

CANOPY ARCHITECTURE AND WATER PRODUCTIVITY IN SORGHUM

by

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B.S., Kerala Agricultural University, Kerala, India, 2007

A THESIS

submitted in partial fulfillment of the requirements for the degree

MASTER OF SCIENCE

**Department of Agronomy
College of Agriculture**

**KANSAS STATE UNIVERSITY
Manhattan, Kansas**

2011

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Abstract

Increasing crop water use efficiency (WUE), the amount of biomass produced per unit water consumed, can enhance crop productivity and yield potential. The objective of the first study was to evaluate the factors affecting water productivity among eight sorghum (*Sorghum bicolor* (L.) Moench) genotypes, which differ in canopy architecture. Sorghum genotypes, grown under field conditions, showed significant differences in (a) biomass production, (b) water use, (c) intercepted radiation, (d) water productivity and (e) radiation use efficiency (RUE; the amount of biomass produced per unit of intercepted radiation which is suitable for photosynthesis). WUE and RUE were more strongly correlated to biomass production than to water use or intercepted radiation, respectively. RUE was positively correlated to WUE and tended to increase with internode length, the parameter used to characterize canopy architecture. These results demonstrate that increased utilization of radiation can increase water productivity in plants. Sorghum canopies that increase light transmission to mid-canopy leaves can increase RUE and also have the potential to increase crop productivity and WUE. The objective of the second study was to develop a quantitative model to predict leaf area index (LAI), a common quantification of canopy architecture, for sorghum from emergence to flag leaf stage. LAI was calculated from an algorithm developed to consider area of mature leaves (leaves with a ligule/collar), area of expanding leaves (leaves without a ligule/collar), total leaf area per plant and plant population. Slope of regression of modeled LAI on observed LAI varied for photoperiod sensitive (PPS) and insensitive (non-PPS) genotypes in 2010. A good correlation was found between the modeled and observed LAI with coefficient of determination (R^2) 0.96 in 2009 and 0.94 (non-PPS) and 0.88 (PPS) in 2010. These studies suggest that canopy architecture has prominent influence on water productivity of crops and quantification of canopy architecture through an LAI simulation model has potential in understanding RUE, WUE and crop productivity.

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Acknowledgements

It is with immense gratitude that I acknowledge my major advisor Dr. Robert M. Aiken for his constant support, encouragement, constructive criticism and inspiration from the initial to the final level of my works. Without his guidance and persistent help this thesis would not have been possible. I would like to thank my co-advisor Dr. Vara Prasad for his valuable advice, and cooperation. It is my pleasure to thank my committee members Dr. Zhanguo Xin and Dr. Jianming Yu for their suggestions, encouragement and assistance.

I wish to thank Ralph Wolf, Ray Duffey and Alicia Oien for their great efforts to explain and teach different tools and techniques to me. I would like to express my deepest appreciation to all student workers of crops lab, Northwest Research Extension Center, Colby, Kansas, for their ideas and assistance during my research.

I am indebted to my husband, Predeesh Chandran, my joy and guiding light, for his love, care and support through every step of the way. I would have been lost without his constant encouragement. I also wish to thank my mother, father and brother for their timely advice and support; despite the geographical distance, they were always nearby!

I am intellectually indebted to my office mate, George Paul for the lively discussions and constructive feedback. I am thankful to all members of crop physiology lab, Manhattan, for always being ready to cooperate with me. I am extremely thankful to my fellow graduate students of agronomy department for providing a stimulating and fun environment to learn and work. I am very thankful to all of my friends at Manhattan, especially Tony Grace, Ginny Antony, Amy Mathew and Vinod Mony for their emotional and moral support. Lastly, I offer my regards to all of those who supported me in any respect during the completion of this project.

Dedication

To all farmers who have been planting trees of hope on our planet

Chapter 1 - Literature review

Importance, origin and distribution of sorghum

Sorghum (*Sorghum bicolor* (L.) Moench) is the 5th most important cereal crop in the world after rice (*Oryza sativa* L.), wheat (*Triticum aestivum* L.), maize (*Zea mays* L.) and barley (*Hordeum vulgare* L.; www.fao.org). It is used for food in Africa and many parts of Asia, cattle feed in the US and Australia, bioenergy, brewing beer and for the manufacture of starch (Prasad and Staggenborg, 2009). It is adapted to the hot, semiarid tropical and dry temperate areas of the world (Kidambi et al., 1990; Blum, 2004).

Sorghum is better suited to high temperature and moisture stress conditions biochemically and physiologically than C₃ cereals like rice, wheat and barley (Dowens, 1972). Global sorghum production is 64.6 million tons and the area was 43.8 million hectares in 2007 (Prasad and Staggenborg, 2009). Major sorghum growing states in the US are Kansas, Texas, Oklahoma, Nebraska, New Mexico, and Missouri (Prasad and Staggenborg, 2009). Now sorghum has reached the second position as feedstock for grain based ethanol in the US after maize (Xin et al., 2008). As the global population and fresh water demand is continuously increasing, dry land farming and sorghum crop are gaining importance (Stewart et al., 1983).

Cultivated sorghum is believed to have originated near Lake Chad in Africa 3000–5000 years ago and is widely distributed through out the continent (Prasad and Staggenborg, 2009). Even though, the migration of sorghum out of Africa is not clear, it is believed that human activity may be responsible for this process; from Africa it was carried to Asia and spread in India, Indonesia, China, and Pakistan (de Wet and Price, 1976). Grain sorghum entered the US as “Guinea corn” (Bennet et al., 1990).

Botany, growth and development of sorghum plant

There are five cultivated races for *Sorghum bicolor* subspecies bicolor: Bicolor, Guinea, Kafir, Caudatum, and Durra; intermediates are produced by hybridization (Dahlberg, 2000). Sorghum developmental stages, time elapsed from emergence and

major characteristics of the developmental stages (Vanderlip and Reevse, 1972) are given in Table 1.1.

Sorghum germinates in 3–5 d and emerges above ground in about 5–10 d after sowing under optimum soil moisture and temperature conditions (Prasad and Staggenborg, 2009). Sorghum is a determinate, short day plant and it completes vegetative growth in about 30–40 d after sowing. The sorghum seed has 6–7 embryonic leaves. Sorghum plant needs 3–6 d to produce a leaf under optimum temperatures. A sorghum plant typically produces about 12–18 leaves arranged in alternate fashion on the culm. The top most leaf, also known as flag leaf or boot leaf, is generally short and broad (Prasad and Staggenborg, 2009). Most commercial varieties of sorghum cultivated in the US show a unimodal distribution of leaf area, where leaf area increases with leaf number, reaches a maximum and then starts to decline, but tropical varieties under stress exhibit bimodal distribution of leaf area (Mass et al., 1987).

Sorghum inflorescence is known as panicle that can be compact or open. Panicle formation begins at about 4–leaf stage and reaches above ground and begins to enlarge at about 6–leaf stage. According to Dowens (1972), a sorghum plant has potential to flower at 13–leaf stage at optimum day/night temperatures (21/16°C), but high temperature prolongs vegetative phase. The main axis of inflorescence is called rachis and it has primary, secondary, and tertiary branches. Spikelets develop from tertiary primordials.

Anthesis in sorghum starts about 2 d after the complete emergence of panicle from the boot leaf. It starts in the sessile spikelet at the top of the panicle and progresses downwards. It takes 4–15 d for a single panicle to complete blooming (Bennet et al., 1990). Maximum flowering occurs in the period of 3–6 d after the start of anthesis. Anthesis starts around midnight and continues up to 10 hrs. Sorghum is a protandrous crop where anthers protrude before stigma. Anther dehiscence takes place just before or just after anthesis between 6 and 7 hrs. Pollen is alive for 3–6 hrs and stigma is receptive for 10 d. Fertilization happens within 6–12 hrs after pollination (Bennet et al., 1990) and is completed within 2 hrs. Flower remains open for 30–90 minutes because pollen grains require light to germinate. Organ differentiation in the embryo starts at 7th d after fertilization and is completed within about 5 d and the endosperm deposition ends at seed

maturity (Bennet et al., 1990). Night temperature below 13°C leads to male sterility in sorghum (Dowens and Marshall, 1971).

Grain development in sorghum is composed of 3 stages– milk, early (soft) dough, and late (hard) dough. Physiological maturity can be visually identified by the dark brown callus tissue formed at the hilar region. At this stage seed moisture percentage will be 25–30 % and seeds will be fully viable. Sorghum seed, which is a caryopsis, varies in shape, color, and size depending upon the cultivar. Plant population, tillering, panicle size, number of seeds/unit length of primary branch, seed size and seed weight have major influence on yield formation in sorghum. Cultivated sorghum is a ratoon (perennial) crop by nature (Escalada and Plucknett, 1975) though only the seed is capable of surviving freeze conditions (Staggenborg and Vanderlip, 1996).

Constraints for sorghum production

Constraints for sorghum production can be broadly classified in to two categories; biotic and abiotic stresses. Major biotic stresses include weeds, pathogens, insects and birds (Bennet et al., 1990). Major abiotic stresses affecting sorghum production are drought, thermal extremes and nutrient deficiencies. Growth of different plant organs is affected differently by water stress (Asana, 1972). The effect of temperature stress depends upon the stage at which it occurs (Prasad and Staggenborg, 2008). Sorghum is sensitive to moisture deficits at the time of flowering and to heat stress at the time of booting (Pasternak and Wilson, 1969; Sullivan, 1972). Sorghum plant can be killed by frost (Smith and Frederiksen, 2000). Sub–optimal or supra–optimal temperatures reduce germination considerably (maximum germination occurs between 21–35°C) and cause leaf damage. Supra–optimal temperature delays flowering and reduces stem growth, root growth, plant height, pollen and ovule viability, pollen number, stigma receptivity, seed set, seed number, seed filling duration, seed size, and seed yield (Prasad and Staggenborg, 2008).

Effects of water deficit on sorghum

Physiological, biochemical, and molecular components of photosynthesis can be affected by water stress (Prasad and Staggenborg, 2008). Under water stress, stoma tend

to close leading to a reduction in the flow of CO₂ to mesophyll tissues and this results in reduction of photosynthesis (Chaves et al., 2003). The response of respiration to water deficit may vary with age of plant organs (Paulsen, 1994). Water stress affects cell division and expansion even before photosynthesis and respiration (Prasad and Staggenborg, 2008). Leaf expansion is the most sensitive growth process to water deficit (Alves and Setter, 2004).

Under water deficit conditions, sorghum panicle initiation can be delayed about 2–25 d and flowering by 1–59 d; effects will be more severe if plant experiences water stress at both early and late stages of panicle development (Craufurd et al., 1993). Panicle development may even cease under severe water stress (Craufurd et al., 1993). Pre-flowering moisture stress symptoms in grain sorghum mainly include panicle and floral abortion, poor panicle exertion, saddle effect (plants in the alley-ways show increased vigor), leaf rolling, leaf bleaching, excessive leaf erectness, leaf tip and margin burn, delayed flowering and reduced panicle size; post-flowering moisture stress might result in accelerated leaf and plant senescence or death, lodging, susceptibility to charcoal rot and reduced seed size (Rosenow et al., 1983; Mkhabela, 1995). Water deficit during the pre-flowering period in grain sorghum reduces grain yield significantly more than any other growth stage (Krieg, 1983). Post flowering water stress decreases seed filling duration, seed size and seed number leading to reduction in grain yield or even total crop loss (Mkhabela, 1995). Water stress at flowering and seed-filling stages can reduce harvest index substantially (Fisher et al., 1978). Water stress affects seed quality mainly through its impact on nutrient uptake, assimilate supply, partitioning and remobilization of nutrients (Prasad and Staggenborg, 2008).

Tolerance mechanisms to water deficit in sorghum

Grain sorghum has remarkable adaptations for tolerance to water deficits (Mkhabela, 1995). Some of those mechanisms are large efficient root system, relatively small amount of transpiration in relation to increased root water uptake, ability for rolling leaves to reduce transpiration under water stress and the waxy covering on leaves and stem to reduce water loss (Wolfe et al., 1959). If water deficit occurs at vegetative stage

(prior to booting) sorghum plant can become physiologically dormant without much reduction in yield (Bennet et al., 1990).

Tolerance mechanisms for intermittent water stress in grain sorghum include matching phenology with water supply, osmotic adjustment of roots and shoots, increased rooting depth and density, early vigor, leaf maintenance, increased leaf reflectance and dehydration resistance (Ludlow and Muchow, 1990). In case of post flowering water stress, sorghum plant can increase the translocation of pre-anthesis photosynthates to the kernels (Ludlow and Muchow, 1990). Sorghum plant can avoid dehydration by enhanced water uptake through deeper and more extensive root systems and can tolerate dehydration by osmotic regulation (Wright and Smith, 1983; Singh, 1989). The increased tillering capacity of sorghum can provide yield compensation when the main culm is damaged by water stress and provide yield stability in dry land environments (Richards, 1987; Mahalakshmi and Bidinger, 1986). Sorghum can reduce transpirational loss of water through upright leaf habit (Begg, 1980).

Stay green trait is an important mechanism associated with post flowering drought tolerance in grain sorghum (Borrel et al., 2000). Stay green trait can be defined as the extended foliar greenness during grain-filling under post-anthesis drought, achieved by the balance between nitrogen demand by the grain and nitrogen supply; however, nitrogen dynamics may not be the sole reason for increased leaf longevity (Borrel et al., 2000; Borrell et al., 2001). Stay green genotypes usually contain increased cytokinin (McBee, 1984) and sugar contents (McBee and Miller, 1982). Stay green genotypes retain chlorophyll in their leaves and carry out photosynthesis for a longer period and thus possess a higher yield potential (Borrel et al., 2001, Jordan et al., 2003). This trait is associated with enhanced water and light use efficiencies (Borrell et al., 2001). Thomas et al. (2000) proposed five ways through which a plant can 'stay green': (i) senescence initiates at a delayed point but loss of chlorophyll content and photosynthetic capacity proceed with normal rate (ii) senescence initiates normally, but proceeds at a lower rate (iii) senescence starts at normal time but chlorophyll is retained indefinitely (iv) loss the capacity of photosynthesis but retains chlorophyll indefinitely (v) rate of photosynthesis remains the same as normal rate, but the amount of chlorophyll pigment contained in the cells remains larger compared to the normal type.

Components of resource use efficiency for increased productivity

Water use efficiency

Water use efficiency (WUE) is defined as the total biomass produced per unit water consumed (Tanner and Sinclair, 1983); water consumption can be transpiration, evapotranspiration or total water input to the system (Sinclair et al., 1984). It varies between species and within species (Kidambi et al., 1990; Donatelli et al., 1992; Peng and Krieg, 1992; Hammer et al., 1997; Henderson et al., 1998; Mortlock and Hammer, 1999; Xin et al., 2009). Increased WUE is of great importance when yields are maximized with the available water supply in each growing season (Sinclair et al., 2001). Increased WUE is associated with increased evapotranspiration efficiency in field (Ehdaie et al., 1988). Crop dry matter production is the product of WUE and transpiration (Fischer et al., 1978).

Transpiration efficiency (TE), the inherent WUE of crops is the ratio of assimilation rate to transpiration rate and is critical to plant survival, crop yield and vegetation dynamics (Xin et al., 2009). TE is positively correlated to total biomass (Xin et al., 2009) and WUE (Balota et al., 2008). TE can be increased by increasing biomass or photosynthesis, decreasing transpiration or by both (Prasad and Staggenborg, 2008). Passioura (1977) proposed that yield is a function of transpiration, TE and harvest index. Improvement in TE has potential to improve drought resistance in plants (Turner et al., 2001). Improvement in TE improves biomass production or allows the plant to survive for a longer period with limited amount of available water (Xin et al., 2008).

Leaf level TE can be expressed as a ratio of assimilation (A) to transpiration (T); A is the product of stomatal conductance (g_s) and CO_2 gradient from atmosphere to leaf intercellular spaces ($C_a - C_i$); T is the product of g_s to water vapor and a concentration gradient of water vapor from leaf boundary layer to leaf tissue (VPD; Kidambi et al., 1990; Luquez et al., 1997; Condon et al., 2002); thus normalized TE (product of TE and VPD, Tanner and Sinclair, 1983) can be increased by decreasing CO_2 partial pressure within the leaf intercellular spaces (C_i , Farquahar et al., 1982; Tanner and Sinclair, 1983; Von Caemmerer and Furbank, 1999). A lower value of C_i/C_a can be achieved through lower stomatal conductance or higher photosynthetic capacity or a combination of both

(Condon et al., 2002). g_s decreases with the increase in C_i , that in turn decreases transpiration (Messinger et al., 2006). Instantaneous TE which is the ratio of CO_2 assimilation to transpiration at the leaf level is inversely proportional to VPD (Xin et al., 2008). The lower C_i/C_a of C_4 plants (0.3–0.4) compared to C_3 plants (0.6–0.7) helps them to maintain an increased ratio of net photosynthesis to g_s which in turn improves TE (Morison et al., 1983; Bunce, 2005). In C_4 crops like sorghum, a reduction of g_s at low VPD will improve TE since g_s that results in increased C_i above the saturation level results in wastage of water without any increase in net photosynthesis (Bunce, 2005).

TE is affected by environmental factors including temperature, water availability, relative humidity and atmospheric CO_2 concentration, mainly through their effect on stomatal opening (Fischer and Turner, 1978; Van De Geijn and Goudriaan, 1996). Leaf level measurements support the correlation of TE with conductance which is transpiration per unit leaf area (Mortlock and Hammer, 1999).

When temperature increases transpiration rate increases initially, but gradually stomatal resistance increases and limits transpiration; increased temperature can also increase VPD and thus influences TE (Van De Geijn and Goudriaan, 1996). Water availability has significant influence on TE. Under water deficit condition, stomatal conductance decreases that reduces transpiration considerably (Cienciala et al., 1994). Improved root penetration will improve absorption of water and TE (Fisher and Turner, 1978). TE increases with humidity; effect of humidity on TE is mainly through its effect on VPD and g_s (Rawson and Begg, 1977).

Gas exchange efficiency, defined as the ratio of photosynthesis to transpiration, has a positive correlation with TE and productivity (Kidambi et al., 1990). Gas exchange efficiency varies with genotypes (Peng and Krieg, 1992). Field scale measurement of gas exchange can be a direct indication of a crop performance in its growing period (Rochette et al., 1996).

Early reports suggested that TE mostly depends on crop species and VPD and there is not much dependence on variety, soil water status and plant nutrition (Fisher and Turner, 1978; Tanner and Sinclair, 1983; Ehlers et al., 2003). Later, significant genetic variation in TE has been reported within species for several crops under well watered and/or water limited conditions (Hammer et al., 1997; Mortlock and Hammer, 1999; Xin

et al., 2009). Mielke et al. (2000) reported that TE varies with genotypes when the transpiration ratio, which is the inverse of TE, is less than 1. Screening for genetic variation under water-limiting conditions may provide useful insights to increase water productivity (Hammer et al., 1997). Masle et al. (2005) showed an increase in TE in *Arabidopsis thaliana* with increased expression of ERECTA gene that reduces stomatal frequency.

The mini lysimetric method in sorghum directly measures whole plant TE (Peng and Krieg, 1992; Xin et al., 2008) and is a simple, highly efficient, reproducible and low cost technique to measure TE in controlled conditions. Carbon isotope discrimination of plant matter can be a reliable and sensitive marker for TE (Farquhar et al., 1982). Reduced carbon isotope discrimination is associated with increased TE (Xin et al., 2009). Variation in carbon isotope discrimination may be due to bundle sheath leakage of CO₂ that is related to light use efficiency or the difference in the ratio of assimilation rate to stomatal conductance which is TE (Masle et al, 2005). Carbon isotope discrimination can be used as useful screening tool for increased TE for C₃ plants rather than for C₄ plants (Xin et al., 2009) since bundle sheath leakage can confound interpretation of carbon isotope discrimination in C₄ plants. TE can be measured using portable photosynthetic systems by gas exchange analysis (Donatelli et al., 1992; Peng et al., 1998).

Carbon use efficiency

Carbon use efficiency (CUE) is a measure of the efficiency of a plant to incorporate newly fixed carbon into biomass and can be expressed as the ratio of daily carbon gain to gross photosynthesis (Frantz and Bugbee, 2005). Total carbon fixed under photosynthesis and fraction of fixed carbon used for biomass production determine plant dry matter accumulation (Norman and Arkebaur, 1991). Hubbart et al. (2007) and Peng et al. (1991) reported that increase in leaf photosynthetic rate will increase total biomass production and yield potential.

