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Grain Sorghum Water Requirement and Responses to Drought Stress: A Review

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Abstract

Because sorghum is a drought-tolerant crop, it is often preferred by producers in cases of expected water stress. The objectives of this review were to summarize the water requirements, effect of water stress, and hybrid variation in drought tolerance of grain sorghum, and to suggest possible solutions that could help narrow the gap between potential and actual dryland sorghum yield. We reviewed more than 70 reports in peer-reviewed journals, extension publications, books, and websites. Grain sorghum tolerates and avoids drought more than many other cereal crops, but the drought response of sorghum does not come without a yield loss. Water stress at the vegetative stage alone can reduce yield more than 36%, and water stress at the reproductive stage can reduce yield more than 55%. Eighty percent of sorghum production in the world is under dryland conditions. We deduced that by focusing on techniques that can improve water availability in sorghum growing season alone, we can double the current dryland sorghum yield with the existing genetic potential. Results of this review suggest the existence of genotypic variation in drought tolerance among sorghum hybrids due to possible physiological differences or vice versa. We concluded by presenting possible management options to reduce the effects of water stress in dryland conditions and suggesting possible areas of research.

Introduction

Several factors limit sorghum yields including: drought, prolonged dry periods, or delayed rainfall; nutrient deficiencies; weeds, insects, and diseases; cool, wet weather at planting or harvest; lodging; excessive or erratic rainfall; early frost, snow, and extreme cold conditions; washing rain and hail; high temperature; hot, dry summers; high-wind conditions; and bird attacks (3).

Analysis of 52 years of sorghum production in Kansas, USA, reveals that drought was mentioned as a major yield-limiting factor in about 30 of the 52 years (Table 1). Not only was drought the most frequently mentioned factor but it was also one of the most described (i.e., late-summer drought, mid-summer drought, August drought, drought in early and late August, drought and high temperature, drought and early freeze, heat and drought, extensive drought or prolonged dry period, delayed rainfall, and below normal rainfall). These expressions show the complexity of drought in terms of intensity, timing, length, and its conjunction with other factors such as freeze and heat (extreme temperatures).

In addition to its complexity and frequency, drought can be the core cause for other major sorghum production problems. For example, drought can reduce nutrient uptake by roots and induce nutrient deficiency by decreasing the diffusion rate of nutrients from soil to root, creating restricted transpiration rates and impairing of active transport and membrane permeability (1,69). Many sorghum pests and diseases, such as stalk rot diseases (charcoal rot and Fusarium stalk rot) (18,56,75) and sorghum ergot (5), are also caused or aggravated by drought and the resulting weak growth and weak defense system.

Table 1. Yield-limiting factors and years as reported in Kansas State University grain sorghum performance trial reports from 1957 to 2008 (36).

Yield limiting factor		**Years reported**
Abiotic	Late-summer drought, August drought, drought and high temperature, hot dry weather, hot dry summer, heat and drought in July and August, extreme growing season temperature, above-normal temperature and below-normal rainfall	1960, 1962, 1963, 1964, 1965, 1966, 1967, 1968, 1970, 1972, 1973, 1975, 1976, 1978, 1980, 1983, 1984, 1987, 1988, 1989, 1990, 1991, 1994, 1997, 1998, 1999, 2000, 2002, 2003, 2006
	Wet weather at harvest, prolonged periods of mud snow and extreme cold conditions at harvest, early frost, hail, late-season storm, sharp killing frost, high wind and early snow, cool temperature at August and September	1961, 1964, 1967, 1972, 1981, 1982, 1985, 1989, 1992, 1993, 1995, 1996, 1997, 2004, 2005
	Wet weather at harvest, extended rainfall at planting	1961, 1973, 1978, 1982, 1983, 1984, 1992, 1993, 1995, 1999, 2001, 2007
	Excessive rain, lodging, sprouting	1958, 1965, 1960, 1986, 1994, 1995, 2008
Biotic	Bird damage	1959
	Milo disease	1962, 1966
	Head smut, borer in panicle, European corn borer, corn borer, corn leaf aphid, spider mites, yellow sugar cane aphid, two-spotted spider mite	1965, 1966, 1967, 1973, 1974, 1977, 1991, 1994, 1998, 2000, 2001, 2008
	Earthworm, midge, sorghum midge, corn earthworm, armyworms, fall armyworm, headworms, sorghum webworm, cutworms, wireworm, grasshopper, sugarcane rootstalk weevil, caterpillar	1966, 1988, 1989, 1991, 1993, 1995, 1996, 1997, 1998, 1999, 2002, 2003, 2004, 2006, 2007, 2008
	New biotype greenbug, Greenbug	1968, 1969, 1972, 1973, 1974, 1980, 1981, 1988, 1989, 1990, 1991, 1993, 1994, 1996, 1998, 2000, 2001, 2004
	Chinch bugs, false chinchbugs, true chinch bugs	1977, 1978, 1980, 1981, 1988, 1989, 1990, 1991, 1993, 1994, 1996, 1998, 2000, 2001, 2003, 2004, 2007, 2008
	Billbugs	1997, 1998, 2000, 2001
	Maize dwarf mosaic, maize mosaic virus	1972, 1973, 1974, 1980
	Acremonium wilt, sooty strip, sorghum downy mildew, Fusarium stalk rot, charcoal rot, stalk rot, leaf blight, bacterial strip, rough spot, rust streak, Fusarium head rot, head smut, crazy top, head mold, seedling blight (Phythium or Fusarium), sorghum ergot, rootless sorghum syndrome	1989, 1991, 1992, 1993, 1994, 1996, 1997, 1998, 1999, 2001, 2002, 2003, 2006, 2008

