

# Traits Associated For Adaptation To Water Limited Environment Of Cereal Crops A Review Of Literature

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**Abstract:** Cereal crops mainly cultivated as a rainfed crops, where grain yield is often limited by terminal drought stress. Therefore, ability of plants to withstand drought is an important aspect of crop production in water limited conditions. In this context grain yield is closely related to post-anthesis water availability. Hence, grain yield can be increased by restricting pre anthesis water use to maximize post anthesis water availability. Therefore, identification of traits associated with water utilization of crops is important to increase crop productivity under terminal drought stress. The increase of post anthesis water availability could be achieved by manipulating traits associated for increasing water accessibility and reducing water use before anthesis. Root architectural traits that increase the soil volume explored and increase water extraction from explored soil are important aspects for increase water accessibility. Reduced water use before anthesis can be attained through smaller plant size via reducing tillering or early anthesis. Higher harvest index in water limited condition could be achieved by increasing water use efficiency through altering plant size, stomatal regulation, crop growth rate around anthesis and reducing competition between reproductive and vegetative organs. This review provides detailed inside to important crop physiological processes of transpiration, transpiration efficiency and biomass partitioning which determine crop adaptation to drought.

**Key words:** Rainfed agriculture, transpiration efficiency, dry matter partitioning, harvest index, drought tolerance, post anthesis drought stress, phenology, water stress, root system architecture, vapour pressure deficit

## Introduction

Dryland agriculture covers about 40% of the earth's surface (Anon, 2006) and provides large parts of the grain requirement for human food and livestock feed (Passioura and Angus, 2010). The demand for cereal grains is rising due to population growth as well as industrial demand. But expansion of cultivation is often limited to areas that are prone to drought stress. These region are experience high variation of rainfall and subjecting a greater range of pattern of water supply during the growing season. In rainfed agriculture, potential evaporation and transpiration often exceed precipitation (Nagarajan, 2009), which limits water availability for crop production. The potential for irrigation is limited because of rising demand for water for domestic, municipal, and industrial purposes (Tuong, 2000). Hence, drought adaptation of cereals is becoming more important in order to meet the increasing demand for grain. Drought is the most important abiotic stress to limit crop yield (Tuberosa et al, 2003). Conceptually, drought means a lack of precipitation over a prolonged period of time (Hale et al., 1987), which can cause water stress for crops over relatively short periods of time. Globally, drought is the second most (7.5%) extensive hazard after flooding (11%) (Nagarajan, 2009). In the tropics, yield loss of maize alone due to drought has been estimated at 24 million tons a year (Tuberosa et al., 2003). The ability of plants to withstand drought is an important aspect of crop production in water limiting conditions. Cereal crop productivity depends on the establishment of seedlings, and on vegetative and reproductive growth (Maiti and Ebeling, 1998a).

Drought can have a profound effect on any of these growth and development stages and the level of yield decline will depend on the severity and critical stage of exposure. Drought stress in the vegetative phase can reduce stomatal opening, which can affect CO<sub>2</sub> exchange, leaf expansion, and stem elongation (Hale et al, 1987) and ultimately results in reduced crop growth. The most critical stage is the reproductive phase (Saini and Westgate, 2000), because any damage done at that stage cannot be restored as cereals have a determinate growth habit. Crop production under water limited condition is the product of transpiration (T) transpiration efficiency (TE) and harvest index (HI) (Passioura, 1977). In this context grain yield is linked to post anthesis transpiration or crop water used (van Oosterom et al., 2011). Therefore, grain yield can be increased by restricting pre anthesis water use to maximize post anthesis water availability (van Oosterom et al., 2008). yield of grain cereal is the function of grain number and grain filling rate (Richards et al., 2002; Araus et al., 2008) and highly depend on the plant growth rate around the anthesis (D'Andrea et al., 2008; van Oosterom and Hammer, 2008). Therefore, identification of traits associated with water utilization of crops is important to increase crop productivity under water limited condition. Therefore, this review focus on the plant factors that contributes to withstand terminal water stress of cereal crops.