The enzyme, phosphoenolpyruvate carboxylase (PEPC) plays a key role in C₄ photosynthesis and is involved in pH regulation and stomatal opening (Cousins et al., 2007). The high affinity of PEPC for CO₂ increases the efficiency of carbon fixation in C₄ plants (Laisk and Edwards, 1998). The increased temperature tolerance of PEPC

relative to that of RUBISCO (Ribulose 1,5-Bis Phosphate carboxylase/oxygenase) increases the photosynthetic efficiency of C₄ plants at higher temperature compared to C₃ plants (Archana and Edwards, 1996).

The efficiency of C₄ photosynthesis can be determined by quantifying the bundle sheath leakage which is defined as the ratio of CO₂ leakage (diffusion of CO₂ from bundle sheath to mesophyll instead of being fixed by Calvin cycle within bundle sheath) at bundle sheath to the rate of C₄ acid decarboxilation (Hatch et al., 1995; Von Caemmerer et al., 1997). Siebke et al. (1997) reported that the reduction in RUBISCO content in a transgenic C₄ plant, *Flaveria bidentis* led to reduction in CO₂ assimilation rate, increase in CO₂ concentration in bundle sheath and bundle sheath leakage and an increase in ATP requirement per mole of CO₂ fixed.

Quantum yield of photosynthesis

Quantum yield of photosynthesis is a measure of photosynthetic efficiency and is expressed in moles of photons absorbed per mole of CO₂ fixed or O₂ evolved (Singsass et al., 2001). At low light intensities, rate of photosynthesis is determined by product of maximum quantum yield and leaf absorptance of radiation (Long et al., 1993). Quantum yield of photosynthesis is more sensitive to water stress than canopy interception and leaf absorptance of radiation (Earl and Davis, 2003). Quantum yield of photosystem II (Φ_{PSII}) and quantum yield of CO₂ assimilation (Φ_{CO_2}) have a linear relationship (Krall and Edwards, 1991). Rate of CO₂ fixation is strongly related to Φ_{PSII} under varying light intensities (Oberhuber et al., 1993). Φ_{PSII} can be used as a useful indicator of rate of photosynthesis in C₄ plants (Oberhuber et al., 1993; Earl and Davis, 2003).

The light energy absorbed by chlorophyll molecules can be used for driving photosynthesis, dissipated as heat or re-emitted as light (Maxwell and Giles, 2000). Even though chlorophyll fluorescence is only about 1 to 2% of the total light energy absorbed, it is a useful measure of rates of photosynthesis and heat dissipation in C₃ and C₄ plants (Donatelli et al., 1992; Krall and Edwards, 1992; Maxwell and Giles, 2000).

Radiation use efficiency

Radiation use efficiency (RUE) is defined as the amount of dry matter produced per unit of intercepted or absorbed solar radiation that is suitable for photosynthesis

(Monteith, 1977). Total available solar radiation and efficiency with which radiation is transformed into biomass are the most important factors affecting crop growth and yield under water sufficient environments (Russel et al., 1989). Monteith (1977) expressed crop growth as the product of light intercepted by the canopy and RUE. The increased incident and intercepted radiation can make yield of the crop unchanged even in the presence of an associated temperature increase that causes a reduction in the grain filling duration (Muchow et al., 1990). Gas exchange measurements with sufficient sampling of leaf positions within the canopy and chlorophyll fluorometry are useful methods for measuring short term crop RUE (Earl and Davis, 2003).

RUE varies with different species, nitrogen status and stages of crop growth (whether vegetative or reproductive; Rosati et al., 2004). Generally, C₄ plants have higher RUE than C₃ plants (Kiniry et al., 1989). Instantaneous photosynthetic RUE varies with time of the day because canopy photosynthesis can become light-saturated at high PAR (Grace et al., 1995; Ruimy et al., 1995). As PAR interception at solar noon is linearly related to total daily PAR interception, it can be considered as a good indicator of total daily interception of PAR (Earl and Davis, 2003). Seasonal weather condition can influence total incident radiation on crop canopy and the amount of radiation available for crop use (Clegg, 1972). RUE can be greater in cloudy conditions compared to clear sky conditions since RUE increases under diffused radiation as a result of cloudiness (Rochette et al., 1996). Under well watered conditions, RUE decreases when saturation VPD increases; possibly due to decrease in stomatal conductance and photosynthesis (Stockle and Kiniry, 1990). Light saturation of photosynthesis reduces RUE depending up on species, varieties and crop growth conditions (Erik et al., 1999).

Lindquist et al. (2005) reported that variation in estimated values of RUE occurs due to, (i) variation in the measurement of radiation [as total solar radiation or as photosynthetically active radiation (PAR)], (ii) fraction of total incoming short wave radiation considered as PAR (usually ranges between 0.46–0.50), (iii) whether RUE is calculated on intercepted PAR or absorbed PAR basis, (iv) whether plant growth is defined as net CO₂ uptake, total above ground dry matter production or total dry matter production and (v) whether RUE is calculated using short-interval crop growth rate method (RUE is the ratio of crop growth rate between two consecutive harvests to

cumulative intercepted or absorbed PAR during that interval) or cumulative biomass method (RUE is the slope of regression of total above ground biomass accumulation on the cumulative absorbed or intercepted PAR).

Canopy architecture

Canopy architecture refers to the distribution of positions, orientations, areas and shapes of various plant organs like leaves, branches and flowers (Welles and Norman, 1991). Canopy architecture influences the fundamental processes of crop growth including evapotranspiration, photosynthesis and intercepted radiation and precipitation and it controls the interaction between vegetation and its environment (Arkin et al., 1983; Aphalo and Ballare, 1995). Canopy architecture influences light environment inside the canopy, leaf nitrogen distribution and whole canopy carbon gain (Werger and Hirose, 1991). Canopy acquires greater absorptivity than the individual leaves due to the distribution and orientation of leaves within the canopy or canopy architecture (Campbell and Norman, 1998). Shade leaves and sunlit leaves within the canopy behave differently in case of light interception and assimilation (Campbell and Norman, 1998).

Canopy architecture can be quantified by LAI, foliage density or leaf angle distribution or by measuring canopy gap fractions which is the fraction of sky visible through the canopy at various angles (Welles and Norman, 1991). Armbrust and Bilbro (1993) developed equations to describe sorghum canopy characteristics including plant height, leaf area, stem area and canopy cover using cumulative biomass production as the predictive variable.

Leaf area index

Leaf area index (LAI) is defined as total leaf area (m^2) per unit ground area (m^2 ; Welles and Norman, 1991). Tewolde et al. (2005) identified LAI as the key parameter in the analysis of crop growth and productivity. LAI is 0 at the top of the canopy, increases with depth into the canopy and becomes equal to the total LAI of the canopy at its very bottom; a canopy that completely covers the ground surface has an LAI around 3 (Campbell and Norman, 1998). LAI required to intercept 95% of the incoming solar radiation is denoted as critical LAI and it varies with crop species and seasons

(Brougham, 1958; Engel et al., 1987). Specific leaf area, which is the leaf mass per unit leaf area, is nearly proportional to maximum rate of photosynthesis per unit leaf area under light saturated conditions and is controlled by environmental and genetic factors (Fageria et al., 2006).

Dry matter production increases with LAI and reaches maximum at optimum LAI beyond which yield does not increase, because net canopy photosynthesis can not increase indefinitely with LAI due to mutual shading of leaves within the canopy (Fageria et al., 2006). Bhatt (1994) showed that PAR interception and dry matter yield reached maximum in fodder sorghum at an LAI of 5 at optimum plant densities. Fageria et al. (2006) reported that maximum light interception generally coincides with an LAI of 4.

Lunagaria and Shekh (2006) found that row orientation and row spacing have an influence on LAI; north–south oriented, narrow rows lead to more LAI than east–west oriented, wide spaced rows.

Several attempts have been made on nondestructive measurement of leaf area. Many researchers have calculated individual leaf area from leaf length and width (Bueno and Atkins, 1981; Shih et al., 1981; Arkin et al., 1983; Birch et al., 1998; Caliskan et al., 2010). Arkin et al. (1983) modeled component processes of sorghum leaf area using thermal time. Maas et al. (1987) reported that the areas of successive leaves on sorghum are correlated. Zhu et al. (2009) related leaf dimensions to leaf position on the stem. Development of leaf area in sorghum can be explained through three phases; in the first phase, leaf area increases exponentially when the individual leaf areas are less than 60 m², in the second phase, rate of increase in leaf area decreases due to intraplant competition and in the third phase, leaf area starts to decline due to interplant competition and reproductive growth (Maas et al., 1987).

Leaf angle and orientation

Leaf angle influences canopy light absorption and photosynthesis (Gilbert and John, 1979; Deckmyn et al., 2000). Leaf orientation influences available leaf area for light absorption, reflectance, and utilization, and it also affects light saturation of photosynthesis (He et al., 1996; Valladares and Pearcy, 1997; Erik et al., 1999).

Optimization of leaf angle distribution in dense canopies can minimize mutual shading of leaves and maximize light interception and canopy photosynthesis (Werger and Hirose, 1991).

Generally monocot leaves are erect ($90-60^\circ$ from the horizontal) or erecto-patent ($70-30^\circ$ from the horizontal) at their base and become more horizontal towards their tip (Barkman, 1979; Werger and Hirose, 1991). A spherical leaf angle distribution is an appropriate approximation for most real canopies; an ellipsoidal distribution generalizes the spherical distribution and includes flattened and elongated spherical distributions as well (Campbell and Norman, 1998). Leaf angle may become nearly vertical in full sun and horizontal in shade (Goudriaan, 1988; Gilbert and John, 1979). Leaf angle is not expected to be largely associated with diurnal variation in leaf temperature (Erik et al., 1999). Younger leaves may have more vertical orientation than older leaves (Erik et al., 1999).

Zheng et al. (2008) showed that rice plants with vertical leaves at the upper canopy, and increasingly inclined leaves at lower canopy increased light interception. Clegg (1972) observed that sorghum lines with upright leaves had a greater yield response to increased populations than lines with a more horizontal leaf orientation. Ross (1970) stated that leaf angle had no effect on assimilation. Duncan (1971) observed small effect of leaf angles on light interception at normal LAI values in sorghum. Clegg (1972) reported that sorghum plant has an inbuilt ability to maintain light harvest and yield under different plant densities by orienting leaves at more erect fashion.

There are many time consuming and sophisticated ways to measure leaf angle like point quadrant measurement system (Warren-Wilson, 1963), laser beams' angle measurements (Sinoquet et al., 1993), 3-D digitizing devices and mechanical or digital clinometers (Sinoquet et al., 1993; Sinoquet and Rivet, 1997). Deckmyn et al. (2000) calculated leaf angle using the relationship between average leaf blade angle and the ratio of leaf height (distance between soil level and highest point of the leaf) to the leaf blade length.

Canopy extinction coefficient

Extinction coefficient (k) is a measure of the extinction of transmitted light into the crop canopy (Lunagaria and Shekh, 2006). Campbell and Norman (1998) defined k as the ratio of mean beam flux density on an average illuminated leaf in the canopy to the beam flux density on the horizontal plane above the canopy. k can be derived as the slope of the graph between natural logarithm of transmittance and LAI (Lunagaria and Shekh, 2006). k is an index of canopy light interception (Lizaso et al., 2003, Lindquist et al., 2005) and is dependent up on leaf angle, solar zenith angle and LAI. k is unity for a canopy of perfectly horizontal leaves (Campbell and Norman, 1998). k can be expected to change with time of day and stage of crop growth (Sinclair, 2006).

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Table

Table 1.1 Sorghum growth stages, time at which it is expected to happen (expressed in terms of days after emergence – DAE) and major features to characterize the growth stages.

| Developmental stage | Growth stage | DAE | Identifying characteristic |
|---------------------|--------------|-------|---|
| 0 | GS1 | 0 | Emergence |
| 1 | GS1 | 5 | 3 leaf stage |
| 2 | GS1 | 10–15 | 5 leaf stage |
| 3 | GS1 | 25–30 | Growing point differentiation |
| 4 | GS2 | 35–50 | Final leaf (flag leaf) visible in whorl |
| 5 | GS2 | 40–55 | Boot leaf stage |
| 6 | GS2 | 55–65 | Half bloom |
| 7 | GS3 | 35–80 | Soft dough |
| 8 | GS3 | 75–85 | Hard dough |
| 9 | GS3 | 80–90 | Physiological maturity |

Chapter 2 - Canopy Architecture and Water Productivity in Sorghum

Abstract

Increasing crop water use efficiency (WUE), the amount of biomass produced per unit water consumed, can enhance crop productivity and yield potential. The objective of this study was to evaluate the factors affecting water productivity among eight sorghum (*Sorghum bicolor* (L.) Moench) genotypes, which differ in canopy architecture. This study hypothesized that sorghum genotypes differing in WUE measured in greenhouse also differ in WUE and radiation use efficiency (RUE; the amount of biomass produced per unit of intercepted radiation which is suitable for photosynthesis) in field; and that increased WUE and RUE could be associated with differences in canopy architecture. Canopy level WUE was estimated as the slope of the regression of above-ground biomass on cumulative water use for specified sampling intervals. RUE was estimated as the slope of the regression of above ground biomass on the simulated cumulative intercepted photosynthetically active radiation. Internode length was calculated as the ratio of plant height to total leaf number at maturity. Sorghum genotypes, grown under field conditions, showed significant differences in (a) biomass production, (b) water use, (c) intercepted radiation, (d) water productivity, and (e) RUE. WUE and RUE were more strongly correlated to biomass production than to water use or intercepted radiation, respectively. RUE was positively correlated to WUE and tended to increase with internode length. These results demonstrate that increased utilization of radiation can increase water productivity in plants. Sorghum canopies with increased light transmission to mid-canopy layers can increase RUE and also have the potential to increase crop productivity and WUE.

Key words

Sorghum, water use efficiency, radiation use efficiency, productivity, internode length

Introduction

Agriculture accounts for 70 % of all freshwater withdrawals worldwide and ranks as the biggest water consumer in today's world (Bacon, 2004). To meet the rapidly expanding requirements of water for food production, both rain-fed and irrigated agriculture needs to use water more efficiently. Producing more crop per drop is key to sustainably feed around 9 billion people in a world susceptible to climate-change; where rain, temperature and drought are highly unpredictable. The term water use efficiency (WUE), defined as the amount of biomass produced per unit water consumed (Tanner and Sinclair, 1983) is also recognized as 'water productivity' due to the importance of efficient water use for world food security (Kijne et al., 2003). To increase crop yield per unit water requires species, cultivars and agronomic practices suitable for improved WUE (Passioura, 2006). Sorghum (*Sorghum bicolor* (L.) Moench) is one of the most drought tolerant (Blum, 2004) and water efficient cereal crop (Kidambi et al., 1990) currently under cultivation. It is the fifth most important cereal crop in the world and is used as a staple food in arid and semi arid tropics of Africa and Asia and as feed, forage and biofuel in the United States (www.fao.org). Therefore, developing strategies to improve WUE in sorghum is a viable approach to improve water productivity in agriculture as far as there is potential to alter WUE within species.

Increased grain productivity in sorghum may result from improved use of available water, nutrients and solar radiation. Increasing crop transpiration efficiency (TE), the inherent water use efficiency (Xin et al., 2009), defined as biomass produced per unit water transpired, can enhance crop productivity and yield potential. Within species variation in TE has already been reported for sorghum (Kidambi et al., 1990; Donatelli et al., 1992; Peng and Krieg, 1992; Hammer et al., 1997; Henderson et al., 1998; Mortlock and Hammer, 1999; Xin et al., 2009). TE can be increased either by increasing biomass or photosynthesis or by decreasing transpiration or by both (Prasad et al., 2008). Primary physiological mechanisms affecting TE, reported so far in literature, involve stomatal regulation of gas exchange (Xin et al., 2009). Leaf level TE can be expressed as a ratio of assimilation (A) to transpiration (T); A is the product of stomatal conductance (g_s) and CO_2 gradient from atmosphere to leaf intercellular spaces ($C_a - C_i$); T is the product of g_s and vapor pressure deficit (VPD); thus normalized TE (product of

TE and VPD, Tanner and Sinclair, 1983) can be increased by decreasing CO₂ partial pressure within the leaf intercellular spaces (C_i, Farquahar et al., 1982; Tanner and Sinclair, 1983; Von Caemmerer and Furbank, 1999). Farquahar et al. (1989) reported that reduction in bundle sheath leakage of CO₂ can increase leaf level TE; however this can be considered as a membrane effect, not stomatal per se. Masle et al. (2005) showed increase in TE in *Arabidopsis thaliana* with increased expression of ERECTA gene that reduces stomatal frequency. Schulz et al. (2007) demonstrated in *Arabidopsis* that damage to cuticular wax could enhance transpiration. High TE genotypes selected for reduced carbon isotope discrimination ratio use less water and are efficient in transpiration control (Condon et al., 2002; Impa et al., 2005). Xin et al. (2009) suggested that TE based on biomass accumulation is superior over low water use approach to determine and select for high TE genotypes in sorghum. This leads to a question whether processes leading to superior productivity can also improve TE and water productivity.

Current theory suggests that increased biomass production is directly proportional to quantity of radiation absorbed by the canopy in the absence of biotic and abiotic stresses (Monteith, 1977; Kiniry et al., 1989; Russel et al., 1989; Sinclair and Muchow, 1999). The amount of dry matter produced per unit of intercepted or absorbed solar radiation that is suitable for photosynthesis is termed as radiation use efficiency (RUE, g MJ⁻¹, Monteith, 1977). Under favorable growth conditions, crop growth can be expressed as the product of light intercepted by the crop canopy and its RUE (Monteith, 1977; Lizaso et al., 2005). Krall and Edwards (1991) reported that gross photosynthesis had direct linear relationship with absorbed photosynthetically active radiation (PAR) when adjusted for quantum yield of photosystem II. Lindquist et al. (2005) identified the slope of crop growth rate (g m⁻² d⁻¹) regressed on absorbed PAR as RUE. Steduto and Albrizio (2005) assigned equal importance to WUE and RUE for crop growth and yield. Earl and Davis (2003) found that lower RUE was the major limitation to yield in field grown maize (*Zea mays* L.) under water stress. If increased RUE can be proved to be correlated with increased WUE in sorghum, improvement in RUE will be a new approach to engineer water efficient genotypes for sorghum.

Canopy architecture has a prominent role in fundamental processes of crop growth including light transmission and interception, evapotranspiration and

photosynthesis (Arkin et al., 1983; Muchow et al., 1990). The term canopy architecture refers to the distribution of area, shape and orientation of leaves, stems, and reproductive structures; leaf area index (LAI) and leaf angle distribution are commonly used indices for vegetative canopy structure (Welles and Norman, 1991). Sorghum canopy architecture could influence intercepted radiation and use for growth, as well as modify the canopy environment (Clegg, 1972; Arkin et al., 1983; He et al., 1996; Valladares and Pearcy, 1997; Erik et al., 1999). Clegg (1972) found that sorghum lines with upright leaves had a greater yield response to increased populations than lines with a more horizontal leaf orientation. He also reported that increased light penetration into canopies with more erect leaves is important for sorghum productivity. Deckmyn et al. (2000) identified leaf angle as an important parameter that influences canopy light absorption and photosynthesis. Lizaso et al. (2005) included leaf angle distribution in calculations of intercepted radiation, assimilation and growth. Clegg (1972) hypothesized that altered canopy architecture could increase RUE. Kato et al. (2004) reported that LAI and total dry matter increment mainly determine the WUE in a sparse crop in the absence of water stress. Leaf orientation within the canopy also affects canopy radiative properties and controls light saturation of photosynthesis (He et al., 1996; Valladares and Pearcy, 1997; Erik et al., 1999).

Canopy characteristics contributing to increased resource (water and light) use efficiency will help to develop useful selection criteria in sorghum breeding programs to identify improved germplasm with increased productivity. The objective of this study was to evaluate factors affecting water productivity among sorghum genotypes that differ in canopy architecture. The canopy characteristics such as internode length, plant height, LAI and radiation interception were evaluated in this study to investigate their influence on biomass production of sorghum in relation to light and water use efficiencies (above-ground biomass based) at canopy level.

Materials and methods

Field studies were conducted in randomized complete block design (RCBD) in 2009 and incomplete block design (IBD) in 2010 at Colby, Kansas. Periodical destructive harvests quantified above-ground biomass of the selected sorghum genotypes. Crop

water use was calculated from changes in stored soil water, precipitation and irrigation. WUE was estimated as the slope of the regression of above-ground biomass on cumulative water use for specified sampling intervals. RUE was estimated as the slope of the regression of above-ground biomass on the simulated cumulative intercepted PAR (CIPAR). Observations were recorded on internode length, plant height and LAI to investigate their influence on biomass production, WUE and RUE.

