline relative humidity (RH) of 45% and an average temperature of 25°C, and assuming three different scenarios: (1) a 3°C degree and a 1% RH increase over 100 years (small dash); (2) a 3°C degree and a 5% RH increase over 100 years (large dash); (3) a 3°C degree and a 10% RH increase over 100 years (continuous line)

at high vapor pressure deficit when carbon fixation has a high water cost, leaving more soil water available for subsequent grain filling. Similar trends have been reported in semi-arid crops, such as pearl millet at vapor pressure deficit >2.5 kPa (Kholová et al. 2010b) and groundnut (Devi et al. 2010). Work is ongoing to test similar responses in chickpea. In pearl millet, this adaptive physiology has been tagged with quantitative trait loci (Kholová et al. 2010b). Genotypes containing the quantitative trait loci slowed their transpiration rate at high vapor pressure deficit, whereas, in those without the quantitative trait loci, the rate of transpiration responded linearly to increases in vapor pressure deficit above 2.0 kPa.

2.4 Aquaporins as a possible “switch” to control water

Another possibility for regulating water flow at the root level is to use aquaporins to modulate water conductance in the root. Work by Steudle and colleagues (Steudle and Henzler 1995; Steudle and Frensch 1996; Steudle 2000, 2001) indicate that plants with a high flow of water through the symplast (e.g., barley) have lower conductance than plants with high apoplastic water fluxes (e.g., maize). Water transport through the symplastic pathways require aquaporins as membrane transporters to act as water channels. Aquaporins have been shown to be under tight genetic regulation, with differences in expression during the course of the day and related changes in root hydraulic conductance (Beaudette et al. 2007; Parent et al. 2009). Abscissic acid has a role in the control of root conductance (Thompson et al. 2007) and has been shown to regulate the expression of aquaporins (Parent et al. 2009; Beaudette et al. 2007). It appears also that the regulation of aquaporins can also take place at the post-transcriptional level. It has indeed been shown that the gating of aquaporins, by mechanisms of phosphorylation/dephosphorylation, could be a quick way of activating–deactivating them (Törnroth-Horsefield et al. 2006). Clearly, aquaporins play an important role in regulating plant water flow by modulating the hydraulic conductance of roots (Ehlert et al. 2009; Parent et al. 2009) and leaves (Sadok and Sinclair 2010). Understanding the interaction between aquaporins and abscissic acid in regulating root hydraulic conductance and the rate of plant water use may be an important research priority in the adaptation of crops to water limitations expected under climate change.

2.5 Water use efficiency

As societies develop, the use of water for non-agricultural purposes increases. So, the future water availability scenario points to a decreasing amount of water availability for agriculture. Clearly, in combination with climate change, it will be essential to maximize water use

efficiency, i.e., the amount of crop per drop. Water use efficiency (Tanner and Sinclair 1983) is inversely related to vapor pressure deficit (Bierhuisen and Slatyer 1965):

$$Y/T = k/(e^* - e) \quad (1)$$

Where Y represents biomass or grain yield, T is transpiration, e is the vapor pressure in the atmosphere, and e^* is the saturated vapor pressure (the term $e^* - e$ represents the vapor pressure deficit), and k is a constant specific to species. As discussed previously, high vapor pressure deficit conditions leads to lower level of water productivity, following Eq. 1 above.