Grain sorghum is drought tolerant and is often grown in environments where water stress is expected. A recent study showed that grain sorghum had a yield and economic advantage over corn in dryland regions because of better drought and temperature tolerance (57). Grain sorghum is also more capable than corn of taking up nutrients from soil in drought conditions (39). However, sorghum yields under dryland conditions are much less than irrigated sorghum yields (3). From these results we can deduce that drought tolerance is not absolute.

The objectives of the this review were to summarize the water requirements of sorghum, yield loss in dryland sorghum production due to drought, and hybrid differences in drought tolerance, and to suggest possible solutions for narrowing the gap between potential and actual dryland sorghum yields. Potential sorghum yield in this paper is defined as the highest possible yield of sorghum without drought stress and actual sorghum yield is defined as yield of sorghum with the existing drought stress. To attain these objectives, we reviewed more than 70 reports in peer-reviewed journals, extension publications, and websites.

Grain Sorghum Water Requirement

Sorghum water use is mainly affected by its growth stages and environmental demands. Hybrid differences in water use also exist (35) because of differences in growth habit and maturity. For high production, a medium-to-late maturing sorghum cultivar (maturity within 110 to 130 days) requires approximately 450 to 650 mm of water during a growing season (19,64). However, the daily requirement varies greatly depending on the growth stage (Fig. 1).