Crop culture

Field studies were conducted in 2009 and 2010 at Kansas State University Northwest Research Extension Center (NWREC), Colby, Kansas (39° 24' N, 101° 4' W; 963 m above sea level) on a Keith silt loam soil (fine silty, mixed, mesic Aridic Argiustoll). The previous crop for the 2009 study site was sorghum (south half) and sunflower (north half), both harvested in fall, 2008. The previous crop for the 2010 study site was corn harvested in fall, 2009. Tillage in both years included two passes with a disk harrow followed by a roller packer to break clods. Sorghum genotypes (TX 7000, TX 399, TX 2862, PI 584085, Liang Tang Ai, TX 7078, IS 27150 and IS 27111) represented a range of vegetative TE (green house; Xin, Aiken pers comm.), heights and photoperiod sensitivities and were planted in 6.1 m x 6.1 m plots on June 25, 2009 and in 6.1 m x 3.0 m plots on May 28, 2010. Bulk rows were planted in between plots to avoid edge effect on crop growth and resource use. Sorghum seed was sown at a depth of 2 cm using a planter with a fluted coulter and double disk opener. Planting rate was 125,000 seeds ha⁻¹ with a spacing of 10 cm between plants and 76 cm between rows. Supplemental soil fertility included 102 kg N ha⁻¹ and 34 kg P ha⁻¹ banded adjacent as basal dose in both years. Weed control consisted of pre-emergent application of atrazine (2-chloro-4-ethylamino-6-isoprophylamino-s-triazine, 4.68 l ha⁻¹) plus Duall II magnum(2-chloro-N-(2-ethyl-6-methylphenyl)-N-[(1S)-2-methoxy-1-methylethyl] acetamide, 1.52 l ha⁻¹) and post-emergent application of Cornerstone Plus [Glyphosate, N-(phosphonomethyl)glycine, 1.75 l ha⁻¹) plus Starane (Fluroxypyr 1-methylheptyl ester: ((4-amino-3,5-dichloro-6-fluro-2-pyridinyl)oxy) acetic acid,1-methylheptyl ester, 1.02 l ha⁻¹) with a spray volume of 93.54 l ha⁻¹ and spray pressure of 138 kPa in both years. Supplemental in-season irrigation was provided during mid-vegetative

growth (38 mm) and just prior to anthesis (25 mm) for one half of the plots and during mid-vegetative growth (25 mm) for other half of the plots in 2009 and just prior to anthesis (25 mm), post anthesis (38 mm) and during grain filling (25, 38, 38 mm with 7 d interval) in 2010. Irrigation was provided with underground well water via micro furrow method with laterals.

Observations and calculations

Crop growth traits

Periodic observations of crop phenologic development, plant height, leaf number (based on ligule formation) and stem diameter were recorded at approximately bi-weekly intervals for two identified plants in each plot. At maturity or end of the season, plant height was determined as the distance between soil and flag leaf ligule; average internode length was calculated by dividing plant height by total leaf number.

In 2009, biomass was measured by destructive harvest at boot [60 days after planting (DAP)] and post anthesis (82 DAP; as indicated by genotypes with normal flowering period); biomass at mid vegetative growth (35 DAP) was determined by an allometric method; this method calculated biomass from observed values of plant height and average stem diameter of 2010 crop season and a calibrated relationship between above-ground biomass and stem volume (Table A.1). Separate equations were derived for each genotype for estimating biomass by allometric method. Since information needed to calibrate allometric relationship between above ground dry matter and stem volume was absent for the genotype PI 584085, data collected on other genotypes were pooled to derive an equation to calculate biomass for genotype PI 584085. In 2010, biomass harvest followed the method of Lindquist et al. (2005); e.g., five consecutive plants were periodically harvested approximately bi-weekly from each plot between 35 and 105 DAP. Each harvested row was ensured to be bordered by other rows to avoid edge effect. At sampling, height and diameter of each plant were recorded and plants were cut at the soil surface. At grain maturity, panicles and stems were harvested separately from each plot with a harvest length of at least one meter. Harvested plants were dried to constant weight at 60°C in oven at least for 14 d and then the dry weight was determined.

For the estimation of WUE and RUE, biomass was modeled as a second order linear function of DAP in 2009 and as a third order linear function of DAP in 2010 for all genotypes. The fitted coefficients and associated standard error for each genotype are presented in Table 2.1 a.

Leaf area index, canopy radiation interception, and crop water use measurements

Leaf area index was measured by a plant canopy analyzer (LAI-2000, LI-COR, Lincoln, Nebraska, USA) approximately bi-weekly, beginning from 35 DAP in 2009 and approximately weekly, beginning from 40 DAP in 2010. The instrument sensor was shaded when measurements were taken and all measurements were completed before 10:00 am to ensure low sun angles and to meet the manufacturer's specifications of diffuse radiance (avoiding exposure to direct radiance) measurement conditions. Light transmittance (five ranges of view angles) was sampled at three locations within each plot; measure at each location consisted of a single reading of incident diffuse irradiance above the canopy and four readings of diffuse irradiance below the crop canopy (parallel, perpendicular and both diagonals relative to crop row), taken within two minutes to avoid atmospheric variation. Below canopy readings were taken with the sensor within 5 cm of the soil surface.

Canopy light transmittance was measured using a line quantum sensor (LI-191SA, LI-COR, Lincoln, Nebraska, USA) on 36, 49 and 60 DAP in 2009 and on 47, 60 and 69 DAP in 2010. Transmittance was determined by the ratio of quantum flux incident above the canopy to quantum flux transmitted below the canopy, at the soil surface. Five measurements were taken within each plot, one with the sensor placed above the canopies and four with the sensor centered between the rows. The fraction of direct incident radiation transmitted by the canopy (τ) was calculated for each reading as the ratio of below canopy reading to above canopy reading and the mean was taken as the estimate for the plot. In both years, measurements of radiation transmittance were made on days with clear sky within one hour of solar noon. Previous studies have shown that radiation measured near solar noon can be good representative of integrated daily radiation (Tollenaar and Bruulsema, 1988; Earl and Davis, 2003). For the estimation of IPAR, a canopy extinction coefficient (k) was calculated by Beer-Lambert equation ($k =$

$-\ln(\tau)/\text{LAI}$). LAI values used to calculate k were obtained from the LAI measurements done on the same day of τ measurements.

Weather data were obtained from the Cooperative Observer Site (Colby 1SW, located within 500 m from the field), associated with the National Weather Service (NWS). Photosynthetically active radiation (PAR, 400–700 nm; MJ m^{-2}) was calculated from daily shortwave radiation (SR); assuming PAR comprised 47% of SR (Howell et al., 1983). For the estimation of intercepted PAR, LAI was modeled as a quadratic function of DAP in both years (Fitted coefficients and associated standard error for each genotype are presented in Table 2.1 b.). The modeled LAI values together with daily solar radiation data were used to estimate daily IPAR using Equation 1 (Campbell and Norman, 1998).

$$\text{IPAR} = 0.47 \times \text{SR} [1 - \exp(-k \times \text{LAI})] \quad (1)$$

Cumulative intercepted radiation (CIPAR) was calculated from daily values of IPAR from emergence through 82 DAP in 2009 and through 105 DAP in 2010. RUE for each genotype was determined as the slope of above-ground biomass (measured sequentially) regressed against corresponding CIPAR values (Lindquist et al., 2005).

Soil water content was measured at approximately bi-weekly intervals during 32–82 DAP in 2009 and 45–103 DAP in 2010 using neutron thermalization (503DR Hydroprobe, CPN Corp., Martinez, CA). Soil was excavated by hydraulic-driven tube (38 mm diameter) in each plot to a depth of 3.5 m, into which a vertical aluminum tube (38 mm diameter and 3.65 m length) was inserted, providing access to the soil profile. Volumetric water content at 0.30 m depth intervals was determined by the neutron attenuation method, from 0.30 m below the soil surface to 3.0 m depth; the total stored soil water (SSW), to a depth of 3.0 m, was calculated as the sum of the product of individual volumetric water content values at 0.30 m intervals and the depth interval, a procedure that assumes uniform water content within 0.30 m increments. Access tubes were installed in a row that was bordered by other rows from both sides and where crop stand was considered adequate to represent root water uptake. Wheat (*Triticum aestivum* L.) straw was applied on the soil (5 cm depth) in rows with access tubes in 2009 to suppress soil evaporation. Application of wheat straw was not done in 2010. Soil water depletion for a given plot between two sampling dates was calculated as the difference

between SSW between the sampling dates. Crop water use at approximately bi-weekly intervals was determined by the soil water balance method; e.g., the sum of soil water depletion, irrigation, and precipitation during the time interval. Cumulative water use was calculated as the sum of bi-weekly crop water use in successive time intervals between 32–82 DAP in 2009 and 45–103 DAP in 2010. These calculations implicitly include drainage, runoff and evaporative losses of water; evaporation was negligible in 2009 due to the application of wheat straw. For the estimation of WUE, cumulative water use was modeled as a quadratic function of DAP (Fitted coefficients and associated standard error for each genotype are presented in Table 2.1 c.). Water use efficiency (biomass-based, WUE_b) was estimated for the duration of the measured crop water use interval, as the slope of the regression of increment in above-ground biomass (relative to initial value, 35 DAP in 2009 and 45 DAP in 2010) on cumulative water use, calculated from the quadratic function of DAP for corresponding dates. In both years, the beginning of seasonal WUE estimation was near canopy closure.

Statistical analysis

Plots were arranged in RCBD with five replications in 2009 and IBD with five blocks in 2010. Analysis of variance on genotypes utilized MIXED procedure in SAS (Statistical Analysis System, version 9.1.3, SAS institute, Cary, North Carolina, USA) for growth, water use and radiation interception variables. Mean separation was done using LSD tests at 0.05 probability level in macro PDMIX 800, SAS (Saxton, 1998). Genotypes were treated as fixed effect variables. Replications or blocks were treated as random variable. Irrigation was considered as whole plot treatment and genotype was considered as split plot treatment in 2009, but since no significant difference was noticed between two irrigation treatments in 2009, data were pooled over irrigation treatments. Genotype and replication (or block) were treated as class variables. Extinction coefficient was estimated and compared among different genotypes using MIXED procedure in SAS, with genotype as class variable and LAI as covariate. Water use efficiency for each genotype in 2009 and 2010 were estimated by regressing cumulative biomass on cumulative water use using PROC REG in SAS; WUE among genotypes was compared by testing the heterogeneity of slopes among genotypes using analysis of covariance in

PROC MIXED with genotype as class variable and cumulative water use as covariate. Similarly, RUE for each genotype in 2009 and 2010 were estimated by regressing cumulative biomass on cumulative IPAR using PROC REG in SAS; RUE among genotypes was compared by testing the heterogeneity of slopes among genotypes using analysis of covariance in PROC MIXED with genotype as class variable and cumulative IPAR as covariate. To determine the relative contribution of the amount of water use and biomass production to WUE and relationship between internode length and RUE, correlation analysis (PROC CORR, SAS) was performed between WUE and water use, WUE and dry matter increment and internode length and RUE. Heterogeneity of slopes between WUE and RUE of 2009 and 2010 was tested using a pooled t-test at 0.05 probability level.

Results

Environmental conditions

The maximum and minimum temperatures (max/min) during the sampling period varied between 18.9/12.2°C to 37.8/20.0°C in 2009 and 19.4/3.3°C to 40.0/21.7°C in 2010 (Figure 2.1). Precipitation was not typical for the region during both cropping seasons since unusually large amount of rainfall (194 mm in 2009 within 82 DAP and 241 mm in 2010 within 105 DAP) was recorded in both years (Figure 2.2). The increased amount of rainfall prevented the two irrigation treatments (well watered and limited irrigation) from being differentiated in 2009 and data were pooled over irrigation treatments for comparison. In 2010, all plots were maintained as well watered through out the growing season. Crops got longer growing season in 2010 compared to 2009 due to earlier planting in 2010. The delayed planting of 2009 confounded the study because of warmer growing conditions and a killing frost (at 99 DAP) prior to grain maturation. No pest or pathogen problems were observed in both years during the entire cropping season. Due to erroneous planting in 2010, replicate plots were staggered and the experimental design had to be changed from RCBD to IBD.

Phenological development

Emergence was noted at 8 DAP in both years. Plant stand was poor in both years (approximately 60%). Genotype PI 584085 was removed from the 2010 study since it had less than 20% crop stand. All short statured genotypes except TX 399 flowered around 50 DAP in both years. TX 399 and tall genotype IS 27150 flowered around 60 DAP in both years. The photoperiod sensitive genotype IS 27111 flowered around 85 DAP in both years. Due to the killing frost, plants did not survive to grain maturity in 2009. This prevented the above-ground biomass sampling for all genotypes at grain maturity in 2009.

Growth characteristics

Plant height was greater for the late flowering genotype IS 27150 and the photoperiod sensitive genotype IS 27111 relative to all others in 2009 and 2010 (Table 2.2). Plant height and internode length of photoperiod sensitive IS 27111 were nearly half in 2009 compared to that of 2010 (Table 2.2). This is because IS 27111 was sampled for plant height and internode length in 2009 at the same day when other genotypes were sampled at their flag leaf stage (70 DAP), but IS 27111 was not at flag leaf stage at this time. Differences among genotypes in case of internode length became noticeable around 45 DAP (Figure 2.3.e&f). Genotypes started differing in above-ground biomass also around 45 DAP (Figure 2.3.a&b). The tall genotypes IS 27150 and IS 27111 also had longest internodes and the short statured genotype TX 399 had the shortest internodes among all genotypes (Table 2.2). Generally genotypes with greater internode length produced biomass at a greater rate than other genotypes with smaller internodes (Figure 2.3).

The trend in biomass production among sorghum genotypes in 2009 and 2010 cropping seasons is shown in Figure 2.3.a&b. In both years, sorghum genotypes started differing in biomass from the second sampling date (60 DAP in 2009 and 48 DAP in 2010) onwards. After that point, generally, the tall genotypes IS 27150 and IS 27111 had greater biomass production compared to their shorter counterparts during the entire cropping season in both years (Figure 2.3.a&b). In 2009, genotypes increased biomass in a quadratic fashion over time during the sampling period (Figure 2.3.a). In 2010,

genotypes exhibited a cubic fashion for biomass with respect to DAP (Figure 2.3.b). End of the season biomass values for all genotypes in both years are given in Table 2.2. The tall genotypes IS 27150 and IS 27111 had greater biomass production compared to all other genotypes at the final sampling in 2009 (82 DAP) and 2010 (105 DAP); though the increased biomass values of IS 27150 did not differ statistically from that of short statured genotypes in 2010 (Table 2.2). In 2010, there was one additional biomass sampling at grain maturity (146 DAP for genotypes TX 2862 and IS 27111 and 136 DAP for all other genotypes), in which the results were consistent with the above mentioned trends in biomass production (Figure 2.3.b).

Tall genotypes (IS 27150 and IS 27111) did not differ each other in case of harvest index (HI), observed in 2010 (data not shown). Similarly, the shorter genotypes (TX 7000, TX 399, TX 2862, Liang Tang Ai and TX 7078) also did not differ among themselves for HI. Therefore, data were pooled to get a single value for HI for tall genotypes and short genotypes. HI of short genotypes (0.39) was greater than the HI of tall genotypes (0.17).

Leaf area index, cumulative IPAR and crop water use

The trend in LAI among sorghum genotypes in 2009 and 2010 is shown in Figure 2.3.c&d. In both years, genotypes differed in LAI in all measurement dates (except for the first measurement on 40 DAP in 2010). All genotypes reached maximum LAI at 80 DAP in 2010. In 2009, Liang Tang Ai, TX 7078 and IS 27150 reached maximum LAI at 60 DAP, whereas remaining five genotypes continued to increase LAI after that date also; but it was not possible to determine when these genotypes reached maximum LAI since there was no LAI measurement in 2009 beyond 80 DAP. In both years, LAI for the tall genotypes IS 27150 and IS 27111 was greater compared to others during the initial days of growth and then it slowed down (Figure 2.3.c&d). After reaching the maximum LAI, tall genotypes started to reduce LAI at a drastic rate; LAI reduced around 60% within 30 d of maximum LAI.

In both years no differences were detected, among genotypes in transmittance of above-canopy incident radiation to ground level (Table 2.3). Therefore, a common extinction coefficient (k) was derived for all genotypes for a period from emergence to 82

DAP in 2009 and 103 DAP in 2010 (Figure 2.4). The value of k (\pm SE) was greater in 2009 (0.93 ± 0.018) relative to that of 2010 (0.62 ± 0.021).

Genotypes differed in cumulative interception of PAR in both years (Table 2.2). The tall genotype IS 27150 had the greatest amount of cumulative interception among all genotypes in 2009 (82 DAP) and 2010 (105 DAP). Cumulative evapotranspiration also increased with cumulative interception of PAR (Figure 2.5). Genotypes differed in water use in 2009 and 2010. But they did not follow a specific trend for ranking in water use (Table 2.2).

Water use efficiency and radiation use efficiency

Genotypes differed in WUE (Figure 2.6.a&b) and RUE (Figure 2.6.c&d) in 2009 and 2010 (Table 2.4). The relative ranking of WUE and RUE among genotypes was similar in 2009 and 2010. Tall genotypes IS 27150 and IS 27111 generally had greater WUE and RUE compared to the shorter genotypes in both years. WUE increased in proportion to biomass accumulation; WUE was more strongly correlated with increment in biomass (Pearson correlation coefficient, $r = 0.99$ in 2009 and 0.79 in 2010) than with water use ($r = 0.80$ in 2009 and -0.46 in 2010; Table 2.5) in both years. WUE and water use had a negative relationship in 2010 (negative slope between WUE and water use, Table 2.5).

RUE also increased in proportion to biomass accumulation; RUE had greater correlation with biomass ($r = 0.86$ in 2009 and 0.97 in 2010) than with CIPAR ($r = 0.37$ in 2009 and 0.68 in 2010; Table 2.5). RUE and WUE had a positive linear relationship (Figure 2.7). RUE increased with internode length ($r = 0.60$ in 2009 and 0.82 in 2010; Figure 2.8).

The tall genotype IS 27111 had greatest biomass production and was among greatest water use of all genotypes in both years. Among the remaining genotypes, field data do not support a relationship between above-ground biomass production and water use. In contrast, those genotypes with greater biomass also had increased radiation interception, WUE and RUE. For example, the tall genotype IS 27150 had similar water use in 2009 and less water use in 2010 compared to the genotype Liang Tang Ai, but IS 27150 had greater biomass production in 2009 and numerically greater biomass

production in 2010 than Liang Tang Ai; IS 27150 also had greater intercepted radiation and WUE than Liang Tang Ai in 2009 and 2010 and greater RUE in 2010 and numerically greater RUE in 2009 compared to Liang Tang Ai (Table 2.2 and 2.4). Comparison between TX 7000 and TX 7078 also showed the above trend (Table 2.2 and 2.4).

Some other genotypes produced greater biomass compared to their counterparts with similar water use or radiation interception or both. But these genotypes also showed increased RUE compared to the other genotypes with similar water use and radiation interception. For example, PI 584085 had the same amount of water use and intercepted radiation, but greater biomass than TX 7078 in 2009; RUE for PI 584085 was greater than that of TX 7078 (Table 2.2 and 2.4). Comparison between IS 27111 and TX 7000 also showed the same results (Table 2.2 and 2.4).

Discussion

Smaller biomass values for sorghum genotypes in 2009 compared to 2010, reported in Table 2.2 may be mainly because crops were harvested 20 calendar d earlier in 2009 compared to 2010. Final harvest was done in 2009 just after heading. Therefore, the crops lost the period of peak growth in 2009 while crops were maintained up to maturity in 2010. Also, crops were planted with 15 d delay from the end of optimum planting season for this region as per the recommendations of grain sorghum production handbook, Kansas State University. This delayed planting also reduced crop growth and robustness of sorghum genotypes in 2009 compared to 2010. The lower HI of tall genotypes (IS 27150 and IS 27111) compared to their short statured counterparts was expected since the tall genotypes were not selected based on the increased HI. The smaller LAI observed in 2009 compared to that of 2010 may be due to considerably later planting, which altered the temperature environment during leaf development (Rawson and Hindmarsh, 1982; Arkebauer and Norman, 1995). The smaller LAI in 2009 also led to lower interception of radiation compared to 2010. The smaller biomass in 2009 may result from reduced PAR absorption, which was primarily due to the lower LAI in that year which seemed as insufficient to reach the maximum radiation interception. The larger estimates of k in 2009 than that of 2010 may be due to the increased amount of

dead leaves altering leaf angles and interception of radiation since the delayed planting and drier growing environment compared to 2010 might have hastened the onset of leaf senescence in crops.