This equation stipulates that water use efficiency of a crop depends on vapor pressure deficit, except for a constant k that is crop-specific. Steduto et al. (2007) elaborates that only C_4 and C_3 plants would have differences in the k constant and not between species within each of the C_3 or C_4 group. However, it does not impede the ratio of biomass to transpirational losses to vary between genotypes (Sinclair and Muchow 2001). Steduto et al. 2007 indeed agree with a growing number of experimental data showing intra- and interspecific differences in water use efficiency in several crops (Bhatnagar-Mathur et al. 2007; Krishnamurthy et al. 2007; Condon et al. 2004; Rebetzke et al. 2002). Steduto et al. (2007) attribute the differences in water use efficiency with genotypic variation in the metabolic costs of respiration. So, while there have been no studies reporting differences in the k factor in any plant species, there are reports of differences in water use efficiency, i.e., the ratio of biomass to water use, across crops. For water-limited environments, whether higher water use efficiency can lead to higher yields in specific environment/crops is still a major question mark. In groundnut, higher water use efficiency leads to higher yield under intermittent stress conditions (Wright et al. 1994; Ratnakumar et al. 2009), but more work is needed in other legume crops. In any case, the definition of water use efficiency by Bierhuisen and Slatyer (1965) indicates it will decrease at a rate that is proportional to the vapor pressure deficit increase. For climate change conditions, it will be important to assess whether water use efficiency follows a similar decline with vapor pressure deficit increase in all genotypes. Preliminary data on water use efficiency in groundnut and pearl millet genotypes, measured at different vapor pressure deficit level ranging between 0.7 and 3.2 kPa using controlled environment growth chambers, indicate that genotypes have a different rate of decrease in water use efficiency upon increasing vapor pressure deficit (Vadez et al. unpublished; Kholova et al. unpublished). Clearly, screening for possible identification of germplasm capable of maintaining high levels of water use efficiency under high vapor pressure deficit is needed.

3 Growth and development processes

3.1 Matching phenology to growing season

Arguably, the most important adaptive criterion in annual crops is appropriate phenology that minimizes exposure to climatic stresses and maximizes productivity in target environments. Given that most Mediterranean and semi-arid legume crops are indeterminate and therefore capable of continuing vegetative growth after the onset of reproduction, the key phenological stage is the onset of flowering, regulated by responses to day length, ambient, and low temperature (i.e., vernalization; Nelson et al. 2010). Photo-thermal modeling suggests that tropical and sub-tropical crops tend to be vernalization unresponsive short day plants, while Mediterranean and temperate crops are more likely to be vernalization-responsive long-day plants (Roberts and Summerfield 1987; Summerfield and Roberts 1987). In agricultural ecosystems that combine moderate winter temperatures with strong terminal drought (i.e., Mediterranean-type climates in southern Australia or the south Asian post-rainy season, stored soil moisture winter cropping system), the vernalization response has been selected against, having been eliminated in chickpea (Abbo et al. 2002; Summerfield et al. 1989) and narrow leaf lupin (Landers 1995). Conversely, legume crops such as faba bean and pea retain their vernalization response (Ellis et al. 1988; Trevino and Murray 1975), as do a range of *Medicago* species (Liu 2007). Vernalization notwithstanding, progress to flowering is a positive linear function of average temperature from a critical minimum base to an upper optimum, for photoperiod-insensitive plants at all-day lengths and for photoperiod-sensitive plants at a given day length (Summerfield and Roberts 1988).

Phenological changes resulting from the anticipated 2–4°C mean temperature increase associated with climate change depend on the relative importance of the environmental triggers outlined above. Phenology will not change in those genotypes regulated largely by photoperiod, will come earlier in ambient temperature-sensitive types, and be delayed in those responding to vernalization. Among the food legume crops such as chickpea or lentils, our understanding of the role of these environmental triggers in specific adaptation to different habitat types is very poor, and as a result, it is difficult to predict where and by how much crop phenology is likely to be affected. Recent work in chickpea has demonstrated that temperature sensitivity is strongly correlated to mean vegetative phase temperatures at the habitat of origin, increasing from winter- to spring-sown Mediterranean genotypes, to Northern India, and finally Central and Southern India (Berger et al. 2011). Among the relatively temperature-insensitive Mediterranean germplasm, there was a strong compensating relationship with day length response.