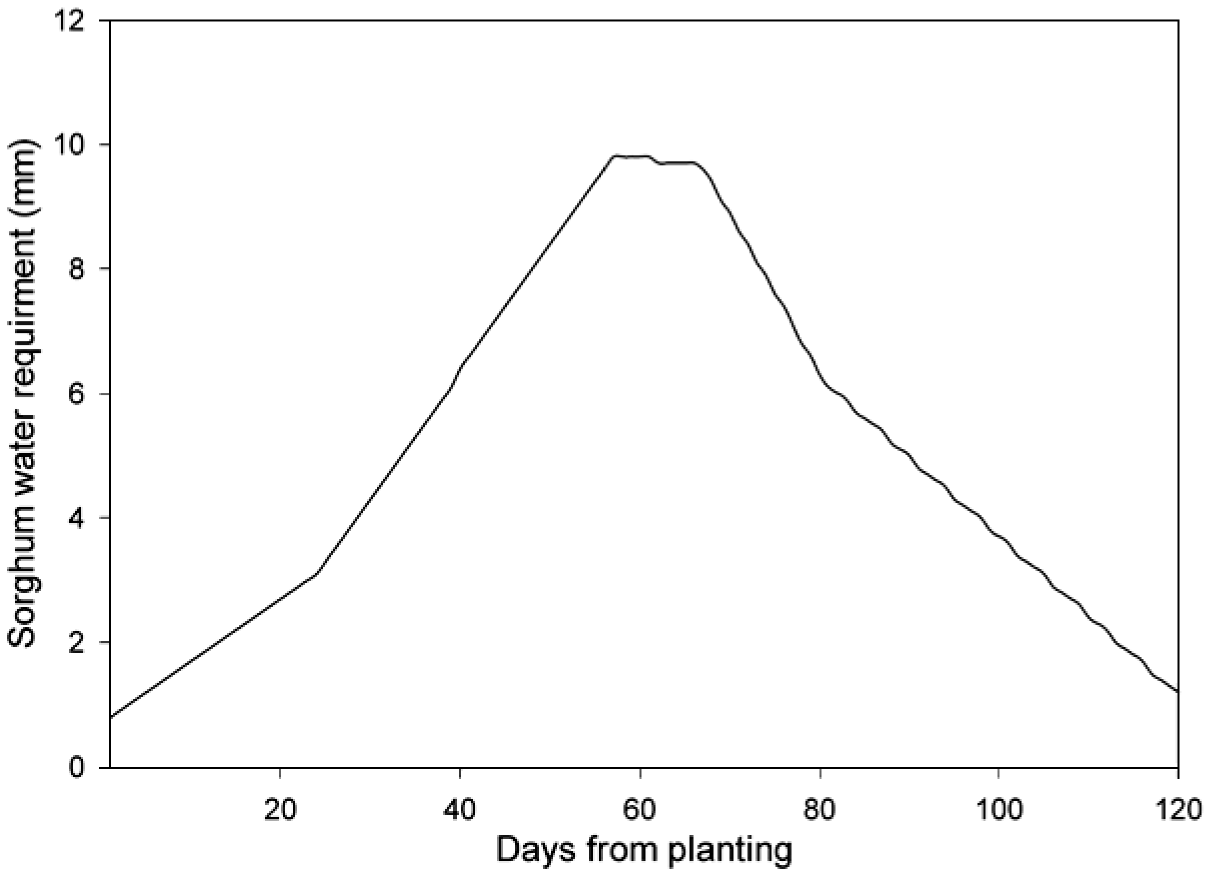

Fig. 1. A hypothetical daily water requirement of grain sorghum maturing in 120 days from planting.

Early in the growing season, average daily water use is low. Approximately 1 to 2.5 mm/day could be enough to avoid water stress. This period is roughly the first 25 to 30 days (up to approximately the 7-leaf stage). The water requirement then increases to around 7 to 10 mm/day until the boot stage. Maximum daily water use occurs from the boot stage until after anthesis. The daily water requirement then decreases gradually during grain fill as the crop begins to senesce leaves and mature (38,46,58).

About 90% of the total water used by sorghum is extracted from a soil depth of 0 to 1.65 m (49). The rooting depth of sorghum, however, can extend to about 2.50 m (60). The water depletion zone for sorghum will vary with growing stage. Water stored at deeper soil depths (below 1.0 m) are an important source of stored water at the end of the growing season (47).

Factors That Can Affect Sorghum Water Use and Water Use Efficiency

Environmental conditions such as rainfall, temperature, relative humidity, solar radiation, and wind can affect water use of sorghum. Crop water use is a function of the crop itself and existing weather conditions. Water use of sorghum is lower under mild climatic conditions than in climates with high evapotranspiration demand (65). A mild climatic condition is defined as moderate temperature (20 to 25°C), low wind speed (< 2 m/sec) and solar radiation, and a humid environment. Even though sorghum is a C_4 plant, elevated atmospheric CO_2 has also been reported to reduce its water requirements (15).

Soils vary in water and nutrient holding characteristics and resistance to root penetration. Tolk et al. (63) showed that sorghum performed well in well irrigated clay soils. In places where irrigation or precipitation is not sufficient, loam soil is preferred for grain sorghum production because of its high plant-available water holding capacity. In soils having high bulk density, root growth might be restricted and water use will be negatively affected.

Soil management practices affect evapotranspiration by altering the heat balance at the soil surface and changing the exchange rate between the soil and the atmosphere (28). Reduced tillage systems, for example, decrease the incoming heat energy, which is capable of evaporating water, and change the exchange rate between soil and atmosphere and trap already vaporized water. Grain yield response to water supply was found to be greater with no tillage than conventional tillage (59). In addition, Unger and Baumhardt (68) showed that the major yield increase in sorghum production since the 1970s is mainly a result of an increase in soil water content due to conservation tillage.

Diseases, insects, and weeds affect sorghum water use by affecting plant physiology and growth. Plant management practices such as application of required nutrients and appropriate disease-, pest-, and weed-control systems will can increase water use efficiency of the plant.

Planting date and planting density can also affect grain sorghum water use by altering canopy development (6). Optimizing planting date and planting population on the basis of the potential supply of water minimizes the opportunity for plant water stress that could be caused by high water demand (38).