Application of wheat straw in 2009 that prevented evaporation of water from soil profile explains the lower water use values in 2009 compared to 2010 as shown in Table 2.2. Since wheat straw was not applied in 2010, the evaporative component of water loss from soil increased the estimates of water use in 2010; but it did not reduce WUE of sorghum genotypes in 2010 compared to that of 2009 since their biomass production was much larger in 2010 compared to 2009. Drainage and run off components of soil water loss were assumed to be minimal in the water use estimations.

WUE values reported here are within the range of those commonly reported for sorghum in literature that ranged between 2.8 to 12.6 g kg⁻¹ (Briggs and Shantz, 1913; Hammer et al., 1997; Henderson et al., 1998; Mortlock and Hammer, 1999). WUE values of 2009 were consistently lower than that of 2010. This is attributed to delayed planting (due to wet spring conditions) that resulted in diminished growth due to sub-optimal growing conditions (hot summer condition during canopy formation and cool conditions late in the season) as well as final harvest just after heading, when sorghum biomass production is strong. In comparison, the 2010 crop was able to grow through maturity for these measurements. To provide a comparison with the previously reported results in literature, a few genotypes (TX 399, PI 584085, Liang Tang Ai and TX 7078) were included in this study those were already tested for TE (pot) by Xin et al. (2009). These genotypes that differed for TE in controlled conditions (Xin et al., 2009) also differed for WUE in field conditions. The relative ranking of water productivity among these genotypes in the present study was similar to the relative TE ranking by Xin et al. (2009) except for the genotype Liang Tang Ai. In 2009, PI 584085, IS 27150 and IS 27111 showed a slightly non-linear relationship when biomass regressed on cumulative water use due to the increased amount of late season biomass, relative to the linear relation (Figure 2.6.a); changes in biomass composition can cause non linear WUE (Steduto and Albrizio, 2005).

RUE values reported here are within the range of published values of seasonal RUE for sorghum that vary from 2.3 to 4.0 g MJ⁻¹ absorbed PAR (Howel and Musick,

1985; Rosenthal et al., 1989; Kiniry et al., 1989; Muchow 1989; Rosenthal et al., 1993). The slightly larger values of RUE in 2009 compared to 2010 can be attributed to the greater estimate of k in 2009 (0.93) than that of 2010 (0.62). In both years RUE varied among genotypes. Previous literature supports the fact that RUE varies among cultivars (Foale et al., 1984; Rosenthal and Gerik, 1991). The relative ranking of RUE among genotypes was similar in both years. The increased biomass production, CIPAR and RUE of the tall genotype IS 27150 could imply that RUE and biomass production can be increased with increased incident or intercepted radiation and this is in contrast to the report of negative response of canopy photosynthesis and RUE to incident PAR by Rochette et al. (1996). Genotype IS 27111 tended to have non-linear RUE in 2010, due to the effect of large biomass production towards the end of the season. Steduto and Albrizio (2005) reported that such trends of loss of linearity of RUE due to the possible effects of increased biomass composition are possible. Figures 2.6.c&d report RUE from emergence through near grain maturity; here RUE did not decline during grain fill. This result is in accordance with the reports of Lindquist et al. (2005) who attributed this response to the optimized crop growth rate ($\text{g m}^{-2} \text{d}^{-1}$) when assimilate supply is likely maintained nearly equal to the demand, under optimal growth conditions.

Genotypes with similar water use but different biomass production proved that the superior biomass production exhibited by the promising genotypes was not due to increased water use. Instead the increased biomass production exhibited by these promising genotypes (IS 27150, IS 27111, PI 584085 and TX 7000) was in response to increased WUE, radiation interception or RUE or a combination of these traits. The stronger correlation of WUE to biomass than to water use implies that the increased WUE exhibited by certain genotypes was due to increased biomass production rather than reduced water use. This result is in accordance with previous literature (Xin et al., 2009). In the present study, genotype IS 27111 had greater WUE than TX 7000 even with greater water use than TX 7000. These imply that a substantial improvement in WUE is possible through the improvement in other traits leading to increased biomass production. This contradicts Tanner and Sinclair's (1983) inference that TE for total biomass is relatively constant within a species. Up to this point of time, the primary mechanism accounting for increased TE involved lower CO_2 partial pressures in the sub-stomatal

cavity, with a concomitant decrease in the transpiration ratio (Farquahar et al., 1982; von Caemmerer and Furbank, 1999; Xin et al., 2009). However, the results from this study support an expanded scope of inquiry regarding water productivity: processes that increase plant utilization of radiation can also increase water productivity.

There was a positive linear relationship of WUE and RUE of sorghum genotypes observed in this study (Figure 2.7). In addition, interception of radiation was directly related to water use (Figure 2.5); this result is expected from the primary role of absorbed radiation in evaporation potential (Penman, 1948). The difference in the intercepts in 2009 and 2010 when cumulative water use regressed over cumulative IPAR (Figure 2.5) arises due to the difference in the planting date and starting date of crop water use estimation in 2009 and 2010. Crop water use estimation began at 32 DAP in 2009 and 105 DAP in 2010.

WUE of a crop can be expressed as, $WUE = \text{biomass}/\text{water use}$ (2)

RUE can be expressed as, $RUE = \text{biomass}/\text{IPAR}$ (3)

From Figure 2.5, it is evident that crop water use (WU) can be expressed as,

$WU = m \times \text{IPAR}$, where m is a constant (4)

In that case, the term water use in Equation (2) can be replaced by IPAR and then Equation 2 becomes as, $WUE = \text{biomass}/(m \times \text{IPAR})$ (5)

That means equations for WUE and RUE are similar or interchangeable. This demonstrates that increased radiation use provides an additional method for increasing water productivity.

Dercas and Liakatas (2007) reported a negative relationship between WUE and RUE in sweet sorghum. But in that study, high WUE values were associated with water stress condition that was sufficient to reduce foliage expansion, leading to inefficient use of radiation. But in the present study, there was no water stress that adversely affects the expansion of developing foliage of the crops during any of the growing seasons, thus increased WUE values were associated with increased RUE values.

Our current study also showed that tall genotypes with increased internode length were superior in biomass production and had greater water and light use efficiencies compared to the shorter genotypes. One of these tall genotypes was a photoperiod sensitive one (IS 27111). Large WUE values associated with tall genotypes with

increased growth and biomass production do not support the common perception that high TE genotypes (selected through carbon isotope discrimination method) are often slow in growth and poor in biomass production under nonstressed conditions (Condon et al., 2002; Impa et al., 2005). Figure 2.8 demonstrates increment in RUE among sorghum genotypes with increase in average internode length. This suggests that plants with open canopies can utilize light energy for dry matter production in a very efficient way. Nobel (1983) articulated the positive relation of total daily PAR with net assimilation rate for obligate sun plants, indicating the significance of increased radiation. Light distribution within the canopy could influence the efficiency with which radiation is utilized. Clegg (1972) reported that sorghum genotypes with erect leaves exhibited a greater growth response to increased plant densities than genotypes with more horizontal leaf angles. He attributed this response to the increased light penetration into canopies with more erect leaves. The current study demonstrated a positive relation between light utilization and internode length; supporting the inference of increased productivity of more open canopies with greater penetration of light into mid-canopy layers. To illustrate, leaves of upper vegetative canopies generally receive full sunlight while mid-canopy leaves tend to be shaded. Light harvesting complex in leaves (e.g. chlorophyll; Connelly et al., 1997) commonly exhibit diminished quantum yields at full sunlight (i.e. $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$), but utilize light more efficiently for growth at intermediate intensities (i.e. $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$, Krall and Edwards, 1991; von Caemmerer and Furbank, 1999). Therefore, canopies with intermediate light intensities in mid-canopy are likely to exhibit greater RUE than canopies with small transmittance of radiation to mid-canopy elements. In this study, canopies with greater internode length transmitted more light to mid-canopy layers than more compact canopies (data not shown). The distribution of radiation among upper- and mid-canopy elements is likely to alter the efficiency of radiation use in biomass production. As an application, canopy characteristics that can increase light utilization can be used to identify and develop crop varieties that also increase water productivity.

Muchow (2003) has reported a positive correlation between increased biomass production and grain yield in sorghum over a wide range of yield estimates. He also observed that differences in biomass production accounted for 95% of variation in grain yield in his study on sorghum. Thus a follow up of present study would be converting the

increased biomass production achieved through efficient use of light energy to increased grain yield with an improvement in HI.

Conclusion

Sorghum genotypes differed in water productivity and RUE. WUE was more strongly correlated to biomass production than to water use. RUE generally increased with internode length and plant height, and was positively related to WUE. Increased utilization of radiation can increase water productivity in plants. Sorghum canopies that increase light transmission to mid-canopy layers can increase RUE and also have the potential to increase crop productivity and WUE.

Acknowledgement

This project benefited from the capable technical support of Ralph Wolf, Ray Duffey, Alicia Oien and Rhett Martin. We would like to thank Leigh Murray and Christopher Juarez for statistical consult. This research was supported in part by the Ogallala Aquifer Program, a consortium between USDA–Agricultural Research Service, Kansas State University, Texas AgriLife Research, Texas AgriLife Extension Service, Texas Tech University and West Texas A&M University.

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Figures and Tables

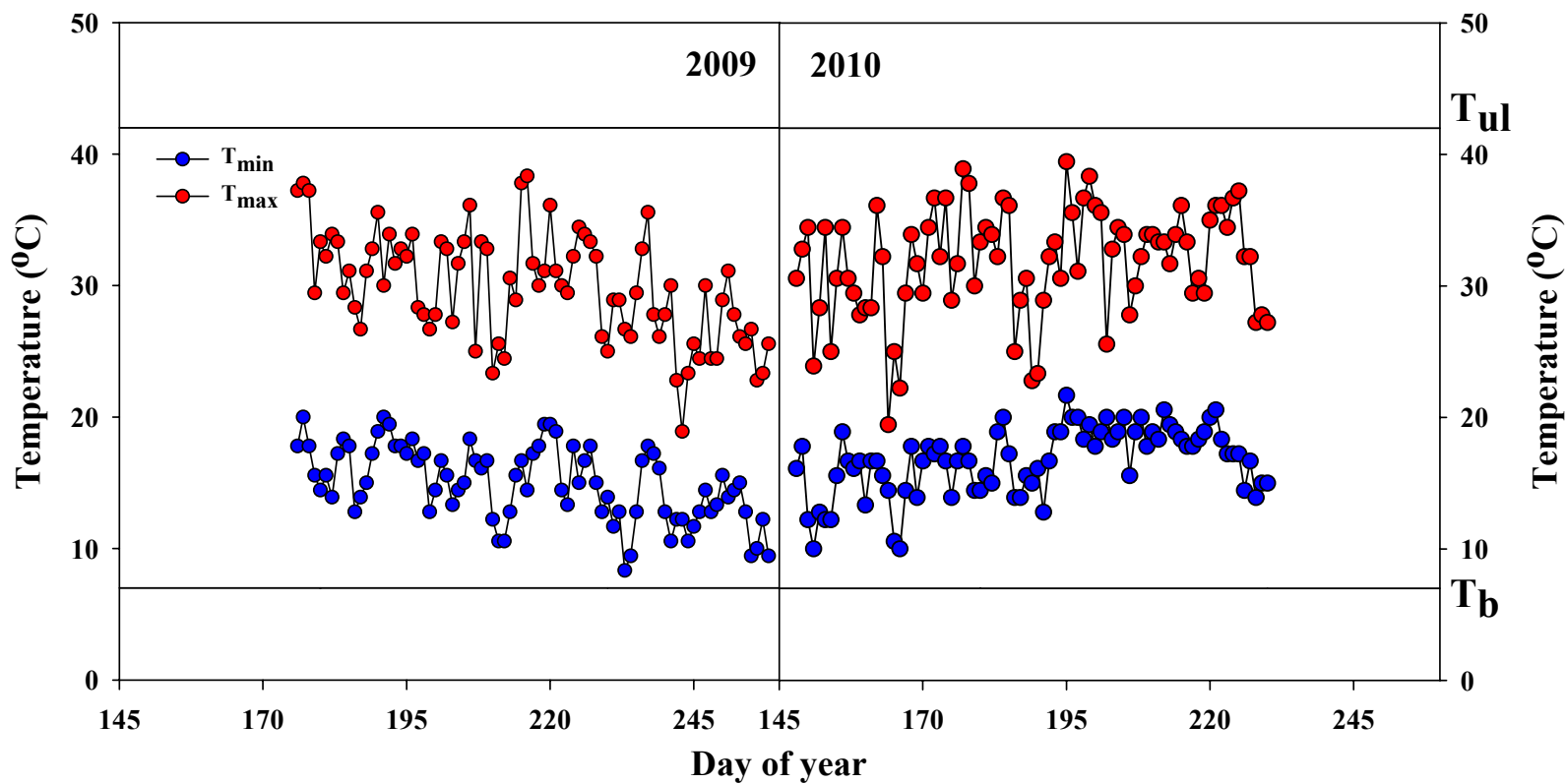


Figure 2.1. Daily minimum (T_{\min}) and maximum (T_{\max}) temperatures from planting through end of the season [82 days after planting (DAP) in 2009 and 136 DAP in 2010] for sorghum genotypes grown at Colby, KS in 2009 (left) and 2010 (right).

Crops were planted 28 calendar days earlier in 2010 compared to 2009.

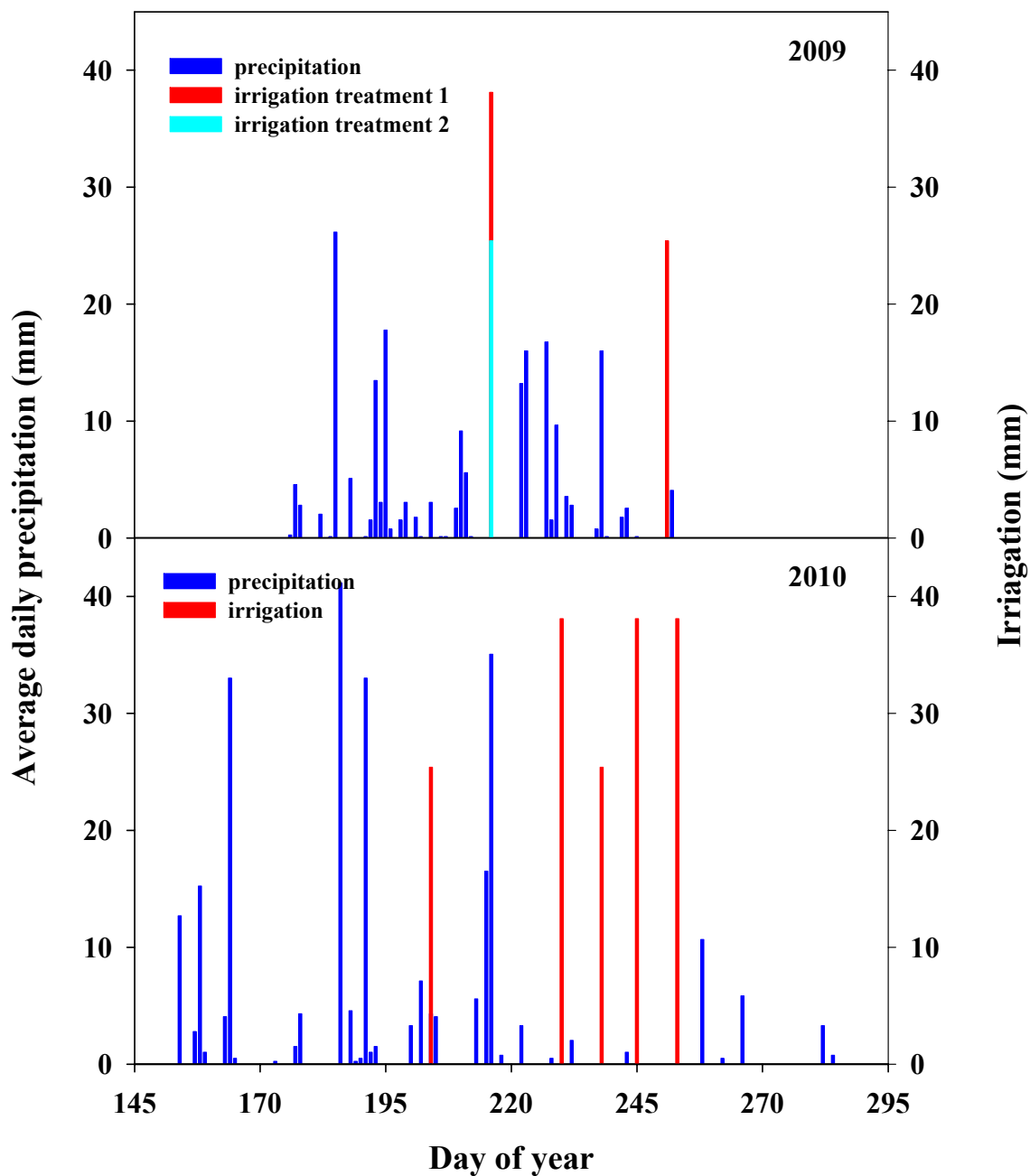


Figure 2.2. Daily precipitation and irrigation from planting through end of the season [82 days after planting (DAP) in 2009 and 136 DAP in 2010] for sorghum genotypes grown at Colby, KS in 2009 (top) and 2010 (bottom).

Crops were planted 28 calendar days earlier in 2010 compared to 2009. There were two irrigation treatments, treatment 1– full irrigation and treatment 2– limited irrigation, in 2009.

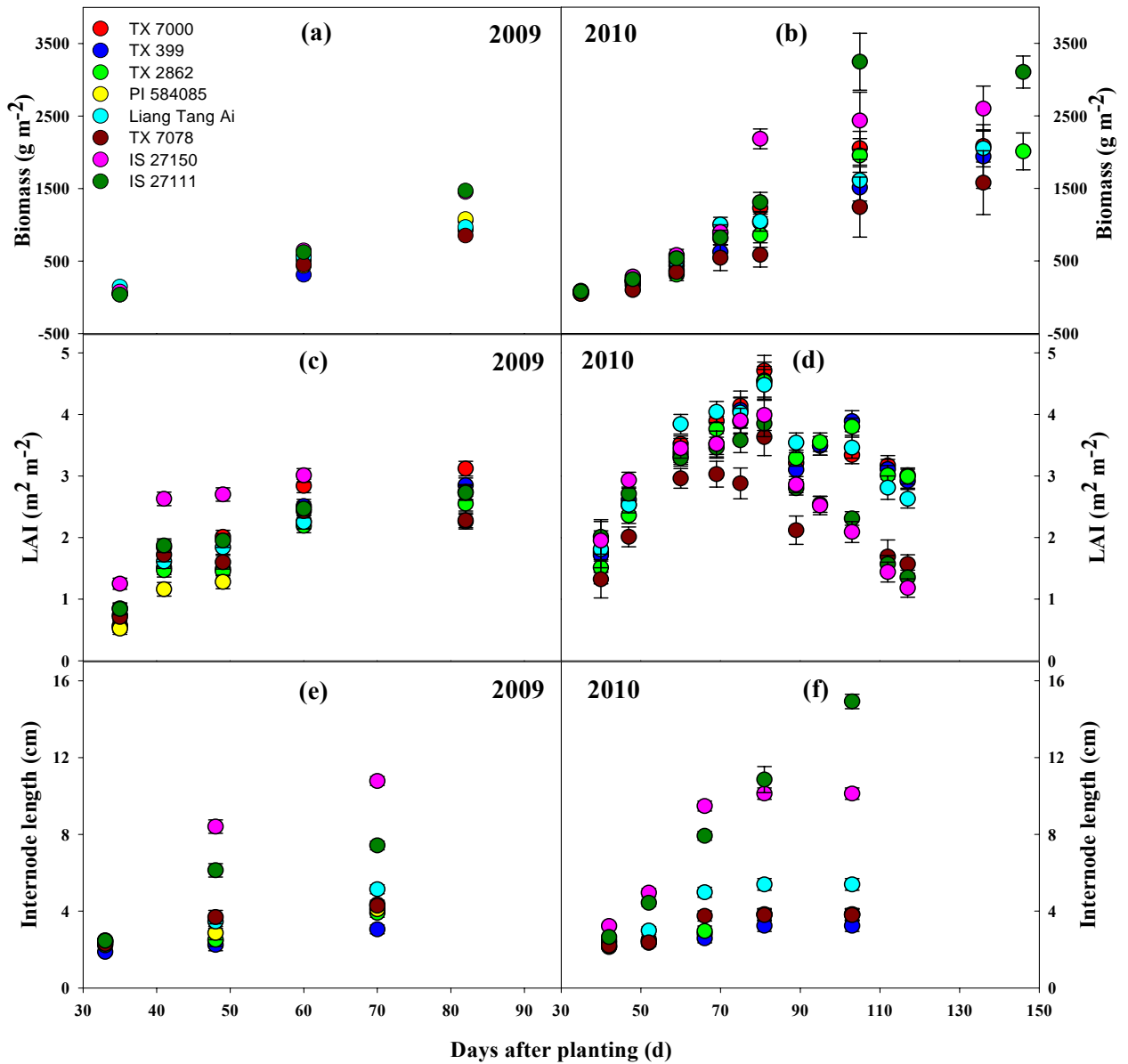


Figure 2.3. Observed [symbols (LSMEANS) and standard error bars] total above ground biomass (a&b), leaf area index (LAI; c&d) and elongation of internodes (e&f) among sorghum genotypes at Colby, KS, in 2009 and 2010.