Accordingly, assuming climate-change-associated temperature increases fall within the linear response range, Indian material will become much earlier than that from the Mediterranean, forcing breeders targeting the latter production area to widen their parental gene pool. Previous work in lentil suggests that this species may respond similarly (Erskine et al. 1990) but needs to be confirmed by genotypic habitat characterization. In the other important Mediterranean and semi-arid grain legume crops, there is no published information on specific adaptation and phenological triggers, let alone cardinal temperatures for flowering (i.e., minimum base and optimal maximum temperatures). Given that, with an increasing frequency of high-temperature events, which already occurs, it is feasible that crops will also experience supra-optimal temperatures that delay flowering, exacerbating terminal drought stress, understanding cardinal temperatures, and identifying heat-tolerant material will become an important research priority. So, even if the timeframe for these changes (>10–20 years) is longer than the timeframe for the development of a new varieties, there are also gaps in the present knowledge of the triggers of flowering and their interactions that would greatly help matching genotypes to current cropping conditions.

Responses to environmental triggers notwithstanding, the length of the growing period in Mediterranean and stored soil moisture environments are likely to be reduced as rising temperatures decrease plant available water as result of increased evapotranspiration. Simulation modeling indicates that the length of the growing period may decreased by up to 20% in some African regions under climate change because of rising temperatures (Thornton et al. 2006) and the delay in reliable opening rains (Tadross et al. 2007). Reducing the cropping cycle leads to a substantial decrease in the magnitude of light capture by the crop canopy, and simulation modeling indicates that this could lead to a substantial yield decline. Increasing the radiation use efficiency to increase the productivity during the shorter growth period could be considered as a compensatory mechanism and has been demonstrated in rice (Zhang et al. 2009). Increasing, early vigor is another option that may compensate for the reduced growing time (Lopez-Castaneda et al. 1995; Turner and Nicolas 1998). However, in nutrient-limited environments where plants need a long cropping cycle to accumulate sufficient nutrients, as in the case of low P soils (Nord and Lynch 2009, 2008), it may not be possible to compensate for the reduced growing season.

3.2 The effects of high temperature and water deficit

High temperature and water deficit decrease net photosynthesis during the period of the constraint, resulting in a reduction of plant growth rate. Final seed number and final

seed weight depend on plant growth rate during the flowering period and the seed filling period, respectively (Guilioni et al. 2003; Pellissier et al. 2007). Thus, high temperature and water deficit indirectly affect seed number and seed weight. Moreover, severe heat stress can cause abortion of flowers, resulting in direct reduction of seed number (Guilioni et al. 1997). However, the indeterminate growth pattern of most legumes provides plasticity to environmental stresses by allowing the development of additional flowers and then seeds under favorable growing conditions.

The temperature during seed filling may influence N partitioning. For example, lowering temperature from 23°C to 13°C with maintained radiation results in an increase in C assimilate availability allowing new vegetative sinks to grow. The increase in vegetative growth seems to attract a part of the N available at the expense of filling seeds (Larmure et al. 2005). On the other side, increasing temperature above 23°C results in a decrease in the rate of N remobilization from vegetative parts to growing seeds (Pellissier et al. 2007; Ito et al. 2009). Eventually, temperature variations can also affect seed N concentration, one of the main criteria determining the quality of grain legume.

Legume plants have the ability to fix atmospheric N₂ through symbiosis with soil bacteria (*Rhizobia*) hosted in specific root organs called “nodules”. Nitrogen nutrition is often sub-optimal and leads to unstable and low yields. Indeed, symbiotic N₂ fixation is highly sensitive to environmental stresses (Sprent et al. 1988), especially to temperature, water, salinity, sodicity, acidity, and nutrient disorders (Chalk et al. 2010; Hungria and Vargas 2000; Jayasundara et al. 1998). As such, climate change may affect symbiotic fixation either directly by impairing *Rhizobia* survival, *Rhizobia* competitiveness, nodule formation, growth, or activity, or indirectly by modifying carbon supply to nodules. Still, effects of environmental constraints on those parameters largely remain to be precisely characterized and quantify, also considering the duration, timing, and severity of stress (Chalk et al. 2010), and simulation modeling to predict symbiotic nitrogen fixation under different conditions would be quite useful (Liu et al. 2010). As a general rule, severe stresses inhibit both legume dry matter accumulation and the proportional dependence on symbiotic N fixation as a source of N. The symbiosis is resilient to low to moderate stress, but there may still be a penalty on legume dry matter (Chalk et al. 2010). Moreover, nodules compete for carbon use with the roots (Voisin et al. 2003). As such, nodulation can limit root growth. The restricted root development of some legume species (Hamblin and Tennant 1987) may limit water and nutrient uptake, especially at late growth stages when environmental stresses are frequent.