Effect of Water Stress on Grain Sorghum Yield

The highest recorded sorghum yield is 20 Mg/ha under optimum conditions (11). Many other studies in the USA reported yields above 8 Mg/ha for fully irrigated sorghum (3). Average yield for dryland sorghum is about a half that of irrigated sorghum.

As with all crops, sorghum grain yield is dependent on water supply (soil water at planting and in-season precipitation). A summary of 30 years of data from Tribune, KS, indicated that every millimeter of water above 100 millimeter resulted in an additional 16.6 kg of grain (59). However, the relationship between grain yield and water is complex because yield is more sensitive to water deficits at certain growth stages (24). Therefore, grain yield is more dependent on rainfall or irrigation well distributed over the growing season depending on demand at each stage than on total water available through the growing season. Howell and Hiler (29) reported that yield response of grain sorghum was not strongly correlated to seasonal evapotranspiration but was highly dependent on timing of the evapotranspiration deficit.

Sorghum can tolerate short periods of less severe water deficit. However, long-term and severe stress can affect sorghum growth and the final yield. Eck and Musick (17) studied effect of various periods of water stress on irrigated grain sorghum at early boot, heading, and early grain filling stages. Their report indicated that 13 to 15 days of stress did not affect grain yield. A 27- to 28-day stress, however, reduced yield at early boot, heading, and early grain fill by 27, 27, and 12%, respectively. Stress period of 35 and 42 days beginning at boot stage reduced yield by 43 and 54%, respectively. Lewis et al. (40) showed that a soil water potential drop to −13 bars from late vegetative to boot stage reduced grain sorghum yield by 17%. The same water potential drop from boot to bloom and milk through soft dough stages caused 34 and 10% yield reductions, respectively. Inuyama et al. (30) reported 16 and 36% yield reduction due to 16 days and 28 days of water, respectively, deficit during the vegetative stage of sorghum. In same study, 12 days of water deficit during boot stage resulted in 36% yield reduction. Withholding 100 millimeter of irrigation water at the early 6- to 8- leaf stage and at heading and bloom reduced sorghum grain yield by about 10 and 50%, respectively (34).

Effect of Water Stress on Seed Emergence, Stand Establishment, and Vegetative Growth

Moisture is important for seedling germination (2). The embryo in the seed is dormant and highly tolerant to desiccation (water stress). After seeds start to germinate and emerge, however, it is susceptible to moisture stress (8). Water stress at the seedling stage could be caused by drought, high soil temperature, or high salt concentration in soil. Although water stress at seeding stage is a rare occurrence under field conditions, it can affect sorghum seed germination and emergence. Studies have shown that water stress at seeding will reduce endosperm weight of the planted seed as well as growth of the coleoptile, mesoctyl, radicle, shoot, and root of sorghum (4,31). Sorghum stand establishment is dependent on seed germination and emergence. Therefore, drought can cause loss in a sorghum crop even before plant establishment (8).

Water stress reduces the rate of cell expansion and, ultimately, cell size and consequently, growth rate, stem elongation, and leaf expansion (27). Therefore, water stress decreases plant height and rate of leaf appearance. Sorghum leaf area is also reduced because of water stress. Garrity et al. (23) reported that the 14 to 26% reduction in photosynthesis of water-stressed sorghum accounted for a decrease in leaf area. Blum and Arkin (9) also observed a significant leaf area reduction due to drought before there is a decrease in stomatal conductance.

In most cases, the sorghum root-to-shoot ratio has been reported to increase under water stress (51,72). The increased ratio is mainly due to a decrease in shoot growth rather than an absolute increase in root growth under stress. However, there are reports of an absolute root weight increase under stress. This increase is a result of diversion of significant amounts of assimilates to root growth; these assimilates could be used to produce grain under non-water-stressed conditions (71).

Effect of Water Stress on Reproductive Growth

Sorghum sensitivity to drought stress is greater during reproductive stages than during the vegetative stage (16,37). Drought stress from boot stage through approximately 10 days after anthesis will severely affect yield.

Water stress during reproductive stages can stop the development of pollen and ovules, prevent fertilization, and induce premature abortion of fertilized ovules (46,50). Sorghum yield is a function of the number of harvested panicles, seeds per panicle, and individual seed weight. All of which can be affected by duration and severity of drought during reproductive stages. Eck and Musick (17) reported that yield decreases due to water stress at the early boot stage were due to both reduced seed size and seed number and that yield reduction due to water stress at heading or later stages was due to reduced seed size.