## Yield or biomass production under water limited conditions

Under drought stress, production of above ground dry matter is the product of transpiration (T) and transpiration efficiency (TE) (Richards, 1989). As harvest index (HI) represents the fraction of dry mass allocated to the grains, grain yield under drought can be represented by the equation (Passioura, 1977; Richards, 1989; Passioura and Angus, 2010):

$$GY = ET * (T/ET) * TE * HI \quad (1)$$

where ET is evapotranspiration from the crop and soil. Therefore, reduction of grain yield under drought stress is associated with either low biomass (T x TE) or low harvest index. Transpiration can be defined as the loss of water from

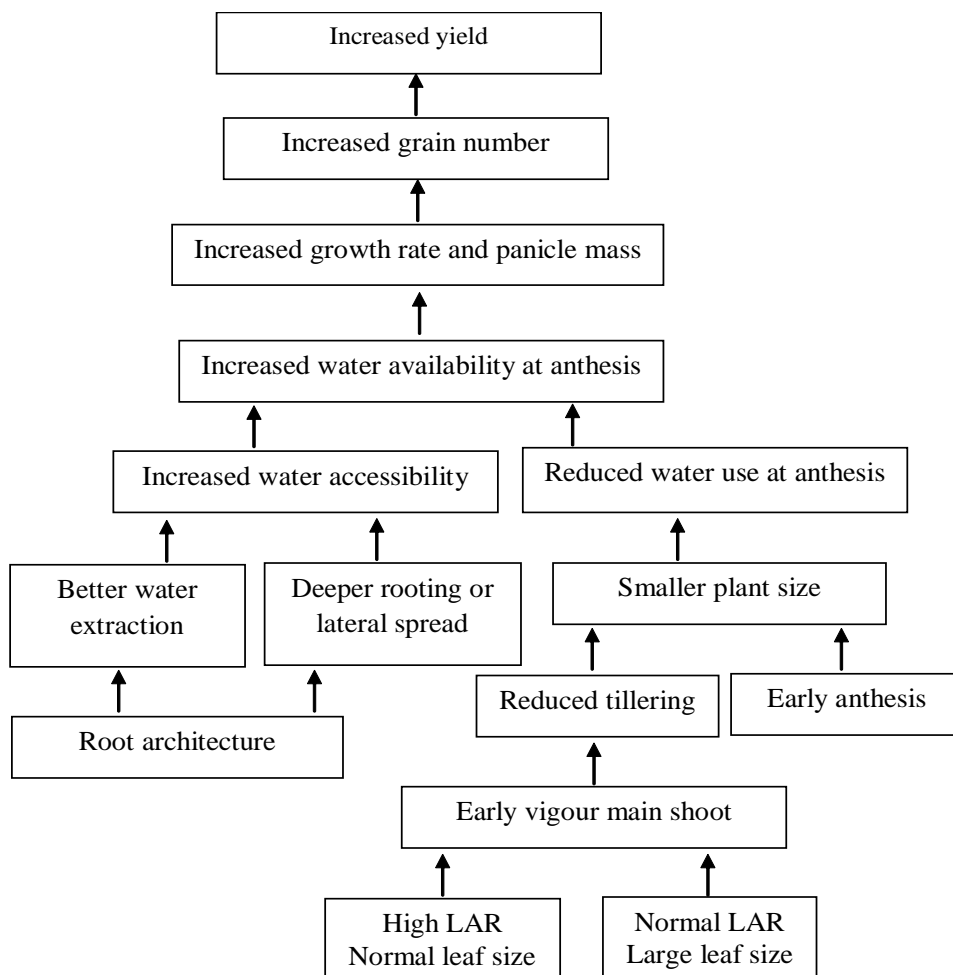
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the plants in the form of vapour (Ehlers and Goss, 2007) and depends on the supply of energy and vapour pressure gradient between evaporating surfaces and the ambient air. The TE is the ratio of the net gain in dry matter over a given period per unit of water transpired. Water deficit can inhibit photosynthesis (Boyer and Wetgate, 2004) and in maize, photosynthesis is reduced when leaf water potential falls below -0.35 Mpa (Fischer and Palmer, 1984). The effect of drought stress on grain yield is complex, as it is the consequence of effects on T, TE, and HI, plus their interactions.