3.3 The effect of heat waves

Climate change is expected to raise the frequency of extremes of cold and heat in different parts of the world (Christensen et al. 2007; Hennessey et al. 2008). Yet, heat waves are common, and current characteristic of the semi-arid tropics and developing cultivars to withstand supra-optimal temperatures is important. It is well known that plant's reproduction is sensitive to heat stress (Prasad et al. 2000, 2002, 2006). Therefore, it will be important to identify genotypes that are capable of setting seeds at supra-optimal temperatures. In doing so, care should be taken with the experimental approach as simply delaying the date of planting to ensure that reproductive development occurs at high temperatures will also affect the radiation received by the crop. To reliably screen for the ability to set seed at high temperatures, controlled environment conditions will be required. Finally, considering the interaction of heat stress with water stress will be critical in semi-arid regions. There are indeed predictions of yield decrease in soybean in future scenarios, which are due to both moisture and heat stress (Carbone et al. 2003).

3.4 The compensating effect of CO₂

High intrinsic water use efficiency, i.e., the ratio of photosynthetic and transpiration rates at the leaf level, is achieved by having a low CO₂ concentration in the sub-stomatal chamber (Condon et al. 2002). A high photosynthetic rate would contribute to that by driving down the CO₂ concentration in the sub-stomatal chamber. Increasing CO₂ concentrations in the atmosphere would maintain optimal CO₂ concentrations in the sub-stomatal chamber at lower level of stomata opening, resulting in lower rates of transpiration saving water. Therefore, we can expect that the higher CO₂ conditions brought about by climate change will have a beneficial effect on the overall plant water balance and productivity, as has been show previously (Muchow and Sinclair 1991; Serraj 2003). Reduced stomatal conductance in a higher CO₂ environment will maintain plant water relations, but may have implications for heat stress as leaf temperature rises with reduced transpiration.

4 Integrating multiple constraints of climate change using models

4.1 The need to approach drought “dynamically”

Controlling leaf water losses and maximizing water capture from the soil profile are two critical ways for plants to adapt to conditions where water is limited, leaving water available for critical plant development stages. Indeed, sufficient amounts of water at key times during the plant cycle may

be more important than availability across the whole cycle (Boote et al. 1982; Meisner and Karnok 1992; Ratnakumar et al. 2009). As seen above, current and climate change conditions will make the control of water use more difficult and therefore the role of roots in water capture will be increasingly important. However, it is difficult to separate leaf's control of water losses from root's maximization of water capture. Shoots are indeed the key driver of water losses (leaf area, conductance, pattern of canopy development) and would directly interact with how much/when root would uptake water. Therefore, it is important to record dynamic data on water uptake by roots, how it interacts with how shoot "manage" water losses, and how the combination of both shoot and root traits interact with the environment, rather than static data on roots, such as biomass, root length density, etc., as outlined below. Despite a substantial number of studies on roots in different crops, most of these studies assessed roots in a very "static" manner, i.e., destructive samplings at one or several points in time, giving virtually no information on the detailed "dynamics" of root functionality and on water per se. As suggested by other authors (McIntyre et al. 1995; Dardanelli et al. 1997), water uptake should be the primary focus of root research. Then, water uptake should be assessed *in vivo* and repeatedly in plants that are adequately watered and are exposed to stress in conditions that mimic field conditions, particularly in relation to soil depths and soil volume per plant. In a previous review (Vadez et al. 2008) and recently published data (Ratnakumar et al. 2009), we have advocated that water uptake by roots should be measured rather than assessing morphological rooting traits, and we have developed a large lysimetric facility to cater for this need (<http://www.icrisat.org/bt-root-research.htm>). This methodological approach should be complemented by a comprehensive study on how roots and shoots capture and regulate water loss in a way that maximizes and matches plant productivity to available water, for example, by having parallel measurement of canopy development/size/conductance (through infrared and visible imaging) and of water extraction dynamics. This would lead to a better integration of different but interactive traits (control of water losses/maximization of water capture) in their role in the plant's adaptation to water limitation, by having a better understanding of the dynamics of plant water use under both well-watered conditions and upon exposure to water deficits. This, in turn, will be crucial to progress towards the identification of genotypes that can match water requirement and availability with climate change.