Effect of Water Stress on Physiology and Biochemical Traits

Severe water stress can cause stomata closure which results in low stomatal conductance and low transpiration rates (14,51). It is also belived that CO_2 assimilation by leaves is mainly reduced because of stomata closure in drought stress conditions (21).

Vinita et al. (70) reported a reduction in photochemical efficiency of photosystem II (PSII), activities of phosphoenolpyruvate carboxylase (PEPcase) and ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) for severe water stress conditions. In addition to stomata closure, a reduction in PEPcase activity, a reduced Rubisco regeneration and functionality, and inhibited functional activity of PSII lowers the net photosynthetic rate (56).

An increase in the rate of photorespiration under severe drought conditions can be attributed to stomata closure, an increase in the internal oxygen concentration, and a decrease in internal CO_2 concentration. An increase in reactive oxygen in cells results in injury to sorghum cells due to peroxidation (21).

A reduction in leaf area and net photosynthesis and an increase in photorespiration rates eventually reduce total dry matter production in drought conditions (48,62).

Drought Tolerance and Avoidance Mechanisms of Sorghum

The prolific root system, the ability to maintain stomatal opening at low levels of leaf water potential, and high osmotic adjustment help sorghum cope with drought (32,43,67). Table 2 summarizes different drought tolerance and avoidance mechanisms in grain sorghum.

Table 2. Grain sorghum drought tolerance/avoidance mechanisms, how the mechanisms contribute to drought tolerance, and limits of the mechanisms.

Drought tolerance / avoidance mechanism in grain sorghum	**How the mechanism help**	**Limits of the mechanism**
Deep root system	Increases water extraction depth	Up to 2.50 meters
Higher root density (secondary roots)	Increases water extraction area	Root density of about 4.1 cm per cm soil
Stomata remain open at wide range of leaf turgor	Maintain CO_2 exchange (photosynthesis)	from 11 bars to 1 bar
Stomata closing at higher level of stress	Avoids further water loss	About −14 bar to −15 bar is lowest leaf water potential where stomata closes
Leaf roll	Avoids further water loss by decreasing surface area of leaf contact with radiation	Starts after about 10 to 14 days of water stress
Forming small vacuoles from large central vacuoles	Avoids cell rapture by maintaining tonoplast integrity	At about a leaf water potential of −37 bar
Production of antioxidant	Protect from lipid peroxidation	Until late in the drought stage
Cuticle and epicuticular wax (waxy bloom substance)	Checks transpiration (decreases water lose from leaves by obstructing the path)	It can check up to 30% of transpiration lose

Sorghum can extract water from deep in the soil profile and remove most of the apparent available water (13) because it has more secondary roots per unit of primary roots than other cereal crops. For example, compared with corn, sorghum has twice as many secondary roots per unit of primary root (44).

Sorghum has the ability to maintain stomatal opening at low levels of water potential and under a wide range of leaf turgors. Turner (67) reported that sorghum guard cells remained open over a wider range of leaf turgor (11 bars to 1 bar) than corn and tobacco guard cells. The same result was reported earlier by Sanchez-Diaz and Karmer (53). This adaptation enables sorghum to maintain a higher rate of CO_2 exchange than other crops at a high level of water stress.

Sorghum also has a high osmotic adjustment. It lowers its osmotic potential because of net solute accumulation in response to water stress. In the case of a high soil water deficit, osmotic potential in the leaves will decline and minimize a significant water loss that could occur from leaf opening (20).

Increasing water stress can cause a decrease in the leaf potential of sorghum. At low leaf potential, around −14 bars, stomata will close, the abscisic acid level will become elevated, and the amount of starch in the bundle sheath chloroplasts will be reduced. If the leaf potential gets much lower than this, near −37 bars, swelling of the outer chloroplast membrane occurs. Reorganization of the tonoplast also occurs to form small vacuoles from the large central vacuoles. This maintenance of tonoplast integrity is an important factor in the ability of sorghum to withstand drought better than other crops such as corn (26).

Under normal circumstances, plants produce antioxidants to detoxify reactive oxygen that can cause lipid peroxidation (45). Water stress can cause lipid membrane peroxidation by activated oxygen species as a result of impairment of the electron transport in plants (73). It has been suggested that lipid peroxidation in sorghum is much lower and occurs later in the drought stage than that in other crops (73). This process contributes to sorghums drought tolerance.

