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Understanding crop physiological processes for climate resilience

VINCENT VADEZ AND JANA KHOLOVA

Crop Physiology Laboratory, Theme Simulation Analysis for Climate Smart Agriculture, ICRISAT, Patancheru 502324, Greater Hyderabad, Telangana, India

As everybody knows, the climate is changing and over the next decade will be putting an increasing strain on agriculture production. This paper aims at putting some focus on what can really be addressed (the change in temperature) from what really cannot be predicted and dealt with (rainfall). But even the effect of one factor like temperature triggers a complex myriad of effects and the paper structures what needs to be done in relation to temperature, and focuses on recently discovered mechanism to adapt to a change in temperature. The paper then briefly reviews its biological basis, the mean to phenotype for it at a high rate and precision, and how the use of crop simulation can help us predict the effect of this trait on yield.

Future climate or how to deal with higher temperature

General circulation models (GCM) for climate consensually predict an increase in the temperature globally, only diverging on the extent of that increase, i.e. 2 to 4 ºC. By contrast, none of the 20 or so models agree with regards to rainfall and whether these would increase or decrease, where and how much. Therefore, an increase in temperature is the only expected change. Before we get on analysing the kind of effects temperature can have on crop productivity, two things need to be kept in mind: (i) there will also be an increase in CO_2 concentration, which is currently on-going. With a current yearly increase over 2 ppm, a concentration around 700 ppm is expected toward the end of the century. High CO_2 leads to stomata closure and expectedly would increase water use efficiency and possibly yields under water limited situation, which would in part alleviate some of the negative effects of increased temperature; (ii) the changes in temperature are foreseen over a time scale of five to ten decades, whereas the time frame in breeding is in the order of one decade. In other words, one thing at a time: we first need to develop the cultivars of the next decade, because there is already enough temperature-related climate vagaries ‘today’ that need to be dealt with, using the same entry points described in the next paragraph. Then as climate changes the environmental context of the breeding program will change and impose a new selection environment in which breeding lines are tested that will likely alter the outcome of breeding selection. Breeders will then need to have their attention focused on what effects temperature is expected to have and what traits are expected to be “promising responses” to these changing conditions.

In relation to temperature stress, yield reductions are caused by three different reasons: (i) higher temperature affects dramatically the reproductive biology and leads to a reduced seed set. This area of research currently receives most of the attention, for instance in rice, wheat, or chickpeas that are known to be indeed sensitive to higher temperature at the time of anthesis; (ii) higher temperature mechanically hastens the phenological development and leads to a shortening of the crop duration with expected negative effects on crop yield. A simple solution to this is about breeding cultivars with an extended crop cycle; (iii) higher temperature will also increase the evaporative demand and have an effect on the plant water balance. In other words, while we often look at drought as being a scarcity of water in the soil profile, the effect of water scarcity in the atmosphere is often overlooked. An increase in the evaporative demand could be seen as a kind of “atmospheric drought”. In this paper, we will expand on that topic, which has so far received little attention and on which major breakthroughs have been recently achieved in relation to how crop respond to this constraint, the range of genetic variations, how to phenotype for it and how to harness genomic regions involved in this trait.

Trait dissection

In the last few years, strong evidences have been acquired that small amounts of water during the reproductive and grain filling period are critical for enhancing grain yield under water limited conditions across dryland legume and cereal crops species. Water availability during grain filling is a consequence of a number of plant traits altering the plant water budget, and operating mostly in the absence of soil water stress. Our current thrust is to crack the plant water budget into simpler “building blocks”, more amenable to genetic analysis and breeding use. One such trait is the capacity of the crop canopy of certain genotypes to restrict transpiration under high vapour pressure deficit (VPD). This trait is highly relevant for drought and climate change adaptation. Genotypic variation for this trait has been identified in soybean (Fletcher *et al*., 2007), pearl millet (Kholova *et al.*, 2010) chickpea (Zaman-Allah *et al*., 2011a), sorghum (Gholipoor *et al*., 2010; Kholova *et al*., 2014), maize (Yang *et al*., 2012), groundnut (Devi *et al*., 2010). It has also been related to increases in grain yield under terminal stress conditions in chickpea (Zaman-Allah *et al*., 2011b) or pearl millet (Vadez *et al*., 2013a). A recent paper reviews the different traits that condition plant water use and in particular the transpiration response to increases in VPD (Vadez *et al*., 2013b). Figure 1 below illustrates the different types of transpiration responses to increases in VPD which were found in different germplasms of different species over the last several years. Another paper then explains how this trait leads to increases in water use efficiency (Vadez *et al*., 2014), basically by lowering the average daytime VPD at the leaf level, which mechanically increases TE according to the theory.