4.2 Ecophysiological model to look at the climate change affected C/N balance

Strong interactions exist between C and N metabolisms in legume plants. For example, photosynthesis depends upon

foliar N (mostly Rubisco), while N uptake requires energy for the synthesis of nodules and for their activity. By modifying both developmental and growth processes, climate change will affect source–sink relationship within the plant, with sometimes antagonistic effects. For example, high temperature and drought result in decrease in dry matter production and symbiotic fixation. On the other hand, even if the increase of CO₂ concentration increases C uptake photosynthesis, it also results in temporary N deficiency in legumes (Rogers et al. 2009) before new nodules are generated and become efficient to sustain the increased growth (Jeudy et al. 2010). As such, the understanding of the effect of climate change on C and N nutrition of legumes necessitates a modeling approach including the effect of temperature, vapor pressure deficit, drought, and CO₂ increase on C and N sources and sinks and their interactions (Liu et al. 2010).

4.3 Simulation modeling to predict crop response to climate change regarding water use

The shortening of the cropping period and the quicker water exploitation from the soil profile due to higher vapor pressure deficit and the temperature-related differences in the canopy development will have antagonistic effects on the overall water balance of the soil profile. Also, as seen above, understanding how the capture of water by the roots matches the water requirement for plant transpiration will require an increased investment in research investigating how essential physiological processes at the organ or cellular level interact with the environment. For example, Reymond et al. (2003) have shown that the process of leaf expansion in maize show genotype-by-vapor pressure deficit or genotype-by-soil moisture interactions, whereby phenotyping is made for a response of a process (leaf expansion) to an environment rather than a measure of the process itself.

Obviously, the framework of processes taking place in the development of a plant is complex and tools to integrate these into a production function will be increasingly needed to assist the search of processes that can make a difference in the productivity of a crop under climate change. As each crop differs in sensitivity to the environment depending on the stage of growth, simulation modeling can consider the timing of each climatic factor at each stage and this is critical for any impact analysis. A comprehensive simulation model which takes into consideration the dynamics of crop–soil–weather interactions and capture the crop physiological principles would be able to explore cropping systems across a range of seasons, soil types, and rainfall zones under various climate change scenarios. Crop–soil models have been shown to be effective tools in extrapolating research findings over time, soil types, and climatic regions. There are clear and

outstanding evidence of the critical role that modeling can play in guiding breeding choices or guiding trait identifications (e.g., Soltani et al. 2000; Sinclair and Muchow 2001; Sinclair et al. 2010). Another example is the Agricultural Production Systems Simulator (Keating et al. 2003) which covers several crop including grain legumes (Carberry et al. 1996; Carberry et al. 2001; Farre et al. 2003; Robertson et al. 2002).