In 2010, there was an additional biomass sampling at grain maturity on 136 days after planting (DAP; on 146 DAP for the genotypes TX 2862 and IS 27111) after the biomass sampling reported in Table 1.

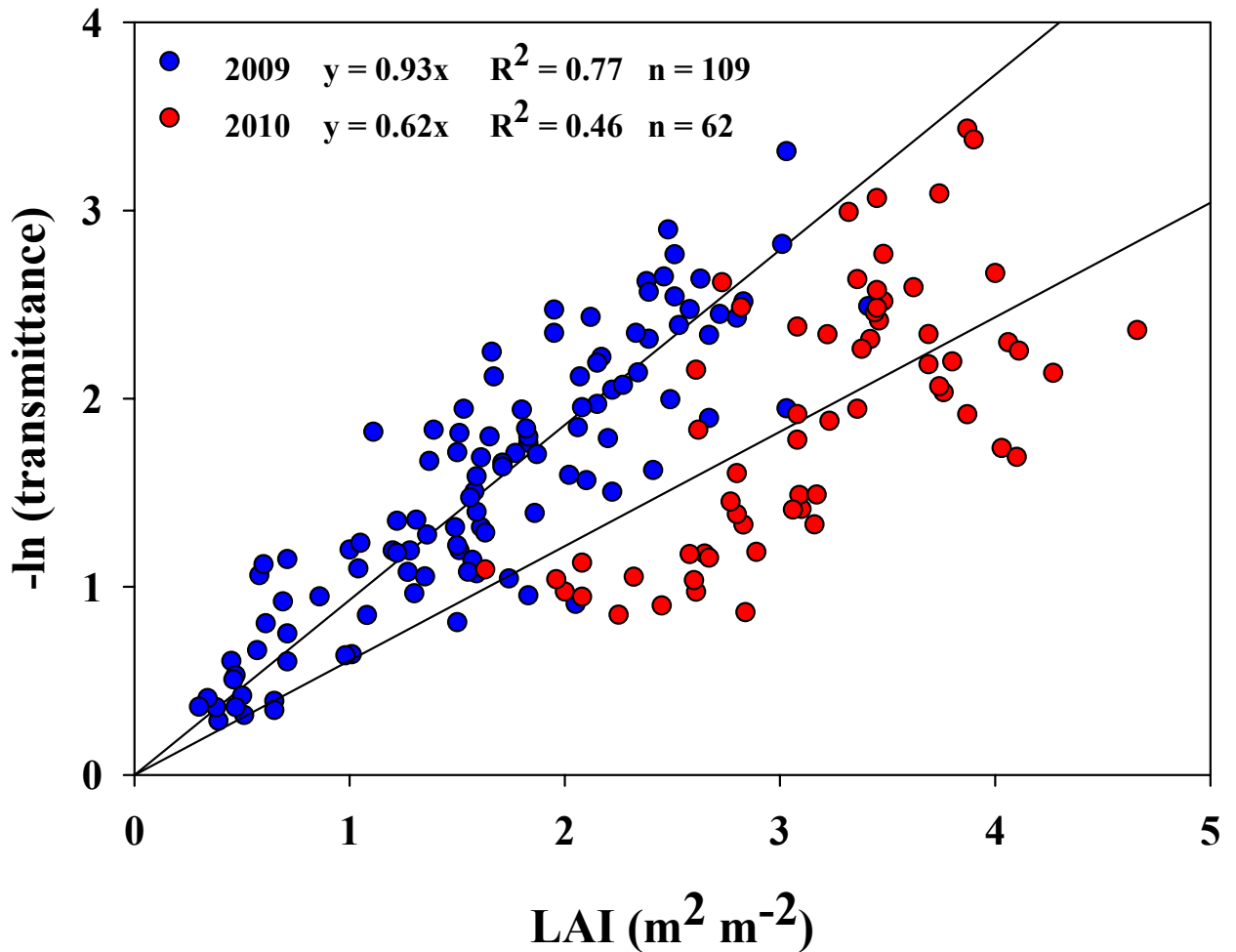


Figure 2.4. Relation between the negative logarithm of the canopy transmittance of radiation and the leaf area index (LAI) in sorghum.

Extinction coefficient (k) was derived as the slope of the regression of natural logarithm of canopy transmittance on LAI ($k = 0.93$ in 2009 and 0.62 in 2010) with suppressed intercept since intercept did not differ from zero. Slopes did not differ among genotypes. So a common k was fit for all sorghum genotypes. Measurement of transmittance and LAI reported in this graph were done on 36, 49 and 60 DAP in 2009 and on 47, 60 and 69 DAP in 2010.

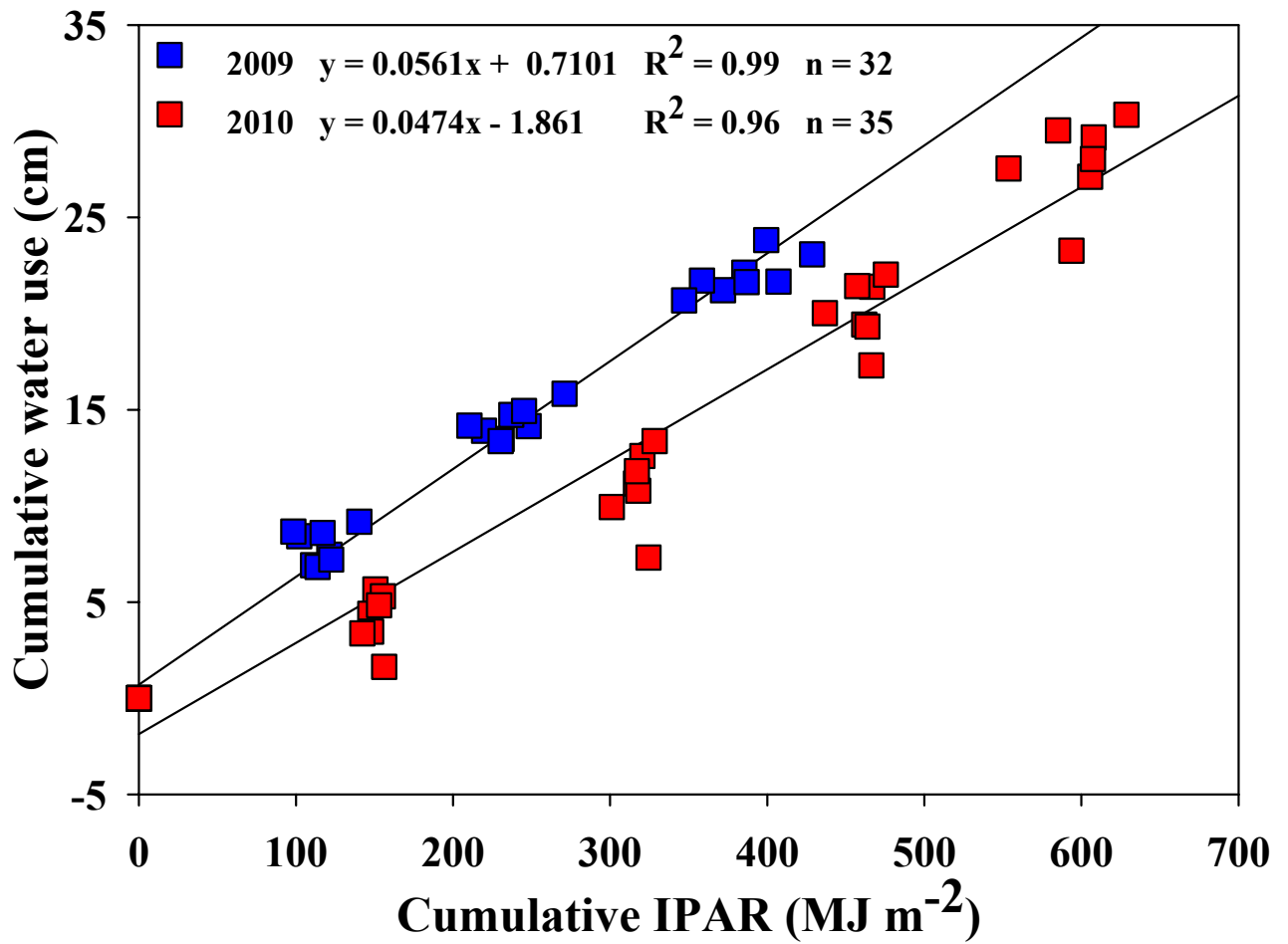


Figure 2.5. Relationship between cumulative intercepted photosynthetically active radiation (IPAR) and cumulative water use in sorghum.

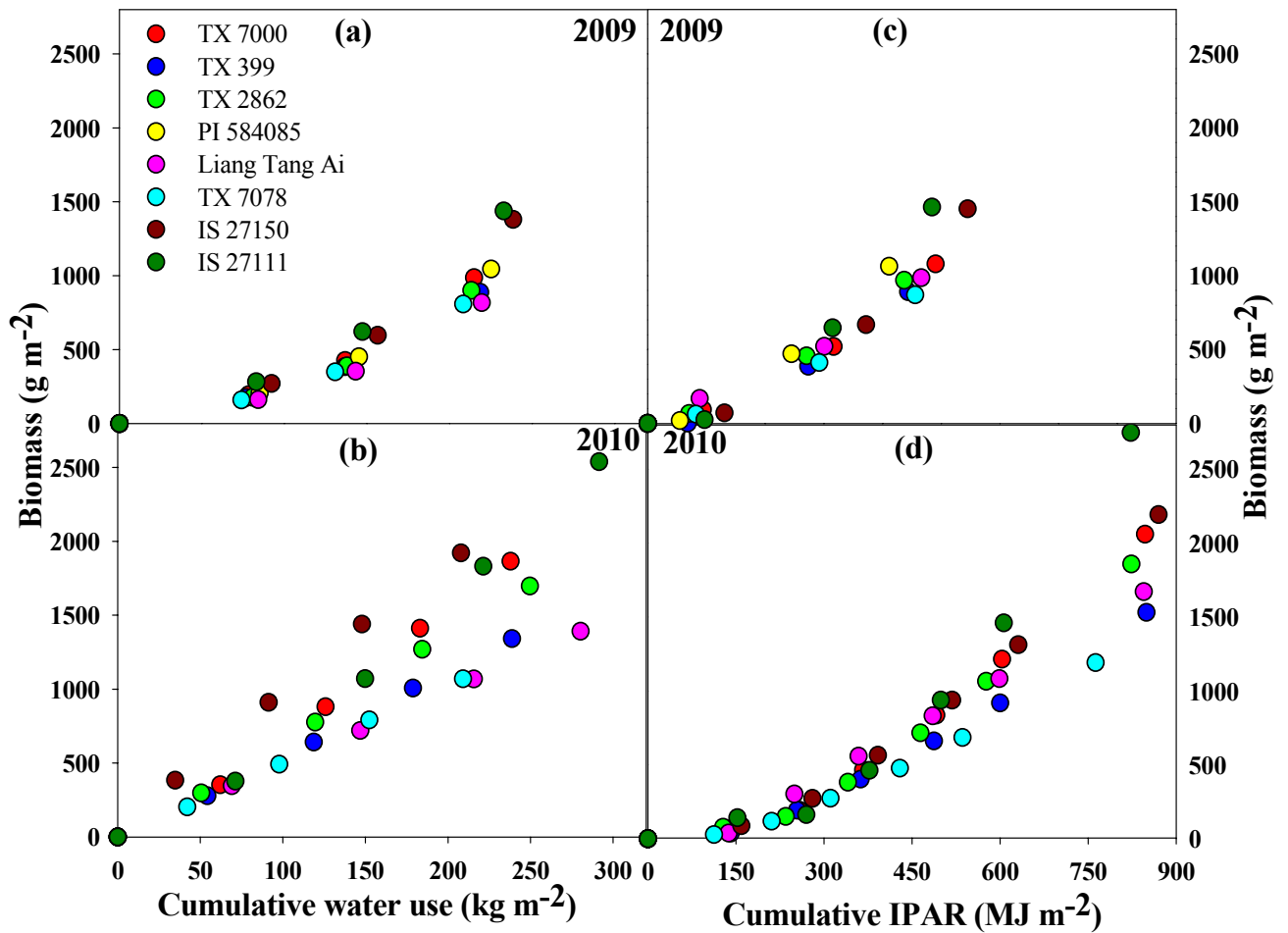


Figure 2.6. Derivation of water use efficiency (WUE; a&b) and radiation use efficiency (RUE; c&d) among sorghum genotypes.

WUE was derived as the slope of the regression of biomass on cumulative water use with a suppressed intercept (since intercept did not differ from zero). RUE was derived as the slope of the regression of biomass on cumulative intercepted photosynthetically active radiation (IPAR) with a suppressed intercept.

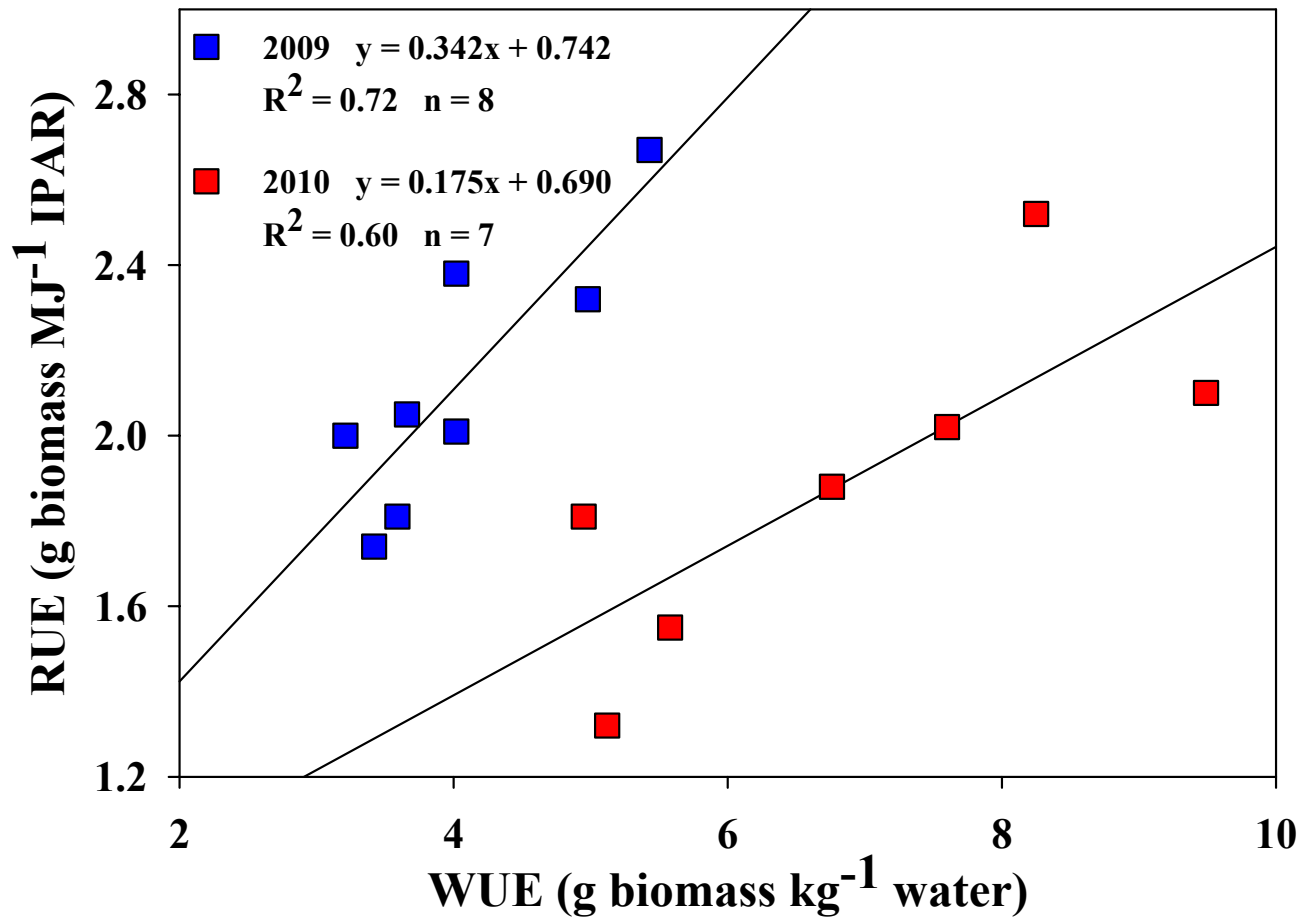


Figure 2.7. Relationship between water use efficiency (WUE) and radiation use efficiency (RUE) for sorghum genotypes differing in canopy architecture. Suppressing the intercept to zero (Since the intercept was not significant for the above relationship in 2009 and 2010 at 0.05 probability level) changed R^2 to 0.99 in 2009 and 0.98 in 2010.

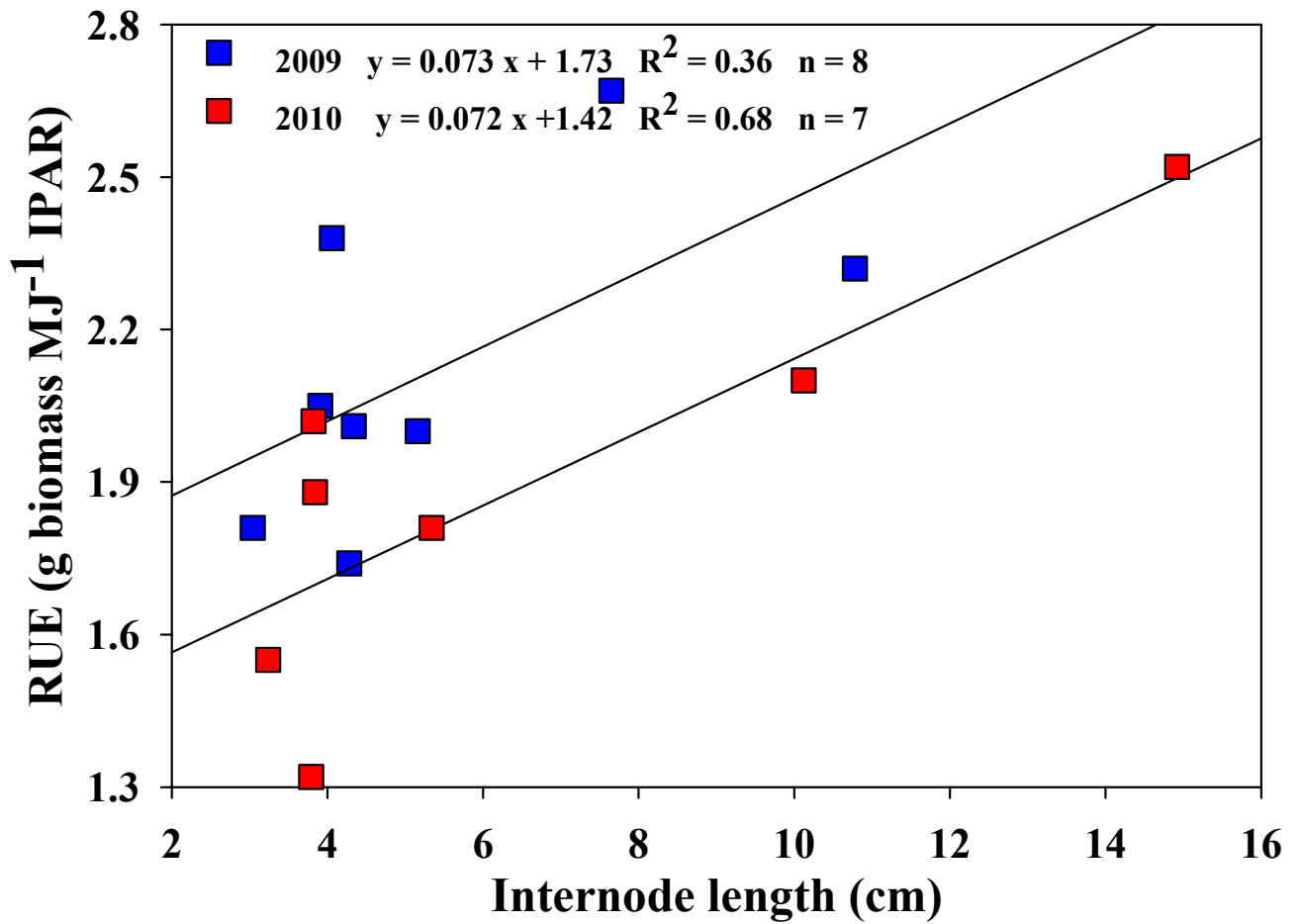


Figure 2.8. Sorghum radiation use efficiency (RUE) in relation to plant height as indicated by average internode length (average distance between stem nodes, corresponding to leaves).