High throughput phenotyping

For many crops, the genomics revolution has given hope that breeding would become easier and more efficient. Phenotyping is now a main bottleneck, especially for complex abiotic constraints, but phenotyping alone is not enough: Relevant phenotyping is needed and implies a thorough understanding of the biological mechanisms, and their interaction with the environment, conferring plant adaptation to abiotic constraints, and the "translation" of this knowledge into large scale and high throughput measurements. For assessing the transpiration response to increases in VPD at a scale that could be applicable to a breeding program, two essential elements were needed: (i) the capacity to assess the leaf area fast, precisely, and dynamically; (ii) the capacity to assess plant transpiration seamlessly and independently of time-consuming and labour intensive weighings. Toward that end, a large phenotyping platform, LeasyScan (Vadez *et al*., 2015) has recently been developed. The imaging platform is based on a novel 3D scanning technique, a scanner-to-plant concept to increase imaging throughput, and analytical scales to combine gravimetric transpiration measurements. The scanning consists in the projection of a laser line at a 940 nm wavelength on top of the crop canopy and in the picturing of its full reflection by the canopy. The assembly of about 80 pictures s^{-1} allows to generate a 3D point cloud from which several plant parameters are computed, including the plant leaf area. Analytical scales are also synchronised in the system and poll the weight of pots every few seconds and integrate the values over an hour, then providing a continuous assessment of the pot weights from which transpiration can be computed. Figure 2 below represents the load cell setup at the LeasyScan platform and gives an example of how transpiration is measured over several days under different maximum VPD conditions in lines of pearl millet know to contrast in their response to increased VPD. As can be seen, the transpiration rate of VPD-insensitive H77/833-2 peaks at the highest VPD in each day, whereas the transpiration rate of VPD-sensitive line PRLT-2/89-33 reaches a plateau is the circa 3 hours of highest VPD in each day. As such, this represents the first experimental evidence of the theory laid out earlier (Sinclair *et al*., 2005).

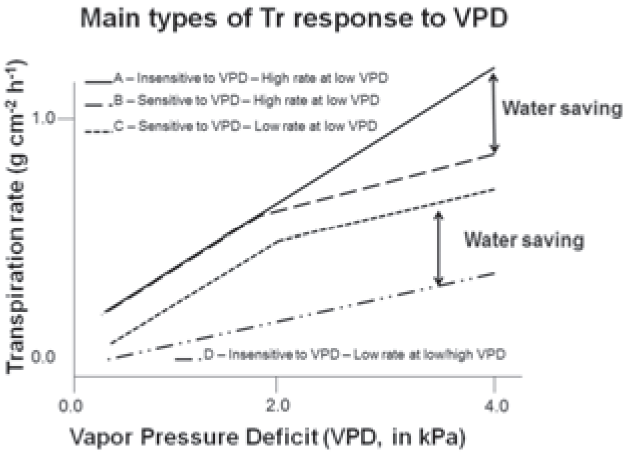

Fig. 1. Main types of transpiration (Tr) responses to increasing VPD conditions found in different germplasm of different species over the last few years. The differences in area between the different curves potentially represent different water savings (reproduced from Vadez *et al*., 2013b)

Modelling of trait effect

The difficulty of breeding for crop adaptation to water limitation is that these limitations are never the same and largely vary with time and geographical scales. Therefore, testing the effects of a given trait on crop yield across a range of environments that would represent the diversity of stress patterns is virtually impossible experimentally. In that context, crop simulation modelling has become a critical tool to be able to predict the effect of such traits / trait-by-management combinations on yield across time and geographical scale, and then to guide the choice of key breeding and agronomic management targets. In the case of the transpiration to increased VPD trait, it has shown that enormous yield benefits could be achieved in soybean across most environments in the US, and more so in dry years (Sinclair *et al*., 2010). Similar results have been obtained for soybean in sub-Saharan Africa (Sinclair *et al*., 2014). In sorghum, evidence has been acquired that the introgression of staygreen QTL elicit a VPD-sensitive phenotype and a modelling analysis has shown also major yield benefit across a large track of *rabi* sorghum in India (Kholova *et al*., 2010).