5 Climate variability and distribution/management of insect pests and diseases

5.1 Impact of climate change on geographical distribution of insect pests and diseases

Low temperatures are often more important than high temperatures in determining global geographical distribution of insect pests and diseases (Hill 1987). Therefore, for species which are currently limited by low temperature, increasing temperatures may result in a greater ability to overwinter at higher latitudes and may increase a pest's chances of extending its range (EPA 1989; Hill and Dymock 1989). Changes in the distribution of insect pests and diseases will be greatly influenced by changes in the range of host crops because of distribution of a pest is also dependent on the availability of a host. However, whether or not a pest would move with a crop into a new area would depend on other environmental conditions such as the presence of overwintering sites, soil type, and moisture (EPA 1989), e.g., populations of the pod borers, *Helicoverpa armigera* and *Maruca vitrata* might move to the temperate regions and attain higher densities in the tropics, leading to greater damage in food legumes and other crops (Sharma 2005, 2010). For all the pest species, higher temperatures below the species' upper lethal limit could result in faster development rates and therefore more rapid increase of pest populations as the time to reproductive maturity is reduced. In addition to the direct effects of temperature changes on development rates, increases in food quality as a result of plant stress may result in dramatic increases in the development rate of pest populations (White 1984). Pest outbreaks are more likely to occur with stressed plants because, under such circumstances, the plants defensive system is compromised and the resistance to pest infestation is lowered (Rhoades 1985)

5.2 Effect of climate change on expression of resistance to insect pests

Increases in global temperature, atmospheric CO₂, and the length of the dry season are all likely to have ramifications for plant/herbivore interactions in the tropics (Coley and

Markham 1998). Problems with new insect pests and diseases will occur if climatic changes favor of non-resistant crops or cultivars. The introduction of new crops and cultivars to take advantage of the new environmental conditions is one of the adaptive methods suggested as a possible response to climatic changes (Parry and Carter 1989). In the enriched carbon dioxide (CO₂) atmosphere expected in the next century, many species of herbivorous insects will confront less nutritious host plants that will induce both lengthened larval developmental times and greater mortality (Coviella and Trumble 1999). Increased CO₂ may also cause a slight decrease in nitrogen-based defenses (e.g., alkaloids) and a slight increase in carbon-based defenses (e.g., tannins). Lower foliar nitrogen due to CO₂ causes an increase in food consumption by the herbivores up to 40%, and unusually severe drought appears to cause herbivore populations to explode. Resistance to sorghum midge breaks down under high humidity and moderate temperatures in Kenya (Sharma et al. 1999). There are indications that stem rot (*Sclerotium rolfsii*) resistance in groundnut is temperature-dependent (Pande et al. 1994).

5.3 Effect of climate change on efficacy of transgenic plants and cost of pest management

There is a big question mark on the stability of Bt genes in transgenic plants, and the possibilities for the breakdown of resistance are real. This scenario is likely to be influenced by climate change. Higher temperatures and prolonged drought lead to increased susceptibility of transgenic cotton to bollworms (Sharma and Ortiz 2000; Sharma et al. 2004). It is therefore important to understand the effects of climate change on the efficacy of transgenic plants in pest management.

With the current trends in global warming and climate change, it is likely that most pests will have a cosmopolitan range wherever the climate is favorable and the hosts are available. Prediction of such changes, and range and diversity in pests niches should help develop better control measures, as well as adapt IPM strategies to minimize pest incidence. There is a need for a greater understanding of the effect of climate change on the efficacy of synthetic insecticides, their persistence in the environment, and development of resistance in pest populations to the pesticides.

5.4 Effect of global warming on the activity and abundance of natural enemies

Relationships between pests and their natural enemies will change as a result of global warming, resulting in both increases and decreases in the status of individual pest species. Quantifying the effect of climate change on the activity and effectiveness of natural enemies will be a major

concern in future pest management programs. The majority of insects are benign to agro-ecosystems, and there is much evidence to suggest that this is due to population control through interspecific interactions among pests and their natural enemies—pathogens, parasites, and predators. Changes in interspecific interactions could also alter the effectiveness of natural enemies (Hill and Dymock 1989). Aphid abundance will be enhanced by increase in CO₂ and temperature. Parasitism rates will remain unchanged in elevated CO₂. Changes to higher temperatures up to 25°C could enhance the natural control of aphids by coccinellids in wheat (Freier and Triltsch 1996).