### Effect of water availability on crop production

Water availability has a direct effect on crop physiological processes such as photosynthesis, photosynthate transport, and dry matter partitioning. Therefore, in water limited conditions, crop productivity is determined by the amount of water available and the efficiency of water used for assimilate production (Xu and Hsiao, 2004). However, plants have several anatomical, developmental, biochemical, physiological, and molecular adaptations to withstand water limited conditions and maintain productivity (Wood, 2005). Water limitation during vegetative stages of development and during late stages of the reproductive phase has a relatively smaller

effect on grain yield than drought around anthesis and early grain filling stages, which can drastically affect grain yield (Goldsworthy, 1984; Petr et al, 1988; Saini and Wetgate, 2000; Ehlers and Goss, 2007) Drought stress around anthesis can have a detrimental effect on grain number per panicle or cob and on grain filling rate via an effect on crop growth rate (Jacobs and Pearson, 1991; Tollennar et al., 1992; Maiti and Ebeling, 1998b; van Oosterom and Hammer, 2008). Therefore, ensuring post-anthesis water availability by any means is an important measure for obtaining higher yield. Hence, in water limited environments grain yield can be increased by restricting pre anthesis water use to maximize post anthesis water availability (van Oosterom et al., 2008). Increase of water availability after anthesis could be achieved by increasing water accessibility and/or reducing water use before anthesis (Figure 1). Increased water accessibility of a crop can be attained through root architectural traits that increase the soil volume explored and/or that increase water extraction from explored soil. Reduced demand for water prior to anthesis can be attained through smaller plant size via reducing tillering or early anthesis. These consequences are discussed in the following paragraphs.



**Figure 1** Schematic illustration of factors affecting post anthesis water availability in field crops (van Oosterom et al., 2011).

### **Reduced pre anthesis transpiration**

In rainfed agriculture, drought stress often increases as the season progresses, because low rainfall is inadequate to replenish water losses due to soil evaporation and transpiration of the existing crop, resulting in a depletion of soil water. Grain yield of cereals under drought is closely related to post-anthesis water use (Turner, 2004), and hence to water availability at anthesis. Therefore, identification of traits that reduce pre anthesis transpiration is a very vital aspect to enhance productivity of dry land farming.

### **Reduced plant size**

Under water stress, biomass production is the product of T and TE. Therefore, if TE is similar, crops with a greater potential for biomass production or greater growth rate require more water prior to anthesis than those that produce less biomass (Figure 1). This will deplete stored soil water at anthesis and hence can have a negative effect on grain yield. Maize plants utilise about half of their seasonal water uptake during the five weeks following attainment of maximum leaf area (Martin et al, 2006). Therefore, when resources (especially soil water) are inadequate to support this vigorous vegetative growth, the rate of biomass production will decrease to a level that can be supported by available soil water (Passioura et al., 1993). In addition, genotypic differences in tillering can be associated with propensity to tiller, which is independent of carbohydrate supply/demand balance. In this case, high tillering hybrids have a low S/D threshold, which could be due to hormonal effects on tillering (Kim et al., 2010a). The unculm growth habit of cereals has also been identified as an important trait in drought prone environments (Sainio et al., 2009) and some genetic regulation of this has been recognized, eg. the *tin* gene in wheat (Richards, 1988) and UC<sub>2</sub> gene in barley (Lundqvist and Franckowiak, 2003). Hence, improvement of crop productivity through increasing post anthesis water availability by manipulation of traits associated with plant size should be a reliable method for grain cereals grown in drought prone environments.

### **Early anthesis**

The adjustment of the crop cycle to water supply via genotypic variation in phenology is a vital means of terminal drought escape (Borrell et al., 2006). Under end of season drought stress, early flowering genotypes yield more grain than later flowering ones, because it enables the plant to escape water stress during the critical stage of yield formation (Figure 1). For example, the faster development of modern wheat cultivars reduces their water use during the vegetative stage and therefore, they have a larger portion of soil water left for the period of grain filling (Ehlers and Goss, 2007). Extreme drought stress can delay anthesis (Barnabas et al., 2008), what will increase pre-anthesis water use and reduce grain yield. Because larger crops are more prone to drought stress than smaller crops, such a delay in anthesis under drought stress is more likely to occur with larger plants, as has been observed in pearl millet (van Oosterom et al., 2003). This can cause genotype x environment interactions for anthesis date. However, under well watered conditions, earliness can negatively affect grain yield, because the shorter crop cycle reduces intercepted radiation and hence biomass accumulation. This can reduce the growth rate of the reproductive organs and hence grain number and grain yield (Blum, 2005; Passioura and Angus, 2010). Therefore, drought

tolerance through early anthesis is preferably achieved with short duration crops that have a vegetative growth rate that is sufficiently high to meet the assimilate demand required for high grain set.

### **Increase total amount of water accessible**

The strategy to reduce pre-anthesis water use by reducing plant size may not be suitable for a crop like maize that does not produce tillers under field conditions. In addition, small plant size could incur a yield penalty under well-watered conditions. Therefore, an ability of plants to access more water from the soil profile is an important aspect to increasing crop productivity where water is a limiting factor for crop growth and productivity.