CONCLUSION

In this brief paper, we have shown that, besides an increase in CO_2, most of the climate change effects that can be predicted would be around an increase in temperature. While the effects of temperature on reducing yield are several, here we

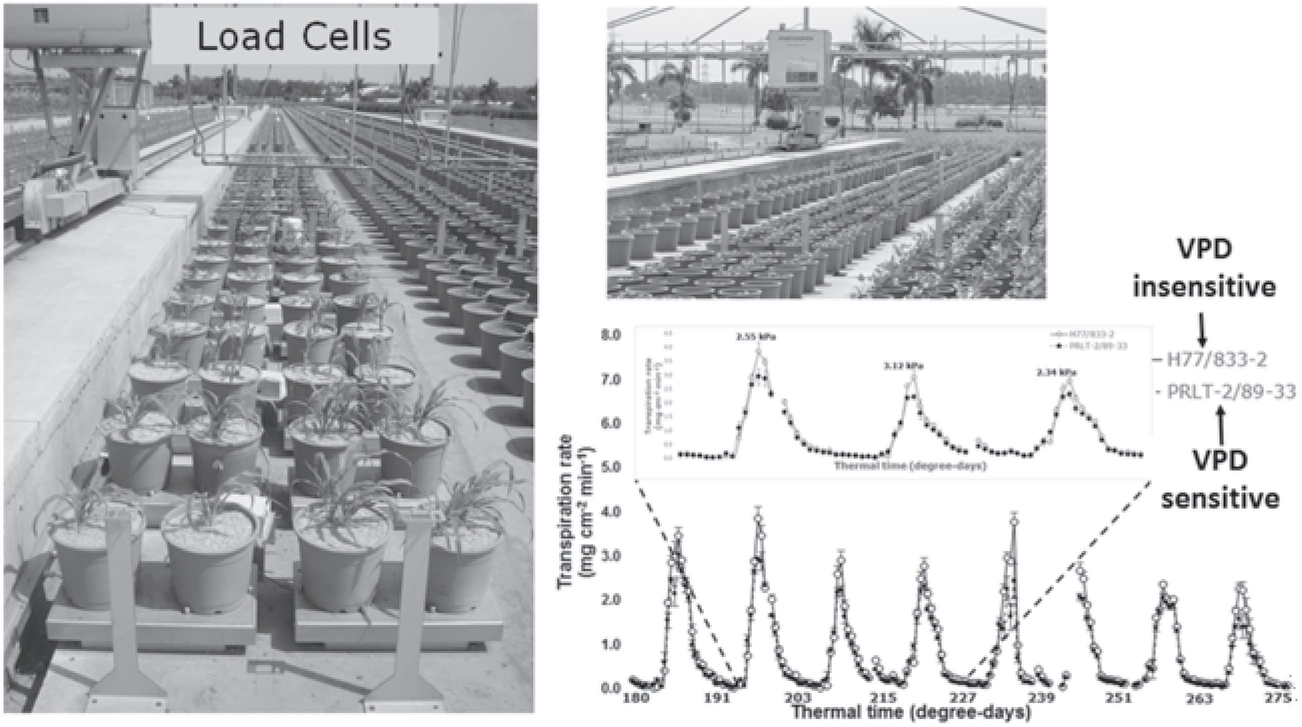

Fig. 2. Pictures of the load cell setup at the LeasyScan platform (left) and of the scanner supporting device (top right). The graph represents the transpiration evolution over several days in two pearl millet lines that were identified earlier as VPD-insensitive or VPD-sensitive (from Kholova *et al*., 2010). The manifestation of this phenotype in the platform is in the plateauing of the transpiration rate in the middle part of the day in the VPD-sensitive line (closed symbols). (Reproduced from Vadez *et al*., 2015)

have focused on the effect of temperature acting from the angle of plant water status via its effect on the vapour pressure deficit. We have shown that plants vary for their capacity to restrict transpiration under high VPD and that this trait confers water savings that are important under drought conditions. While this trait is typically a "climate change" trait, it has importance 'today' itself and is currently used toward breeding of cultivars adapted to high VPD conditions in the semi-arid tropics.

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