Table 2.1. Estimates of fitted coefficients for the prediction equations of biomass, leaf area index and cumulative water use using days after planting (DAP) as the predictive variable for sorghum genotypes grown at Colby, KS in 2009 and 2010.

a. Estimates of fitted coefficients (\pm standard error) for the prediction equations of biomass using DAP as the predictive variable

| Coefficient | Year | Estimate (\pm standard error) | | | | | | | |
|-------------|------|----------------------------------|--------------------|--------------------|--------------------|--------------------|--------------------|--------------------|--------------------|
| | | TX 7000 | TX 399 | TX 2862 | PI 584085 | Liang Tang Ai | TX 7078 | IS 27150 | IS 27111 |
| a | 2009 | – | – | – | – | – | – | – | – |
| | 2010 | –0.0067 (0.002) | –0.0030 (0.002) | –0.0065 (0.002) | – | –0.0015 (0.002) | –0.0028 (0.003) | –0.0051 (0.003) | –0.0096 (0.002) |
| b | 2009 | 0.1792 (0.0161) | 0.1613 (0.0161) | 0.1637 (0.0161) | 0.1898 (0.0161) | 0.4850 (0.0161) | 0.4680 (0.0161) | 0.2500 (0.0161) | 0.2614 (0.0161) |
| | 2010 | 1.594 (0.466) | 0.7306 (0.519) | 1.570 (0.486) | – | 0.3345 (0.513) | 0.6964 (0.674) | 1.2360 (0.629) | 2.430 (0.591) |
| c | 2009 | – | – | – | – | – | – | – | – |
| | 2010 | –88.06 (36.3) | –33.19 (38.9) | –90.86 (37.9) | – | 0.3876 (39.4) | –36.28 (51.2) | –61.75 (45.8) | –150.1 (44.5) |
| d | 2009 | –126.2 (72.61) | –195.4 (72.61) | –133.3 (72.61) | –213.4 (72.61) | –13.49 (72.61) | –18.03 (72.61) | –236.9 (72.61) | –295.1 (72.61) |
| | 2010 | 1488 (865) | 433.8 (889) | 1613 (900) | – | –320.7 (926) | 564.7 (1195) | 953.1 (1012) | 2831 (1022) |

Biomass (BM) was modeled as linear functions of DAP ($BM = b(DAP)^2 + d$ in 2009 and $BM = a(DAP)^3 + b(DAP)^2 + c(DAP) + d$ in 2010)

b. Estimates of fitted coefficients (\pm standard error) for the prediction equations of leaf area index (LAI) using DAP as the predictive variable

| Coefficient | Year | Estimate (\pm standard error) | | | | | | | |
|-------------|------|----------------------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
| | | TX 7000 | TX 399 | TX 2862 | PI 584085 | Liang Tang Ai | TX 7078 | IS 27150 | IS 27111 |
| a | 2009 | -0.0014 (0.0002) | -0.0012 (0.0002) | -0.0010 (0.0002) | -0.0009 (0.0002) | -0.0013 (0.0002) | -0.0015 (0.0002) | -0.0019 (0.0002) | -0.0012 (0.0002) |
| | 2010 | -0.0012 (0.0015) | -0.0011 (0.0015) | -0.0012 (0.0014) | – | -0.0015 (0.0017) | -0.0013 (0.0018) | -0.0014 (0.0016) | -0.0013 (0.0014) |
| b | 2009 | 0.2056 (0.028) | 0.1850 (0.028) | 0.1569 (0.028) | 0.1479 (0.028) | 0.1826 (0.028) | 0.2040 (0.028) | 0.2450 (0.028) | 0.1745 (0.028) |
| | 2010 | 0.1890 (0.024) | 0.1824 (0.023) | 0.1981 (0.022) | – | 0.2341 (0.026) | 0.2002 (0.029) | 0.2060 (0.025) | 0.1810 (0.021) |
| c | 2009 | -4.599 (0.752) | -4.412 (0.752) | -3.648 (0.752) | -3.614 (0.752) | -3.980 (0.752) | -4.560 (0.752) | -4.840 (0.752) | -3.718 (0.752) |
| | 2010 | -3.638 (0.875) | -3.591 (0.853) | -4.310 (0.793) | – | -5.095 (0.953) | -4.496 (1.04) | -3.682 (0.907) | -2.984 (0.784) |

LAI was modeled as linear functions of DAP ($LAI = a(DAP)^2 + b(DAP) + C$) in 2009 and 2010.

c. Estimates of fitted coefficients (\pm standard error) for the prediction equations of cumulative water use (CWU) using DAP as the predictive variable

| Coefficient | Year | Estimate (\pm standard error) | | | | | | | |
|-------------|------|----------------------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
| | | TX 7000 | TX 399 | TX 2862 | PI 584085 | Liang Tang Ai | TX 7078 | IS 27150 | IS 27111 |
| a | 2009 | -0.0018 (0.0003) | -0.0015 (0.0003) | -0.0019 (0.0003) | -0.0019 (0.0003) | -0.0022 (0.0003) | -0.0015 (0.0003) | -0.0025 (0.0003) | -0.0020 (0.0003) |
| | 2010 | -0.0006 (0.001) | -0.00003 (0.001) | 0.0001 (0.001) | – | -0.0010 (0.001) | -0.0006 (0.001) | 0.0009 (0.001) | -0.0004 (0.001) |
| b | 2009 | 0.6458 (0.053) | 0.6229 (0.053) | 0.6466 (0.053) | 0.6699 (0.053) | 0.6938 (0.053) | 0.6006 (0.053) | 0.7657 (0.053) | 0.7121 (0.053) |
| | 2010 | 0.5065 (0.187) | 0.4339 (0.162) | 0.4465 (0.167) | – | 0.6544 (0.167) | 0.2907 (0.167) | 0.2557 (0.167) | 0.5677 (0.162) |
| c | 2009 | -19.02 (1.82) | -18.76 (1.82) | -18.59 (1.82) | -19.28 (1.82) | -19.82 (1.82) | -17.98 (1.82) | -21.77 (1.82) | -21.28 (1.82) |
| | 2010 | -22.02 (7.11) | -20.50 (6.33) | -22.09 (6.73) | – | -28.76 (6.73) | -15.39 (6.73) | -15.10 (6.73) | -26.07 (6.33) |

CWU was modeled as linear functions of DAP ($CWU = a(DAP)^2 + b(DAP) + C$) in 2009 and 2010.

Table 2.2. Least square means (LSMEANS) for growth characteristics, water use and intercepted photosynthetically active radiation (IPAR) of sorghum genotypes differing in canopy architecture and expected water use efficiency grown at Colby, KS in 2009 and 2010.

| Genotypes | Photoperiod sensitivity | Plant height (cm) | | Internode length (cm) | | Biomass (g m ⁻²) | | Crop water use [†] (kg m ⁻²) | | Cumulative IPAR* (MJ m ⁻²) | |
|---------------|-------------------------|-------------------|------------------|-----------------------|-------------------|------------------------------|--------------------|---|-------------------|--|------------------|
| | | 2009 | 2010 | 2009 | 2010 | 2009 | 2010 | 2009 | 2010 | 2009 | 2010 |
| | | | | | | (82 DAP) | (105 DAP) | (32–82 DAP) | (45–103 DAP) | (82 DAP) | (105 DAP) |
| TX 7000 | Normal | 71 ^{cd} | 81 ^{de} | 4.3 ^d | 3.8 ^{de} | 1056 ^b | 2053 ^b | 218 ^c | 249 ^{ab} | 500 ^b | 835 ^b |
| TX 2862 | Normal | 70 ^{cd} | 87 ^{de} | 3.9 ^d | 3.8 ^{de} | 944 ^{bc} | 1953 ^b | 212 ^c | 281 ^{ab} | 436 ^{cd} | 829 ^b |
| PI 584085 | Normal | 74 ^{cd} | – | 4.1 ^d | – | 1079 ^b | – | 226 ^c | – | 422 ^d | – |
| Liang Tang Ai | Normal | 79 ^c | 110 ^c | 5.1 ^c | 5.4 ^c | 968 ^{bc} | 1612 ^b | 232 ^{bc} | 307 ^a | 469 ^{bc} | 829 ^b |
| TX 7078 | Normal | 66 ^{cd} | 74 ^e | 4.3 ^d | 3.8 ^{de} | 852 ^c | 1242 ^b | 223 ^c | 253 ^{ab} | 431 ^d | 723 ^c |
| TX 399 | Late flowering | 57 ^d | 77 ^e | 3.0 ^e | 3.2 ^e | 922 ^{bc} | 1510 ^b | 221 ^c | 254 ^{ab} | 456 ^{cd} | 803 ^b |
| IS 27150 | Late flowering | 179 ^a | 207 ^b | 11.1 ^a | 10.1 ^b | 1452 ^a | 2435 ^{ab} | 247 ^{ab} | 229 ^b | 555 ^a | 876 ^a |
| IS 27111 | PPS | 145 ^b | 319 ^a | 7.4 ^b | 14.9 ^a | 1472 ^a | 3246 ^a | 260 ^a | 285 ^{ab} | 495 ^b | 822 ^b |
| LSD | | 20 | 16 | 0.7 | 0.9 | 202 | 1058 | 20 | 65 | 34 | 36 |

[†]Drainage and run off components of soil water loss were assumed to be minimal in the estimation of crop water use.

*Cumulative IPAR was computed from emergence (8 DAP).

LSMEANS estimates with different letters are significantly different according to LSD test at $P < 0.05$.

Table 2.3. Analysis of covariance for the effect of genotypes and leaf area index (LAI) on transmittance of radiation by crop canopies to ground level in 2009 and 2010.

| Source of variation | df | | F-value for type III tests of fixed effects | |
|---------------------|------|------|---|------------|
| | 2009 | 2010 | 2009 | 2010 |
| Genotype | 7 | 6 | 1.03 | 0.69 |
| LAI | 1 | 1 | 324.64 **** | 37.17 **** |
| Genotype*LAI | 7 | 6 | 0.63 | 0.65 |

* indicates significance at $P < 0.05$

** indicates significance at $P < 0.01$

*** indicates significance at $P < 0.001$

**** indicates significance at $P < 0.0001$

Table 2.4. Water use efficiency (WUE) and radiation use efficiency (RUE) of sorghum genotypes grown at Colby, KS in 2009 and 2010.

| Genotypes | WUE (g kg ⁻¹) | | RUE (g MJ ⁻¹ IPAR) | |
|---------------|------------------------------|-----------|----------------------------------|-----------|
| | 2009 | 2010 | 2009 | 2010 |
| TX 7000 | 4.02±0.46 | 7.60±0.23 | 2.01±0.17 | 2.02±0.20 |
| TX 2862 | 3.66±0.44 | 6.76±0.09 | 2.05±0.16 | 1.88±0.19 |
| PI 584085 | 4.02±0.48 | – | 2.38±0.22 | – |
| Liang Tang Ai | 3.21±0.40 | 4.95±0.01 | 2.00±0.10 | 1.80±0.10 |
| TX 7078 | 3.42±0.37 | 5.12±0.03 | 1.74±0.16 | 1.32±0.12 |
| TX 399 | 3.59±0.39 | 5.58±0.05 | 1.81±0.20 | 1.55±0.13 |
| IS 27150 | 4.98±0.63 | 9.49±0.17 | 2.32±0.31 | 2.10±0.19 |
| IS 27111 | 5.43±0.60 | 8.25±0.37 | 2.67±0.34 | 2.52±0.35 |

Canopy level WUE was estimated as the slope of the regression of above-ground biomass on cumulative water use for specified sampling intervals. Canopy level RUE was estimated as the slope of the regression of above ground biomass on the simulated cumulative intercepted photosynthetically active radiation (IPAR).

Table 2.5. Relationship between resource use efficiencies [water use efficiency (WUE) and radiation use efficiency (RUE)] and their components.

| Variables | Year | Equations | R ² | RMSE |
|------------------------|------|-------------------------|----------------|-------|
| x = biomass; y = WUE | 2009 | $y = 0.0032 x + 0.7616$ | 0.98 | 0.118 |
| | 2010 | $y = 0.0022 x + 2.925$ | 0.63 | 1.15 |
| x = water use; y = WUE | 2009 | $y = 0.0390 x - 4.938$ | 0.65 | 0.495 |
| | 2010 | $y = -0.0296 x + 14.68$ | 0.20 | 1.67 |
| x = biomass; y = RUE | 2009 | $y = 0.0011 x + 0.8882$ | 0.75 | 0.170 |
| | 2010 | $y = 0.0006 x + 0.7655$ | 0.93 | 0.109 |
| x = CIPAR; y = RUE | 2009 | $y = 0.0026 x + 0.8852$ | 0.14 | 0.312 |
| | 2010 | $y = 0.0057 x - 2.781$ | 0.47 | 0.308 |

Chapter 3 - Allometric Model to Quantify Sorghum Canopy Formation

Abstract

Canopy architecture has a prominent role in fundamental processes of crop growth including light interception, evapotranspiration and photosynthesis. Leaf area index (LAI; leaf area per unit land area) is a common quantification of vegetative canopy structure. The objective of this study was to develop a quantitative model to predict LAI for sorghum (*Sorghum bicolor* (L.) Moench) from emergence to flag leaf stage. Measurements included LAI, individual leaf area, leaf number, leaf length and maximum leaf width for eight sorghum genotypes under water- and nutrient-sufficient field conditions in two years. LAI was calculated from an algorithm developed to consider the area of mature leaves (leaves with a ligule/collar), area of expanding leaves (leaves without a ligule/collar), total leaf area per plant and plant population. The leaf shape factor (slope of the regression line between leaf area and product of leaf length and maximum width) was constant (0.73 in 2009 and 0.81 in 2010) for all mature leaves irrespective of genotype. Phyllochron (thermal time between ligule development of successive leaves on the culm) varied among genotypes. Linear functions quantified leaf length from leaf sequence number and maximum leaf width from leaf length for all mature leaves. Area of mature leaves was calculated as the product of length, maximum width and shape factor. Area of expanding leaves was linearly related to length, relative to expected mature length and was modeled assuming linear leaf expansion rates. Slope of regression of modeled LAI on observed LAI varied for photoperiod sensitive (PPS) and insensitive (non-PPS) genotypes in 2010. A good correlation was found between the modeled and observed LAI with coefficient of determination (R^2) 0.96 in 2009 and 0.94 (non-PPS) and 0.88 (PPS) in 2010. The proposed model has applications in canopy light distribution and interception studies and identification of drought stress on crops.

Key words

Leaf area, leaf length, leaf width, LAI, phyllochron, mature leaves, expanding leaves, sorghum, canopy formation

Introduction

Canopy architecture has a prominent role in fundamental processes of crop growth including light transmission and interception, evapotranspiration and photosynthesis (Arkin et al., 1983; Muchow et al., 1990a). The term canopy architecture refers to the size, number and spatial arrangement of plant organs such as leaves, stems, and reproductive structures upon the plant body (Cici et al., 2008). Leaf area index (LAI), defined as the total leaf area (m^2) per unit ground area (m^2) is a commonly used parameter for analyzing vegetative canopy structure and it can directly quantify canopy architecture (Welles and Norman, 1991). Leaf area at individual leaf level or crop level and LAI influence photon capture, photosynthesis, assimilate partitioning, growth and yield formation (Yin et al., 2000; Launay and Guerif, 2003; Rosenthal and Vanderlip, 2004; Tsialtas and Maslaris, 2008a). LAI impacts the exchange of energy and gases such as water vapor and CO_2 between crop canopy and the atmosphere (Sellers et al., 1986; Bonan, 1993; Canadell et al., 2000). Muchow and Carberry (1990) reported that leaf area development is a major determinant in amount of radiation intercepted by the crop and thus affects crop photosynthesis and soil water balance. LAI is a key parameter in the analysis of crop growth and productivity (Tewolde et al., 2005) and serves as an input for many crop growth and evapotranspiration models (Arkins et al., 1983; Birch et al., 1998). Kato et al. (2004) reported that LAI and total dry matter increment determine the transpiration efficiency and water use efficiency in a sparse crop. Quantification of LAI has potential in understanding resource (water and radiation) use efficiency and productivity of a crop.

Direct or destructive measurements of LAI are laborious and time consuming (Gower et al., 1999; Hyer and Goetz, 2004). Indirect or nondestructive LAI measurements require sophisticated and expensive equipments and prone to contain errors with the variability in the atmospheric or environmental parameters such as incident radiation and solar zenith angle (Hyer and Goetz, 2004; Camas et al., 2005). Large errors are possible in the indirect estimates of LAI even with small errors in the measurement conditions. Thus, quick, easy and efficient estimation of leaf area under field conditions through simulation models are of great importance. Also, simulation of

leaf area and LAI is essential in crop models those predict crop growth and yield (Birch et al., 1998).

Simulation of LAI requires the knowledge of the relevant environmental factors contributing to leaf growth and control leaf area development. Temperature is a major environmental factor that controls leaf area production in plants especially in cereals (Gallagher, 1979; Warington and Kanemasu, 1983; Ong and Monteith, 1985; Baker et al., 1986; Sinclair et al., 2004). Several workers have simulated leaf area dynamics in sorghum (*Sorghum bicolor* (L.) Moench) using thermal time (Arkin et al., 1983; Hammer et al., 1987a; Rosenthal et al., 1989; Muchow and Carberry, 1990) which is the temperature-weighted measure of time. Another environmental factor that affects phenology and leaf area production in sorghum is photoperiod (Geric and Miller, 1984). Photoperiod affects leaf area indirectly through its effect on total leaf number production and duration of vegetative phase by controlling the time of initiation of floral primordium (Quinby et al., 1973; Hammer et al., 1989; Muchow and Carberry, 1990). Water and nutrient availability also affect leaf area production. Even though it is difficult to incorporate those effects into simulation models, attempts have been made in that direction (Zhu et al., 2009).

Several models, differing in level of complexity, have simulated leaf area in field crops at whole crop level (O'Leary et al., 1985; Hammer et al., 1987b), whole plant level (Sinclair, 1984; Jones and Kiniry, 1986; Hammer et al., 1987a) and individual leaf level (Porter, 1984; Muchow and Carberry, 1989, 1990). Arkin et al. (1983) developed a leaf area model for sorghum consisting of five component processes of leaf growth which were total number of leaves produced, leaf appearance interval, leaf expansion duration, expansion rate and longevity of individual leaves. Hammer et al. (1987a and 1993) observed that investigation of leaf area production is relatively simpler at whole crop level and more complex at whole plant level and individual leaf level that require more inputs and involve more queries on components of leaf area and mechanisms underlying leaf growth.

Early attempts to simulate leaf area in sorghum used the relationship between area of a single leaf and total leaf area of the whole plant (Bueno and Atkins, 1981). But this method was not successful for estimating leaf area with crop development and was

largely influenced by genotype, location and plant population (Arkin et al., 1983). Charles-Edwards (1979) and Lainson and Thornley (1982) addressed the physiological mechanisms related to leaf growth and expansion in their models; Arkin et al (1983) reported difficulties in use of their models in crop growth simulation studies (e.g. validation and calibration steps). Arkin et al. (1976) estimated daily increment in leaf area using leaf appearance and expansion rates with considerations of leaf senescence in their model, but the model was difficult to use due to the requirement of detailed inputs. Even though all the component processes of individual leaf growth were simulated in sorghum leaf area model proposed by Arkin et al. (1983), the accuracy of predictions was not high considering the intensive measurements needed to use the model (Muchow and Carberry, 1990). Rosenthal et al. (1989) developed the grain sorghum growth simulation model SORKAM; a derivative of SORGF model (Arkin et al., 1976), to calculate individual leaf area based on leaf number and maturity classes. They calculated leaf expansion rates ($\text{cm}^2 \text{ heat unit}^{-1}$) as a function of leaf number in their model. Rosenthal and Vanderlip (2004) further modified SORKAM to make it independent of maturity classes. Hammer et al. (1987a) estimated leaf area produced and senesced with thermal time after emergence using logistic equations; examined genotypic effects on leaf area dynamics in grain sorghum hybrids from a single sowing and found that genotypic differences were mainly observed for maximum leaf area attained and rate of leaf senescence rather than the intrinsic rate of LAI production. They also reported genotypic differences in distribution of leaf area between main culms and tillers. But their model lacked a thorough inclusion of expanding leaf area dynamics. Muchow and Carberry (1990) developed a leaf area model of a tropical grain sorghum hybrid considering the component process of leaf initiation as a function of photoperiod and thermal time; they calculated leaf appearance using thermal time and individual leaf area using leaf position on culm. They considered fully expanded and expanding leaf areas separately, but used a common equation to simulate them. To calculate area of expanding leaves, they assumed that the area of expanding leaves at a given time was equal to the fully expanded area of the next 1.6 sequential expanding leaves. They included leaf senescence also in their model. Hammer et al. (1993) modeled genotypic and environmental control of leaf area dynamics for unicum and tillering grain sorghum at whole plant level and individual leaf

level and incorporated leaf area senescence into their approaches. But the models proposed by Muchow and Carberry (1990) and Hammer et al. (1993) suffer from lack of details of leaf area dynamics especially for expanding leaves. The objective of the current study was to develop a simple quantitative model to predict LAI of sorghum with emphasis on details of leaf area production especially for expanding leaves.