### **Root system architecture to increase soil volume explored**

Soil is a heterogeneous medium (Pages, 1999). Supply of resources (nutrients, water) from the soil can be limited, can vary throughout the season, and resources can be unevenly distributed throughout the profile (Lynch, 1995). The extractable volume of water from a soil profile depends on root distribution within the profile and the difference between field capacity and permanent wilting point (Ehlers and Goss, 2007). Hence, root system architecture, which is defined as the spatial configuration of the root system (Lynch, 1995), is an important determinant of water uptake capacity of a plant (Bacio et al., 2003). Therefore, root system architecture can be important to manipulate the soil volume explored by the root system in order to access resources. The geometric configuration of roots has important implications for drought adaptation (Manschadi et al., 2008). A vertical distribution pattern of roots (consequence of narrow root angle) has advantages in deep soil which may allow plants to access stored water from deep layers (Hammer et al., 2009; Singh et al., 2010), whereas a more horizontal root distribution may be useful in skip row configurations that will allow the plants to access remaining water in between rows (Whish et al., 2005; Singh, et al., 2010).

### **Root system architecture to increase water extraction from soil**

The capacity of root systems to take up water and nutrients from the soil is of primary importance when considering the functional behaviour of the root system of a plant. Within the context of root system architecture, Manschadi et al. (2006) identified effectiveness and occupancy of the root system as two important parameters. The effectiveness of a root system is associated with root length density and a greater density in the soil profile will result in increased extraction rate of water. The occupancy is associated with branching behaviour of roots in different soil layers and even root branching results in better extraction of available water in explored in parts of the soil profile. In addition to those characteristics, genotypes that have the ability to proliferate or continuously grow during drought may have greater drought tolerance and enhanced water extractability (Maiti and Ebeling, 1998b). In general, deep (Ehlers and Goss, 2007), more branched, compact, and uniform (Manschadi et al, 2006) root systems provide a better adaptation to drought by enhancing water extractability. Better occupancy within the soil profile that has been explored by roots may increase water availability under drought. Thus,

these different root architectural traits are very vital in cultivar development for drought tolerance.

### Maximize transpiration as fraction of evapotranspiration

Evapotranspiration means the water used by crops as transpiration and evaporation from soil surface during the cropping season. Therefore, evaporation is the non productive water use and transpiration is the productive water use by the crop (Atwell et al., 1999). In drought prone environments, maximising transpiration as a fraction of evapotranspiration is an important aspect to increase crop water use and hence crop production. Agronomists have developed various cropping systems and ground cover methods to reduce surface water losses. As skip row configurations are used in environments with irregular rainfall, the increase in soil evaporation is limited. It is possible that root angle, through an effect on the horizontal distribution of roots, may affect the adaptation of genotypes to skip row configuration. Because roots can only extract soil water from the skip row later in the season, crops in skip row configuration tend to use less water pre-anthesis than crops in solid planting and hence have more water available post-anthesis during drought and can yield more grain (Routley et al., 2003). Water use efficiency is higher in skip row configuration at low and medium rainfall sites than in solid planting configuration in these sites (Abunyewa, 2010). In addition, clumps planting technique of sorghum has been reported as a promising method to reduce pre anthesis water use by reducing tillering and as a consequence increasing grain yield under post flowering water limited conditions (Bandaru et al., 2006). The TE of a crop declines with increasing vapour pressure deficit (VPD) (Kemanian et al., 2005). The normalised TE, adjusted for VPD, is around 9 g kg<sup>-1</sup> for both maize and sorghum (Tanner and Sinclair, 1983), but lower for C<sub>3</sub> species (Mortlock and Hammer, 2000). Under drought stress, the TE tends to be greater than under well watered conditions (Mortlock and Hammer, 2000), because under well-watered conditions biomass accumulation is limited by radiation, indicating luxurious levels of water uptake. As there appears to be no interaction between genotype and water treatment (Mortlock and Hammer, 2000), TE under well-watered conditions is important to drought adaptation.