5.5 Changing scenario of diseases/pathogens

Climate change will affect plant pathosystems at various levels viz. from genes to populations and from ecosystem to distributional ranges, from host vigor to susceptibility, and from pathogen virulence to infection rates. Climate change is likely to have a profound effect on geographical distribution of host and pathogens, changes in the physiology of host–pathogen interactions, changes in the rate of development of the pathogens, e.g., increased over summering and overwintering of pathogens, increased transmission and dispersal of pathogens, and emergence of new diseases.

In the tropics and sub-tropics, with prevailing high temperatures, crops are already growing at a threshold. Under elevated CO₂ levels, the morpho-physiology of the crop plants is significantly influenced. Elevated CO₂ and associated climate change have the potential to accelerate plant pathogen evolution, which may, in turn, affect virulence. Chakraborty and Datta (2003) reported loss of aggressiveness of *Colletotrichum gloeosporioides* on *Stylosanthes scabra* over 25 infection cycles under elevated CO₂ conditions. On the contrary, pathogen fecundity increased due to altered canopy environment. The reason attributed was to the enhanced canopy growth that resulted in a conducive microclimate for pathogen's multiplication. McElrone et al. (2005) found that exponential growth rates of *Phyllosticta minima* were 17% greater under elevated CO₂.

Recent surveys and reports from SAT regions indicated that dry root rot (*Rhizoctonia bataticola*) in chickpea and charcoal rot (*Macrophomina phaseolina*) in sorghum increased many folds in last 2–3 years due to high temperature and prolonged moisture stress that leads to drought at the flowering and reproductive growth stages (Sharma et al. 2010). Similarly, prolonged moisture may create a new scenario of potential diseases in SAT crops, such as anthracnose, collar rot, wet root rot, and stunt diseases in chickpea; *Phytophthora* blight and *Alternaria* blight in pigeonpea; leaf spots and rusts in groundnut; blast and rust in pearl millet; and leaf blight and grain mold complex in sorghum. Preliminary analysis of weather

indicated that outbreak of *Phytophthora* blight of pigeonpea (*Phytophthora drechsleri* f. sp. *cajani*) in SAT regions in last 5 years may be attributed to high intermittent rain (>350 mm in 6–7 days) in July–August (Pande and Sharma 2009).

Extensive research is lacking in this domain to develop adaptation and mitigation strategies for sustained food security. Efforts are needed to underway research across laboratories to forecast the changing scenarios of pathogens and diseases of SAT crops under variable climatic conditions through simulation modeling and targeted surveys. Studies are also need to be initiated to understand behavior of the vectors of pathogens from the point of view epidemic development as well as biosecurity.

6 Conclusions

As seen in this review, the challenges related the changes in climate will be various. Many of them will in fact exacerbate current constraints, like water deficits or heat. Therefore, reinforcing current work on drought by including the dimensions of the physical environment that will prevail under climate change is important, such as a possible increase in the evaporative demand, or temperature-led changes in phenological cycle. New methods are needed to evaluate how plants respond currently to water deficit to better understand how they will respond to climate change as an added layer of complexity. Many disciplines are likely to be involved, in particular, plant physiology, crop simulation modeling, GIS, and breeding. The potential of exploiting genetic diversity to identify new traits suiting crops to a new environment will be critical. Simulation modeling will be a must to help tackle the complexity of having other dimensions overlapping the already fairly complex issue of adapting grain legumes to the current climate conditions and variability. Changes in the climate variability and increase in temperature will modify the pest and disease distribution and how these need to be managed, having consequences on the economics of pest control measures and on the economic thresholds. In particular, sensitivity to the environment of host plant resistance, biological control, synthetic insecticides, spinosads and avermectins produced by fungi, nuclear polyhedrosis viruses, and *Bt* toxins may render many of these control tactics to be relatively less effective. Therefore, there is a need to adapt appropriate strategies for pest management in food legumes that will be effective under climate change.

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