Leaves and stems of many sorghum varieties are covered with a waxy bloom substance. This is an adaptation for drought avoidance. The cuticle and epicuticular wax structure and composition determine hydraulic permeability of the leaf. Most cultivated sorghum genotypes have a close-to-maximum epicuticular wax (33).

Under water stress, sorghum leaves can become erect and roll. This will decrease the leaf surface area exposed to incoming solar radiation and, consequently, water loss. Lower leaves in the canopy and older leaves can senesce during water stress that occurs during grain filling and this also allow sorghum to maintain yield under severe stress.

Water Use and Drought Response Variation within Sorghum

Briggs and Shantz (11) reported variation in water requirement within plant species, specifically in sorghum. Other researchers have also shown differences in water use among grain sorghum by directly comparing water use and yield of different sorghum cultivars (24,25,42) and indirectly by measuring differences in gas exchange between hybrids (54).

Drought response variation among sorghum hybrids is similarly evident. The existence of yield variation among sorghum hybrids is the basis for breeding programs in dryland regions. Blum et al. (10) reported grain yield variation of 184 to 943 g/m^2 under drought stress between sorghum hybrids. Variation in phenology, plant height, panicle, peduncle length, leaf area, and plant weight have also been reported (22,41).

Agronomic and physiological differences such as osmotic adjustment (61), epicuticular wax content (10), leaf water potential, canopy temperature, leaf rolling, leaf carbon exchange rate, and stomatal conductance (10) are some reasons that have been indicated for drought response variation between sorghum varieties. Correlation between root variation and osmotic adjustment among sorghum genotypes was also mentioned (61). However, variation between roots of sorghum has been investigated less than the other aspects.

Conclusions

Determining the water requirement of a crop is not as easy as determining the nutrient requirement because the former is highly dependent on the environmental requirement. Therefore, it is often impossible to identify a specific number as the water requirement of a crop. Rather, a range is suggested on the basis of various experimental results to accommodate environmental conditions, hybrid differences, and their interactions. Maximum grain sorghum yield requires 450 to 650 mm of water. Most importantly, this amount of water should be well distributed throughout the growing season depending on the crop's stage of development and environmental demand because yield is sensitive to water deficits at certain growth stages.

Numerous studies have attempted to address water stress and water stress effects in sorghum. From the approach of these studies alone, one can understand how complex the problem is. Some studies attempted to address water stress from the level-of-stress point of view (intensity) that is by imposing different levels of water stress. Other studies attempted to impose a stress for different lengths of time. Studies that attempted to study water stress in different growth stages are also numerous. And studies also include a factorial combination of these water stress effects. However, in practice, water stress can happen in any complex combination. There is no cure for avoiding stress other than understanding the water requirement of sorghum and ensuring that water resources are well distributed in required amounts at the appropriate growth stage.

If the total amount of water needed is not going to be met, and water stress is expected, understanding that some growth stages of sorghum are more sensitive than others is important. Armed with this knowledge producers can optimize planting date or prioritize the irrigation scheme. Planting sorghum so that growth stages with high water demand can occur in months when better rainfall is expected is one choice, and harvesting water and irrigating at those growth stages should also be considered.

In addition to management options, hybrid selection can also play a major role. By selecting the best drought-tolerant hybrid and practicing the best management possible (i.e., optimum plant population, no-till, application of required nutrients and appropriate disease, pest and weed control systems) producers can meet the water requirement and narrow the difference between potential and actual sorghum yield in dryland conditions.

Sorghum is more drought tolerant than other crops because of its root system, ability to maintain stomatal opening at lower levels of leaf water potential, high osmotic adjustment, waxy bloom substance in leaves and stem, better adjustment in leaf angle, and leaf rolling in low water conditions. These characteristics vary among sorghum hybrids. Therefore, this variation among varieties of sorghum should be well utilized as a source for drought tolerant hybrids selection rather than relying on yield differences alone.

To date, the focus of the majority of drought-tolerant sorghum selections seems to be finding a cultivar that produces more grain from given amount of water (i.e., high water use efficiency). Existence of variation between varieties and importance of water use efficiency is undeniable. However, we likely will not eventually find or develop a hybrid that can produce a yield without water or nutrients. Therefore, future focus of sorghum breeders should be finding a hybrid that efficiently recovers available water resources from its surroundings. For this reason, understanding root variations among sorghums should be well investigated and should be a major component in development of future hybrids.

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