Materials and Methods

A dynamic, quantitative model of canopy formation can be formulated from concepts of leaf and stem formation and duration. The proposed model quantifies sorghum canopy formation through allometric estimation equations for leaf area production. The scheme of the model is illustrated in Figure 3.1; terms are defined when introduced in the text. The model description, in the following sections, is preceded by details of field experiments and measurements at field and laboratory required to develop the algorithm predicting LAI production. Coefficients fit for the empirical model of leaf area dynamics were based on field observations. Model evaluation utilized independent field data.

Field experiments

Field studies were conducted in 2009 and 2010 at Kansas State University Northwest Research Extension Center (NWREC), Colby, Kansas (39° 24' N, 101° 4' W; 963 m above sea level) on a Keith silt loam soil (fine silty, mixed, mesic Aridic Argiustoll). Tillage in both years included two passes with a disk harrow followed by a roller packer to break clods. Sorghum genotypes (TX 7000, TX 399, TX 2862, PI 584085, Liang Tang Ai, TX 7078, IS 27150 and IS 27111) represented a range of vegetative transpiration efficiency (green house; Xin, Aiken pers comm.), heights and photoperiod sensitivities and were planted in 6.1 m x 6.1 m plots on June 25, 2009 and in 6.1 m x 3.0 m plots on May 28, 2010. Plots were arranged in randomized complete block design (RCBD) in 2009 and incomplete block design (IBD) in 2010. All genotypes except IS 27111 were photoperiod insensitive (non-PPS). Sorghum seed was sown at a depth of 2 cm using a planter with a fluted coulter and double disk opener. Planting rate was 125,000 seeds ha⁻¹ with a spacing of 10 cm between plants and 76 cm between rows.

Supplemental soil fertility included 102 kg N ha⁻¹ and 34 kg P ha⁻¹ banded adjacent as basal dose in both years. Weed control consisted of pre-emergent application of atrazine (2-chloro-4-ethylamino-6-isoprophylamino-s-triazine, 4.68 l ha⁻¹) plus Duall II magnum (2-chloro-N-(2-ethyl-6-methylphenyl)-N-[(1S)-2-methoxy-1-methylethyl]acetamide, 1.52 l ha⁻¹) and post-emergent application of Cornerstone Plus [Glyphosate, N-(phosphonomethyl)glycine, 1.75 l ha⁻¹] plus Starane (Fluroxypyr 1-methylheptyl ester: ((4-amino-3,5-dichloro-6-fluro-2-pyridinyl)oxy) acetic acid, 1-methylheptyl ester, 1.02 l ha⁻¹) with a spray volume of 93.54 l ha⁻¹ and spray pressure of 138 kPa in both years. Supplemental in-season irrigation was provided during mid-vegetative growth (38 mm) and just prior to anthesis (25 mm) in 2009 and just prior to anthesis (25 mm), post anthesis (38 mm) and during grain filling (25, 38, 38 mm with 7 d interval) in 2010. Irrigation was provided with underground well water via micro furrow method with laterals. Weather data were obtained from the Cooperative Observer Site (Colby 1SW, located within 500 m from the field), associated with the National Weather Service (NWS).

Measurements

Periodic phenologic development was recorded at approximately bi-weekly intervals for two identified plants in each plot. Observations included total number of mature leaves (TLN) and length (L, length of midrib from leaf tip to ligule/collar) and maximum width (W, measured at about two-third of the final blade length from the ligule/collar) of all even numbered mature leaves not sampled in the previous measurement, on the main culm. A leaf was considered as mature or fully expanded when its ligule/collar became completely visible above the leaf sheath. The leaf collar refers to the thickened and lighter colored region between leaf blade and leaf sheath of grasses (www.biology-online.org) which supports the ligule which is either a projected membrane-like tissue or series of hair-like structures (www.wikipedia.org). In this write-up, when it's referred to ligule, it's also implicitly referring to the collar-supporting tissue. A known leaf number (leaf number 4 in 2009 and 6 in 2010) was marked early in crop growth to identify the leaf number of newly formed mature leaves.

To derive the relationship between length (L), maximum width (W) and area (A_m) of mature leaves based on the principle of self similarity for sorghum leaves, one plant per genotype was sampled in 2009 and two plants per genotype were sampled in 2010. We harvested at least top three even numbered mature leaves per plant in 2009 and at least top four even numbered mature leaves per plant in 2010 approximately at 12 leaf stage and flag leaf stage from plants other than the tagged plants of periodic phenologic observations. The top mature leaf was included in the above measurements even if it was an odd numbered leaf. Leaves were harvested by cutting at the leaf collar, placed in ziploc plastic bags, kept in portable cooler and taken to laboratory where A_m , L and W were measured. A_m was measured using a leaf area meter (CI 203, CID Bio–Science, Camas, Washington, USA). In 2009, the harvested leaves were cut into four or more pieces; the length (L_x) and area (A_x) of each piece was measured to simulate the length and area of expanding leaves (leaves without a ligule) and to derive a relationship between those variables. In 2010, expanding leaves were also included in the destructive leaf harvest; the whole plant whorl was cut at the top ligule and taken to laboratory where the expanding leaves were numbered (starting from the expanding leaf that was one node above the top mature leaf) and cut at the point where the two edges of the leaf lamina just touch each other. Each cut portion was that part of the expanding leaf lamina that had unwound from the whorl. Length and area of each cut portion were measured and denoted as the current length (L_x) and area (A_x) of expanding leaves. A_x was measured by CI 203 leaf area meter. Same symbols represented length and area (L_x and A_x respectively) of leaf segments (2009) and immature leaves (2010) since they were analyzed in identical manner.

LAI was measured by a plant canopy analyzer (LAI–2000, LI–COR, Lincoln, Nebraska, USA) approximately bi–weekly, beginning from 35 DAP in 2009 and approximately weekly, beginning from 40 DAP in 2010. The instrument sensor was shaded when measurements were taken and all measurements were completed before 10:00 am to ensure low sun angles and to meet the manufacturer's specifications of diffuse radiance (avoiding exposure to direct radiance) measurement conditions. Light transmittance (five ranges of view angles) was sampled at three locations within each plot; measure at each location consisted of a single reading of incident diffuse irradiance

above the canopy and four readings of diffuse irradiance below the crop canopy (parallel, perpendicular and both diagonals relative to crop row), taken within two minutes to avoid atmospheric variation. Below canopy readings were taken with the sensor within 5 cm of the soil surface.

Theory and model parameterization

Overview of the structure of the LAI estimation model: LAI was calculated from an algorithm (Figure 3.1) considering the area of mature leaves, area of expanding leaves, total leaf area per plant and plant population. Area of mature leaves was calculated from length, maximum width and a leaf shape factor. Total number of mature leaves was calculated using phyllochron concept. Area of expanding leaves was calculated as proportional to their length relative to the maximum expected length and expected mature area, assuming linear leaf expansion rates.

Leaf appearance

Sorghum leaf appearance and maturation are quantified by the phyllochron concept of synchronous development with thermal time (Rickman and Klepper, 1995). Linear developmental response to temperature was assumed for sorghum plants to estimate thermal time or degree days. Growing degree days (GDD) were calculated by Equation 1 (Robinson, 1971; Arkin et al., 1983; Hammer et al., 1987; Richie and NeSmith, 1991; Aiken, 2005).

$$GDD = \frac{T_{\min} + T_{\max}}{2} - T_b \quad (1)$$

where T_{\min} and T_{\max} are daily minimum and maximum temperatures respectively and are limited in value to a T_b (base temperature) of 7°C (Vanderlip and Arkin, 1977; Mass and Arkin, 1978; Arkin et al., 1983; Muchow and Carberry, 1990) and a T_{ul} (upper limit) of 42°C (Alagarswamy et al., 1986). If T_{\min} on a particular day is less than T_b , then T_{\min} is set equal to T_b ; similarly if T_{\max} on a particular day is greater than T_{ul} , then T_{\max} is set equal to T_{ul} . Cumulative thermal time (cGDD) was computed from day of planting in both years.

Phyllochron (P), defined as the interval between similar developmental stages of successive leaves on the same culm (Wilhelm and McMaster, 1995) was estimated in

thermal time (GDD) under water sufficiency conditions. P was determined as the inverse of the slope of TLN (measured through 16–20 leaves in 2009 and 2010) regressed on observed cGDD with a suppressed intercept (since intercept was not significantly different from zero; Equation 2).

$$TLN = P^{-1} \times cGDD \quad (2)$$

The slope, P^{-1} in the above equation is rate of leaf appearance (leaf °Cd⁻¹); the inverse of which is phyllochron. P was an input for the proposed leaf area production model.

Shape factor

Area of a mature sorghum leaf (A_m) was assumed to be proportionate to L and W, following the principle of self-similarity (Equation 3). The shape factor (F) was an important leaf characteristic that was used as an input for the model to calculate individual leaf area. F for mature sorghum leaves was derived by regressing observed A_m on the product of observed values of L and W (Bueno and Atkins, 1981; Shih et al., 1981; Arkin et al., 1983) with a suppressed intercept, since intercept was not different from zero (Equation 3).

$$A_m = F(L \times W) \quad (3)$$

Area of mature leaves

Characteristic L was assumed to vary with leaf order on a stem (McMaster et al., 1991; Zhu et al., 2009), here quantified by a third order linear function of leaf sequence number (LN; Equation 4). Characteristic W was assumed to vary with L (Zhu et al., 2009), here quantified by a third order linear function (Equation 5).

$$L_k = f(LN_k); \quad f(LN_k) = a_l(LN_k)^3 + b_l(LN_k)^2 + c_l(LN_k) + d_l \quad (4)$$

$$W_k = f(L_k); \quad f(L_k) = a_w(L_k)^3 + b_w(L_k)^2 + c_w(L_k) + d_w \quad (5)$$

where LN_k is leaf sequence number of leaf k, L_k is length of leaf k, W_k is maximum width of leaf k and a_l , b_l , c_l , d_l , a_w , b_w , c_w and d_w are fitted coefficients. These relations are based on the assumption that L and W of a leaf are constant at maturity, prior to senescence. An intercept was fit for the prediction equations of L and W to improve the goodness of fit. A_m was calculated from the estimated values of L and W using Equation 6.

$$A_m = L \times W \times F \quad (6)$$

Total number of mature leaves on the main culm at j days after planting (TLN_j) for genotype i with a phyllochron P_i was calculated using Equation 7.

$$TLN_j = cGDD_j / P_i \quad (7)$$

where $cGDD_j$ is cumulative thermal time at j DAP. Total area of all mature leaves on a plant at j DAP (TMA_j) was calculated by Equation 8.

$$TMA_j = \sum_{k=1}^{TLN_j} A_{m_k} \quad (8)$$

Area of expanding leaves

This model relates the leaf area dynamics of expanding leaves to thermal time by means of apparent leaf age (ALG_x , °C d). ALG_x of r^{th} expanding leaf at a given point of time indicated thermal time elapsed from the tip appearance of r^{th} expanding leaf in the whorl. The concept of ALG_x is based on the fact that it takes one phyllochron for a leaf to expand completely (Wilhelm and McMaster, 1995). ALG_x of r^{th} expanding leaf for i^{th} genotype ($ALG_{x_{ir}}$) was calculated as,

$$ALG_{x_{ir}} = P_i - \frac{r \times P_i}{n_x} \quad (9)$$

where n_x is the maximum number of expanding leaves observed in the whorl such that $TLN + n_x \leq FLN$, FLN being the flag leaf number. Value of n_x was assumed to be constant in Equation 9. $r = 1$ for the expanding leaf that will be at one node above the top mature leaf. ALG_x is zero for the youngest expanding leaf ($r = n_x$) in the whorl. If Equation 9 conceptually extends to top mature leaf ($r=0$), ALG_x becomes one phyllochron and that is in accordance with Wilhelm and McMaster's (1995) finding that the duration between tip and ligule appearance of a leaf is one phyllochron.

Leaf area dynamics of expanding leaves was assumed to be proportionate to their expected mature area [$E(Ax_m)$], length relative to the expected mature length (RL_x) and area relative to the expected mature area (RA_x). Expected mature area of r^{th} expanding leaf [$E(Ax_{mr})$] was calculated as,

$$E(Ax_{mr}) = E(Lx_{mr}) \times E(Wx_{mr}) \times F \quad (10)$$

where $E(Lx_{mr})$ and $E(Wx_{mr})$ were expected length and expected maximum width (respectively) of r^{th} expanding leaf at maturity and were calculated using Equations 4 and 5 respectively. Leaf sequence number of r^{th} expanding leaf is $TLN+r$. $E(Ax_{mr})$, $E(Lx_{mr})$ and $E(Wx_{mr})$ indicated the area, length and maximum width respectively of r^{th} expanding leaf when it completes expansion with the formation of a ligule. Ratio of current length of r^{th} expanding leaf (Lx_r) to $E(Lx_{mr})$ was denoted as its relative length (RLx_r ; Equation 11).

$$RLx_r = Lx_r / E(Lx_{mr}) \quad (11)$$

Similarly, ratio of current area of r^{th} expanding leaf (Ax_r) to $E(Ax_{mr})$ was denoted as its relative area (RAx_r ; Equation 12).

$$RAx_r = Ax_r / E(Ax_{mr}) \quad (12)$$

RLx was calculated by the model using the linear relationship observed between RLx and $ALGx$; Equation 13).

$$RLx_r = f(ALGx_r) ; \quad f(ALGx_r) = c_g(ALGx_r) + d_g \quad (13)$$

where c_g and d_g are slope and intercept respectively. Similarly, RAx was calculated by the model using the linear relationship observed between RAx and RLx (Equation 14).

$$RAx_r = f(RLx_r) ; \quad f(RLx_r) = c_q(RLx_r) + d_q \quad (14)$$

where c_q and d_q are slope and intercept respectively. Ax_r contributing to the total leaf area of the plant at any time was calculated using equation 15.

$$Ax_r = RAx_r \times E(Ax_{mr}) \quad (15)$$

The individual area of expanding leaves was accumulated to get the total area of expanding leaves at j DAP (TXA_j) as,

$$TXA_j = \sum_{r=1}^{n_j} Ax_r \quad (16)$$

where n_j is total number of expanding leaves at j DAP. Total leaf area per plant at j DAP ($TPLA_j$) was calculated as,

$$TPLA_j = TMA_j + TXA_j \quad (17)$$

Finally, LAI at j DAP (LAI_j) was estimated as,

$$LAI_j = TPLA_j \times PLN \quad (18)$$

where PLN = average observed plant population for sorghum genotypes.

Model evaluation

Given inputs of daily T_{\max} and T_{\min} , P_i , PLN , F and fitted values of coefficients for the prediction equations developed in the model, LAI was simulated for data sets where LAI was measured independently by plant canopy analyzer. Accuracy of predictions was tested by regressing predictions against observed values. Goodness of fit was quantified by coefficient of determination (R^2). Predictive bias was identified by significant deviation of intercept and slope from the 1:1 line. Deviations were quantified in the units of the data of interest by error indices (Legates and McCabe, 1999) such as

root mean square error (RMSE, $\left[\left\{ \sum_{i=1}^n (M_i - O_i)^2 \right\} / n \right]^{0.5}$; where n is total number of observations and O_i and M_i are observed and predicted values respectively at each comparison point i), percentage RMSE (% RMSE, $\frac{RMSE}{\frac{\sum_{i=1}^n O_i}{n}} \times 100$), mean absolute error

[MAE, $\frac{1}{n} \sum_{i=1}^n (M_i - O_i)$] and percent bias (PBIAS, $\frac{\sum_{i=1}^n (M_i - O_i)}{\sum O_i} \times 100$).

Statistical analysis

Experimental design was RCBD with five replications in 2009 and IBD with five blocks in 2010. Analysis of variance and mean separation on the genotypes utilized MIXED procedure and MEANS procedure respectively in SAS (Statistical Analysis System, version 9.1.3, SAS institute, Cary, North Carolina, USA) for plant population and leaf dimension variables at 0.05 probability level. Analysis of covariance utilized the MIXED procedure in SAS to (i) compare P among genotypes (cGDD as covariate), (ii) test the significance of the fitted coefficients a_i , b_i , c_i , d_i (Equation 4), a_w , b_w , c_w and d_w (Equation 5) in the prediction equations of L and W (third, second and first order terms of LN as covariates) and to compare them among genotypes, (iii) test the significance of the fitted coefficients c_g and d_g in the prediction equation of RLx (Equation 13; $ALGx$ as covariate) and to compare them among genotypes, (iv) test the significance of the fitted coefficients c_q and d_q in the prediction equation of RAX (Equation 14; RLx as covariate)

and to compare them among genotypes and (v) compare F among different genotypes and leaf sequence number (LN and product of L and W as covariates). Genotypes were treated as fixed effect variables and replication or block was treated as random effect variable. Genotype and replication (or block) were the class variables. Regression analysis utilized the REG procedure in SAS for model evaluation by regressing modeled LAI on observed LAI; intercept and slope of the linear regression equations were tested for significant departure from 0 and 1 respectively.

Results

Environmental conditions and crop growth

The maximum and minimum temperatures (max/min) during the sampling period varied between 18.9/8.3°C to 38.3/20°C in 2009 and 19.4/10.0°C to 39.4/21.7°C in 2010 (Figure 3.2). Large amount of precipitation was recorded during both cropping seasons (194 mm in 2009 and 238 mm in 2010 within 82 DAP, Figure 3.3) that was not typical for the region. Increased amount of rainfall together with supplemental irrigation and fertilization ensured that neither water nor nutrients limited crop growth in both years. No pest or pathogen problems were observed during the entire cropping season in both years.

Crops got a late start in 2009 compared to 2010 due to delayed planting in 2009. Due to erroneous planting in 2010, replicate plots were staggered and the experimental design had to be changed from RCBD to IBD. Emergence was noted at 8 DAP in both years. Plant stand was poor in both years. Data on observed plant population are presented in Table 3.1. Since plant stand for genotype PI 584085 was less than 20% in 2010, that genotype was excluded from LAI measurements by plant canopy analyzer in 2010.

Phyllochron

T_{\min} never deceeded T_b (7°C) and T_{\max} never exceeded T_{ul} (42°C) during the entire sampling period in both 2009 and 2010 (Figure 3.2). Linear relationship was observed between leaf number production and cGDD (Figure 3.4). Analysis of covariance reported significant difference among genotypes for P^{-1} , even though the difference was small (Table 3.2). Estimates of P^{-1} for different genotypes in 2009 and 2010 are presented in

Table 3.2. P varied between 58°C and 66°C in 2009 and 58°C and 69°C in 2010 among genotypes.

Characteristic dimensions of mature leaves

The observed TLN per plant (mean±SD) at flag leaf stage varied between 17±1.2 and 20±0.74 in 2009 and 19±0.89 and 20±1.4 in 2010 among genotypes. No differences in L were detected among genotypes prior to LN 14 (2009) or LN 12 (2010); but genotypes differed for L for subsequent leaves (Figure 3.5). Genotypes differed for W from LN 6 (2009) or LN 8 (2010) (Figure 3.6). Generally, the tall and PPS sorghum genotype (IS 27111) tended to have longer and narrower leaves compared to short statured and non PPS genotypes during mid vegetative growth.