### Dry matter partitioning

The ultimate objective of crop cultivation is to get maximum grain yield with available resources. In order to achieve potential grain yield, it is necessary to convert or transform more biomass into grain. Therefore, understanding of physiological processes involved in dry matter partitioning to grains is vital for improved grain yield and also for crop improvement. Grain yield can be improved either by increasing biomass production or by converting more biomass to grain yield, which is a higher harvest index (HI) (Otegui et al., 2000). The HI is defined as the ratio of grain yield to total crop biomass (Hay and Porter, 2006):

$$\text{Grain yield} = \text{Total Biomass} \times \text{HI} \quad (2)$$

Therefore, grain yield is proportional to HI (Donald and Hamblin, 1976). Since the green revolution, improved HI has been the main determinant of yield improvement of cereal crops (Sinha, et al., 1982), as crop biomass has not increase substantially (Hay and Gilbert, 2001). Increased HI was

principally associated with a reduction in plant stature. Although HI is a heritability character (Hay, 1995), it is associated with environmental conditions and phenology (Hammer and Broad, 2003). The role of environmental factors may become more prominent under stress conditions (Hay and Gilbert, 2001). In this context, there are two determinants of HI that can be genetically manipulated to maximize HI to achieve higher grain yield (Richards et al., 2002). The first one is the potential yield (HI) of a crop in a given environment and is independent of drought. The second one is drought dependent HI and depends largely on water availability during grain filling. The HI of modern cereal varieties falls within the range of 0.4 - 0.6 (Hay, 1995). Although, HI of cereal crops is close to the upper limit under optimum conditions, a better understanding of the physiological traits associated with higher HI under rainfed conditions could potentially increase grain yield under drought stress, which is known to reduce biomass and HI.

### HI related to temporal patterns of transpiration

Under water limited conditions, biomass production is a function of water use (WU) and water use efficiency (WUE). Therefore, Eq 3 can be rewritten as follows (Passioura, 1996):

$$\text{Yield} = \text{WU} \times \text{WUE} \times \text{HI} \quad (3)$$

Water use has two components: transpiration from the crop and evaporation from the soil. Soil evaporation can be manipulated through agronomic practices, although that effect is expected to be relatively minor (Richards et al., 2002). In rainfed agriculture, water deficit is generally most prevalent during the reproductive phase of the crop, because of low rainfall during this period (Blum, 2009). It has been well documented that water availability during anthesis (flowering) is critical for yield formation in cereal (Maiti, 1996; Maiti and Ebling, 1998a; Saini and Westgate, 2000; Ribaut et al., 2009) and HI can be increased with the fraction of total crop transpiration used after anthesis (Hammer, 2006). Therefore, restrictions of pre anthesis water use for transpiration can conserve soil water for utilisation post anthesis. Because grain yield is closely related to post-anthesis water use (Turner, 2004), HI does depend on the seasonal pattern of water use. Therefore, the components of Eq 3 are not independent of each other. As discussed in an earlier section, pre-anthesis transpiration is largely determined by plant biomass and leaf area (Mortlock and Hammer, 2000; Narayanan, 2010) and time to flowering. The amount of biomass produced by crops depends on the amount of PAR intercepted by the crop, which is a function of leaf area (Lizaso, et al., 2003). As example, increased internodal length and leaf area increased transpiration of sorghum (Narayanan, 2010). Restriction of plant size can be achieved by restricting tillering (van Oosterom et al., 2011) and reducing leaf area of the main culm (Hammer et al., 1993). Tillering is associated with the growth rate of the main culm and carbohydrate supply/demand index (Kim et al., 2010b). Sorghum plants with vigorous main shoot growth have less carbohydrate excess available for tillering and hence produce fewer tillers and have smaller plant size than plants with less vigorous main shoot growth (Kim et al., 2010b). Therefore, transpiration in sorghum can potentially be reduced utilising traits associated with plant size. However, as tillering is not important in maize, pre-anthesis transpiration in that crop can be manipulated through early flowering, which is a function of final leaf number and leaf expansion rate (Birch et



al., 1998). Early flowering reduces pre-anthesis transpiration through a reduction in leaf area and plant size, but, more importantly, through a reduction in the duration of pre-anthesis water use. Genotypic variation in response of timing of anthesis to temperature and photoperiod can affect pre-anthesis water use (van Oosterom et al., 2011). In addition to altering plant size, stomatal regulation of transpiration in water deficit conditions can be utilised to reduce transpiration. In general, transpiration rates increase with increasing VPD (Kholova et al., 2010; Gholipour et al., 2010). In several crops, including sorghum (Gholipour et al., 2010) and pearl millet (Kholova et al., 2010), genotypic differences in the relationship between transpiration rate and VPD have been observed, with some genotypes reducing their transpiration rate at high VPD. Because actual TE is inversely related to VPD, a restriction in transpiration rate under high VPD can result in an increased TE (Sinclair et al., 2005). Simulation studies for sorghum indicated that small amounts of water saved prior to anthesis would generally increase grain yield in dry environments compared to genotypes that have a greater transpiration rate under high VPD. According to this observation, these limits on transpiration rate restrict the amount of water transpired from the crop during the mid day period, when actual TE is lowest (highest VPD). This could improve HI by conserving soil water content during the vegetative phase.

### **HI not related to temporal patterns of transpiration**

Genotypic differences in HI that are not related to temporal patterns of water use are independent of drought (Richards et al., 2002). Grain yield depends on its components, which are the number of panicles (ears) per unit area, number of grains per panicle, and mean weight per grain. Grain yield represents dry matter partitioning to the grain. Therefore, improvement of HI requires an understanding of the physiological processes that determine yield components (Fischer and Palmer, 1984). The number of ears or panicles per unit area is a function of tillering and this has already been discussed earlier. Therefore, the focus here is on factors that affect grain number and grain size. Grain number is the main yield determining factor of cereals (Petr et al., 1988; Richards et al., 2002; Araus et al., 2008). The demarcation of potential number of florets in a panicle occurs during the last half of stem elongation (Kirby, 1988). In sorghum, final grain number is a linear function of crop growth rate around anthesis (van Oosterom and Hammer, 2008). In both maize (D'Andrea et al., 2008) and sorghum (van Oosterom and Hammer, 2008), genotypic differences in this relationship between crop growth rate and grain number have been identified. These differences could be explained by differences in the allocation of dry mass to the panicle or ear around anthesis (van Oosterom and Hammer, 2008; D'Andrea et al., 2008). In sorghum (van Oosterom and Hammer, 2008), grain number is highly correlated to ear or panicle growth rate around anthesis. Nonetheless, genotypic differences in the relationship between grain number and ear growth rate have been reported for maize (Echarte and Tollenaar, 2006). The observed genotypic differences in dry mass partitioning to the ear or panicle around anthesis can be related to differences in organ size. For sorghum, for example, genotypic differences in the proportion of dry matter partitioning to reproductive organs were associated with differences in plant height (van Oosterom and Hammer, 2008). In maize, genotypic differences in ear growth and kernel number per plant were associated with plant

growth rate during the period of kernel set (Echarte and Tollenaar, 2006; D'Andrea et al., 2008). In addition, genotypic differences in the position of the main ear could affect biomass partitioning among leaf blade, leaf sheath, and stem above the ear and this could potentially affect competition for assimilates with the developing ear (van Oosterom et al., 2008). Fischer and Palmer (1984) reported that reducing stem weight at flowering from 60 – 40% of total shoot weight was associated with increased ear dry weight by 2 -3.2% of total dry matter at flowering. Therefore, less stem demand during grain set of maize can increase the assimilate availability to the ear and as a result grain number per ear can increase. In conclusion, differences in dry mass partitioning to the ear or panicle around anthesis can affect grain number and HI independent of drought stress. Partitioning of assimilates to the grain is influenced by source (supply) and sink (demand) for photosynthate and is moderated by vascular connections (Tollenaar and Dwyer, 1999). Individual grain mass of maize is considered to be sink limited, because an increase in canopy photosynthesis does not increase grain yield and because the canopy generally produces more photosynthate than required for grain filling (Westgate et al., 1996). For sorghum, individual grain mass is generally source limited, as it closely related to assimilate availability per grain (van Oosterom et al., 2011). Assimilate partitioning can be modified by growing condition. Drought stress and low nitrogen status can increase allocation of dry matter to roots (Tollenaar and Dwyer, 1999), possibly as a consequence of inadequate sink capacity (grain number) (van Oosterom et al., 2011). In contrast, if plants cannot meet the sink demand from current photosynthesis, non-structural carbohydrate is mobilised from vegetative plant parts, in particular the stem, to the grain to meet the short fall. As a consequence, remobilisation percentage of carbohydrate increases under water stress, as observed for sorghum (Beheshti, 2010). However, in a shading experiment with sorghum, Kinery et al. (1992) observed that the grain yield from stored assimilates was less than the theoretical amount, suggesting that the contribution of stored carbohydrate has low importance in yield formation. Hence, understanding the physiological mechanisms that underline differences in dry matter partitioning among plant organs will provide valuable information for cultivar development.

### **Conclusion**

The crop production and cultivation is limited by water availability, yield improvement can be achieved by identifying traits associated with reduced pre anthesis water use without compromising grain yield and traits that can increase biomass partitioning to the grain.

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