Leaf characteristic L was a third order linear function of LN (Figure 3.5) in 2009 and 2010. Characteristic W was a second order linear function of L in 2009 and a third order linear function of L in 2010 (Figure 3.7). The value of the fitted coefficient c_1 in the prediction equation of L (Equation 4) was not significantly different from zero in 2009 and 2010. Value of the fitted coefficients a_1 , b_1 and d_1 in the prediction equations of L (Equation 4) differed among genotypes in 2009 while the value of only d_1 differed among genotypes in 2010. Value of the fitted coefficients a_w , b_w , c_w and d_w in the prediction equation of W (Equation 5) were significantly different from zero in 2010 while only b_w , c_w and d_w showed significance in 2009; genotypes differed for the coefficients b_w and d_w (Equation 5) in 2009 and only for d_w (Equation 5) in 2010. Values of the fitted coefficients in the predictive equations of L and W (Equations 4 and 5) are presented in Table 3.3. F did not vary with different genotypes or different leaf sequence numbers (Figure 3.8). The value of $F(\pm SE)$ was 0.73(±0.013) in 2009 and 0.81(±0.006) in 2010 (Figure 3.8).

Area of expanding leaves

RLx exhibited a linear relationship with ALGx ($R^2 = 0.89$; Figure 3.9). No differences were detected among genotypes in the prediction equation for RLx from ALGx (Equation 13). Intercept was significant for the regression line between RLx and ALGx. RAx increased with RLx in a linear fashion (Figure 3.10). Coefficients of prediction equation for RAx from RLx (Equation 14) differed among genotypes in 2009,

but the differences were only minor (Table 3.4). Also there was no improvement over R^2 and only a very slight reduction in CV and RMSE (with a magnitude of 0.87 and 0.005 respectively) by fitting different coefficients for different genotypes. Therefore, common coefficients were fit for all genotypes using pooled data in Equation 14 in 2009. In 2010, coefficients did not differ among genotypes in Equation 14. R^2 was 0.98 in 2009 and 0.97 in 2010 for the linear relationship between RAx and RLx (Figure 3.10). Intercept turned to be significant for the regression of RAx on RLx (Equation 14) in both years.

Model evaluation

The adequacy of the general framework was verified by simulating TPLA over time using the prediction equations. Testing of this model was done on independent data collected by actual measurements in field. Model evaluation parameters are presented in Table 3.5. Slope of regression of modeled LAI on observed LAI varied for photoperiod sensitive (PPS) and insensitive (non-PPS) genotypes in 2010. A good correlation was found between the modeled and observed LAI with R^2 0.96 in 2009 and 0.94 (non-PPS) and 0.88 (PPS) in 2010 and RMSE ($m^2 m^{-2}$) 0.349 (19%) in 2009 and 0.234 (8%; non-PPS) and 0.524 (17%; PPS) in 2010 (Figure 3.11; Table 3.5). Intercept for the fitted line was not significantly different from zero in 2009. A negative bias in projected LAI values was detected in 2009 (slope \pm SE = 0.807 \pm 0.027); and for non PPS genotypes in 2010 (slope \pm SE = 1.04 \pm 0.05, intercept \pm SE = 0.552 \pm 0.15). Model over predicted the LAI values of the PPS genotype in 2010 (slope \pm SE = 1.70 \pm 0.32, intercept \pm SE = -2.14 \pm 1.01). The observed LAI for the sorghum genotypes considered in this study ranged from 0.52 to 3.12 $m^2 m^{-2}$ in 2009, 1.20 to 4.14 $m^2 m^{-2}$ for non-PPS genotypes in 2010 and 1.82 to 3.86 $m^2 m^{-2}$ for PPS genotype in 2010.

Discussion

This model provides a general framework to simulate LAI in sorghum using daily thermal time as the sole independent variable; provided the model meets with the calibration requirements (summarized in Table 3.6). The prediction range of this model was from emergence to flag leaf stage (maximum leaf number production). The model predicted LAI for 8 genotypes in 2009 and 7 genotypes in 2010 including a PPS genotype

under well watered conditions. Thermal time brought the major control of environment over plant leaf area production in the model. Leaf area was highly dependent up on accumulated heat units as suggested by Arkin et al. (1983). Equations 4, 5 and 6 incorporated the effect of leaf characteristic dimensions on LAI in the model. Use of specific genotypic coefficients in equation 4 and 5 accommodated genotypic control over leaf area dynamics.

The major contribution of this study is the introduction of a new and detailed method to calculate the area of expanding leaves. It calculates area of expanding leaves using a different algorithm than that used for fully expanded leaves. This is to accommodate the completely different behavior of expanding leaves compared to fully expanded leaves in relation to leaf area production. All other sorghum leaf area models use common equations to simulate leaf area production by mature and expanding leaves or use a single equation to simulate TPLA without separating mature and expanding leaf areas (Arkin et al., 1983; Hammer et al., 1987a; Muchow and Carberry, 1990; Hammer et al., 1993; Carberry et al., 1993).

This model calculates thermal time from a linear function of temperature since it assumes a linear developmental response of sorghum plants to temperature. This method is more convenient than the optimized developmental response method for GDD calculation which estimates GDD from a broken linear function of temperature, supported by maximum, optimum and base temperatures (Hammer et al., 1993; Aiken 2005). Alagarwamy et al. (1986) reported a T_b of 8°C and Nelson (1986) found a T_b of 10°C for sorghum leaf appearance. However, Nelson (1986) also reported adequacy of taking any value for T_b within the range of 7–10°C for sorghum which justifies the T_b of 7°C in this model.

This model utilized a single value for P for each genotype during the vegetative development. This method is simple (Aiken, 2005) and reasonable since P in sorghum has been reported as constant from seedling stage to flag leaf expansion (Muchow and Carberry, 1990; Birch et al., 1998; Craufurd et al., 1998) or for first 20 leaves (Clerget et al., 2008). This is in contrast with the earlier reports of variation in accumulated thermal time between successive leaf appearances during vegetative development in sorghum (Castleberry, 1973; Arkin et al., 1976). Phyllochron has been reported to vary with

environmental factors including temperature (Cao and Moss, 1989; Masle et al., 1989; Boone et al., 1990), nitrogen availability (Longnecker et al., 1993), water (extreme levels of water stress; Bauer et al., 1984; Baker et al., 1986), salt concentrations (Maas and Grieve, 1990), CO₂ concentrations (Boone and Wall, 1990), light (quality, quantity and duration; Friend et al., 1963; Kirby and Perry, 1987; Barnes and Bugbee, 1991) and day length (Baker et al., 1980). Craufurd et al. (1998) observed that P was constant at the temperature range of 10–18°C to 30°C and it increased above 30°C. Arkin et al. (1983) reported that leaf appearance rate (based on leaf tip appearance) in the whorl was constant up to panicle initiation and after that it decreased. However, the constant leaf appearance rate based on the formation of a ligule was adequate to simulate the leaf area dynamics in this model.

Accumulation of thermal time (cGDD) began at planting for the calculation of leaf appearance in this model, but emergence was recorded at 8 DAP corresponding to a cGDD of 164°C in 2009 and 138°C in 2010. Therefore, an intercept can be expected for the regression of TLN on cGDD (Equation 2). However, the intercept did not turn to be significant at 0.05 probability level for different genotypes in both years. Also, fitting an intercept reduced R² in the relationship between TLN and cGDD; in addition, the phyllochron estimates resulted from this type of calculation over predicted TLN by 2–4 leaves. Thus, considering the logical and statistical reasons, intercept was set to be zero for the regression of TLN on cGDD (Equation 2; Figure 3.4).

Variation of P⁻¹ among genotypes in this study is supported by the reports on differences in P among genotypes in grasses (Kirby et al., 1985; Baker et al., 1986; Syme, 1974). Estimate of P for different genotypes in this study (ranged between 58 and 65°C in 2009 and 58 and 69°C in 2010; Table 3.2) are within the range of those reported for sorghum in literature. Craufurd and Qi (2001) reported a range of 40–70°C for leaf appearance in sorghum. Muchow and Carberry (1990b) found a constant rate of 69°C for leaf appearance in their sorghum genotype.

The maximum number of leaves produced by sorghum genotypes in this study was less than or equal to 20. Prasad and Staggenberg (2009) reported that a sorghum plant typically produces 12–18 leaves. Arkin et al. (1983) reported a maximum number

of leaf production of 20–22 in late maturing sorghum hybrids and Clerget et al. (2008) reported evidences for more than 22 leaves in PPS sorghum genotypes.

This model calculates L as a third order linear function of LN and W as a second (in 2009) or third (in 2010) order linear function of L. The simplicity of linear functions is an advantage of this approach (Lu et al., 2004; Tsialtas and Maslaris, 2008b). Similar approaches are reported in literature also. Zhu et al. (2009) modeled leaf length and leaf width as quadratic functions of leaf sequence number and leaf length respectively in rice (*Oriza sativa* L.). McMaster et al. (1991) modeled leaf length and maximum width as exponential functions of leaf number in winter wheat (*Triticum aestivum* L.).

Estimate of F was greater in 2010 compared to that of 2009. This shows that leaves had blunter tip in 2010 than in 2009, which may be a result of environmental conditions (delayed planting in 2009) that led to a slight change in leaf expansion and shape in 2010 compared to 2009. Value of F in 2009 (0.73 ± 0.013) was similar to that reported in literature (Clements and Goldsmith, 1924; Bueno and Atkins, 1981; Shih et al., 1981; Arkin et al., 1983; Birch et al., 1998; Sinclair et al., 2004) whereas F was slightly greater in 2010 (0.81 ± 0.006) than the commonly reported values; however Rinaldi et al. (1990) has reported an estimate of F for sorghum (0.79) that was similar to the 2010 estimate of F in this study.

Since RL_x attained values slightly greater than 1 in 6 cases out of 61 expanding leaves in 2010, (Equation 11), approximately 10% chance of a slight negative bias in the prediction equation of L from LN (Equation 4) can be expected in 2010. The approach of deriving a single prediction equation for RA_x from RL_x (Equation 14) in 2009 even though the coefficients differed among hybrids is supported by Hammer et al. (1987) who derived a common equation for different sorghum hybrids to predict tiller leaf area from leaf length when the fitted coefficients in the predictive equation significantly differed among hybrids, but the differences were small and had no practical implication. The intercept of the regression of RA_x on RL_x (Equation 14) indicates the area of the triangular leaf tip.

The difference in slopes of regression of predicted LAI on observed LAI for PPS and non-PPS genotypes in 2010 and the absence of this trend in 2009 may be a result of delayed planting in 2009 compared to 2010. One month earlier start of crops in 2010

compared to 2009 might have magnified the effect of day length on leaf expansion (Cookson et al., 2007) in 2010.

Variations in leaf dimensions among genotypes for same leaf sequence number (Figure 3.5 and 3.6) can be attributed to differences in cell number or cell size or combinations of the two (Francis, 1992; Granier and Tardieu, 1998; Granier et al., 2000); which are in turn controlled by mechanisms at the molecular or cellular level. Leaf expansion is primarily governed by biochemical processes that regulate cell expansion and cell division (Charles-Edwards, 1979; Arkebauer and Norman, 1995, Van Volkenburgh, 1999). Cell expansion is controlled by several factors such as plant hormones– auxins and gibberellins (Coartney et al., 1967; Vanderhoef and Dute, 1981; York et al., 1984; Keyes et al., 1990), cell wall pH (Baydoun and Brett, 1984; Gaspar et al., 1985), different enzymes (Morris and Arrthur, 1984), synthesis of cell wall material (Lainson and Thornley, 1982), hydraulic and osmotic properties of the cell (Arkebauer and Norman, 1995; Van Volkenburgh, 1999) and environmental factors including light (Cosgrove and Green, 1981; Van Volkenburgh and Cleland, 1981; Kigel and Cosgrove, 1991; Van Volkenburgh, 1999; Cookson and Granier, 2006), water, salt and nutrient stresses (MacAdam et al.1989; Alves & Setter 2004; Assuero et al., 2004; Aguirrezabal et al. 2006; Cookson & Granier, 2006), temperature (Pritchard et al., 1990), daylength (Cookson et al., 2007) and atmospheric CO₂ concentration (Taylor et al., 1994, 2003). Cell division and cell number can be affected by carbohydrate supply (Dale 1988; Chapin, 1991) and cell temperature – through its effect on length of cell cycle (Series of events taking place in a cell leading to the duplication of its genetic material and division of genetic material and cell mass; Arkebauer and Norman, 1995); but very little is known about the mechanisms controlling cell division which in turn regulate leaf expansion (Van Volkenburgh, 1999). Arkebauer et al. (1995) found that water potential outside the cells and cell temperature can control leaf length and leaf area in maize (*Zea mays* L.) through their effects on cell division and cell expansion. Tisne et al. (2008) reported the role of ERECTA gene on leaf epidermal cell expansion. Genetic studies in Arabidopsis (*Arabidopsis thaliana*), maize and many other species have identified several mutations and enzyme activities regulating leaf expansion (Van Volkenburgh, 1999). Cookson et al. (2007) reported the effect of day length on cell size in Arabidopsis that is partially

controlled by whole plant mechanisms related to floral transition timing. Combinations of these factors likely influenced differences in leaf dimensions among sorghum genotypes and between years.

A follow up of this study can be the molecular level investigations of the mechanisms contributed to differences in leaf dimensions among genotypes. Changes in leaf length and width may affect mutual shading between leaves which in turn influence canopy light interception. If so, the above studies can also analyze the mechanisms at the molecular or cellular level those have implications on light interception and use by the plant canopy and thus crop productivity.

This model can successfully predict whole plant leaf area for unicum sorghum. Contribution of tiller leaves to TPLA is not considered in this model. Lafarge et al. (2002) has reported a nondestructive method to calculate tiller number per plant in sorghum. In that case, the algorithm proposed by the current model to estimate TPLA can be extended to tillers with moderate accuracy to calculate total leaf area of tillers and to include them in LAI estimation. The fact that tiller leaves' area are not considered in this model explains the under estimation of projected LAI (for all genotypes in 2009 and PPS genotypes in 2010) by this model. This model has not estimated the senesced leaf area, relative to the amount of leaf area already produced, since process of leaf senescence was not incorporated in to the model. As the predicted values were compared with the LAI observations recorded by plant canopy analyzer which estimates total LAI rather than green LAI, this did not reduce the goodness of fit. But with further research on tiller leaf area production and leaf senescence, the current model can be improved.

Daily increase in area of expanding leaves with accumulation of thermal time is not reflected completely in this model since the driving variable for A_x in this model is ALG_x which remains constant until the formation of a new ligule on the culm. This is also a limitation of this model. However, the residual from each daily accumulation of $cGDD$ (Equation 7) can be used to quantify ALG_x progression, with corresponding implementations in RL_x , RA_x and A_x . Thus the current model can be readily extended for dynamic simulation of A_x .

This model compared the genotypes only in one location under water and nutrient sufficient conditions. Water, nutrients and solar radiation affect the component processes

of leaf growth and expansion (Arkin et al., 1983). These environmental variations are not accounted for by this model. Modifications in the model including changes in the estimates of fitted coefficients are necessary to use it in different locations, since various biotic and abiotic factors alter the allometry coefficients (Gower et al., 1999). However, this model provides a general, useful and simple reference framework for simulation studies on leaf area.

Applications

This model has applications in prediction of radiation interception by a crop canopy with a known extinction coefficient since radiation interception by plant canopies can be calculated from information on LAI and extinction coefficient. This model could also be used to identify drought stress on plants at an extent that reduces leaf expansion. As this model predicts leaf area in well watered conditions, drastically less value for observed leaf area compared to predicted value of leaf area can be perceived as the result of a severe water stress that hinders leaf expansion. Thus rate of leaf expansion under water deficit conditions could be used as a criterion for selecting tolerant genotypes as suggested by Ober and Luterbacher (2002). This model has also implications in simulation studies of light distribution within the plant. Since the expanding leaves that are at one or two nodes above the top mature leaves are the most erect leaves in the upper canopy of the plant (Table 3.7), they might have very good influence on the distribution of radiation within the plant canopy. As this model predicts the leaf area of expanding leaves with reasonably good accuracy, it can be used in canopy light distribution studies also.

Conclusion

Sorghum LAI is predictable through a dynamic, quantitative model of canopy formation, relating leaf area to thermal time. LAI can be estimated from an algorithm considering the area of mature leaves, area of expanding leaves, total leaf area per plant and plant population. Total leaf area per plant with a known phyllochron and leaf shape factor can be calculated with given inputs of daily maximum and minimum temperatures

and coefficients required for model calibration, and extended to LAI with the knowledge on plant population

Acknowledgement

This project benefited from the capable technical support of Ralph Wolf, Ray Duffey, Alicia Oien and Rhett Martin. We would like to thank Leigh Murray and Christopher Juarez for statistical consult. This research was supported in part by the Ogallala Aquifer Program, a consortium between USDA–Agricultural Research Service, Kansas State University, Texas AgriLife Research, Texas AgriLife Extension Service, Texas Tech University and West Texas A&M University.

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Figures and Tables

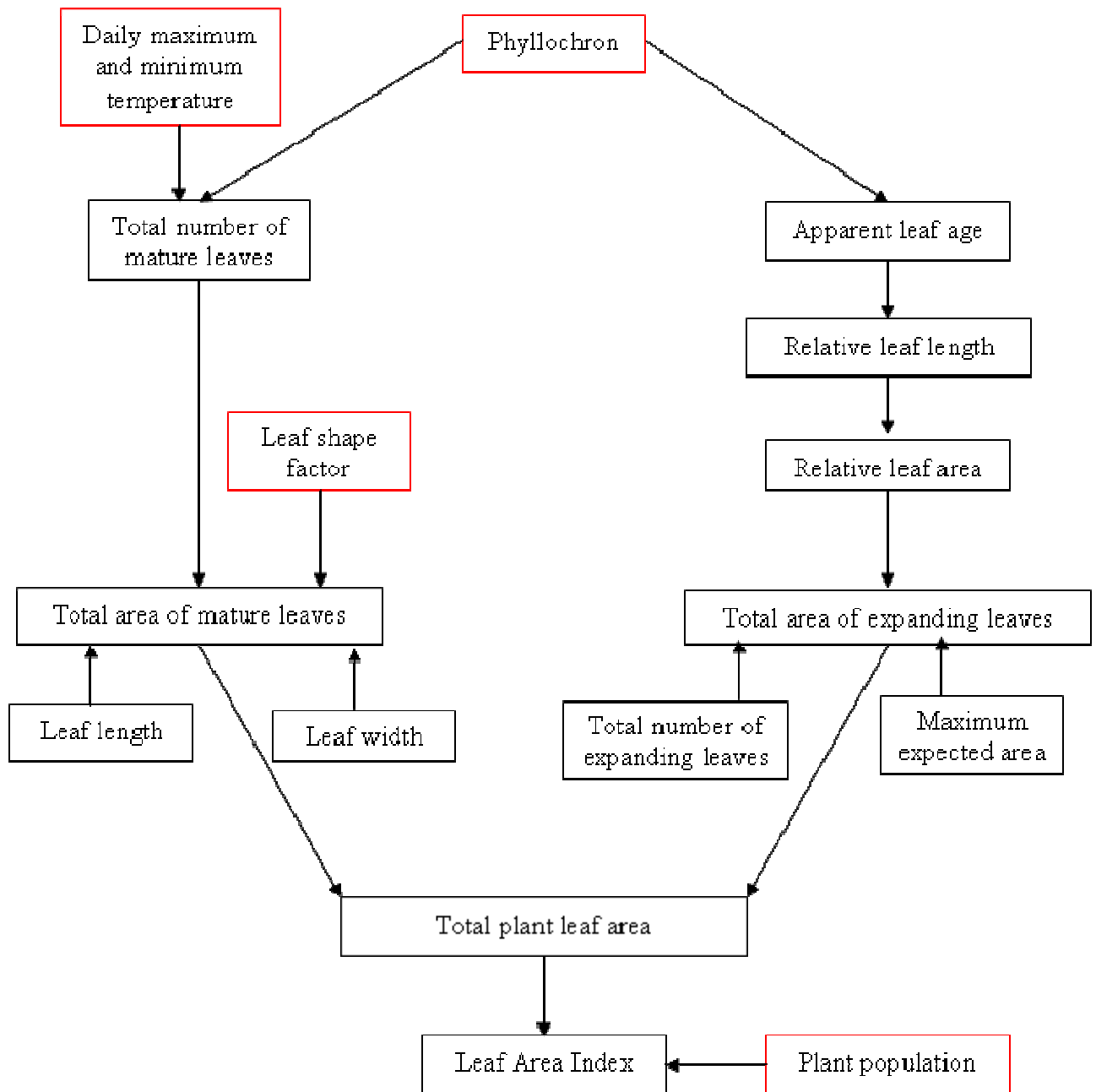


Figure 3.1. Flowchart showing scheme of leaf area production model. Red boxes indicate inputs for the model. Arrows connect the derived variables (towards which they point) and the variables needed to derive them (from which they start).

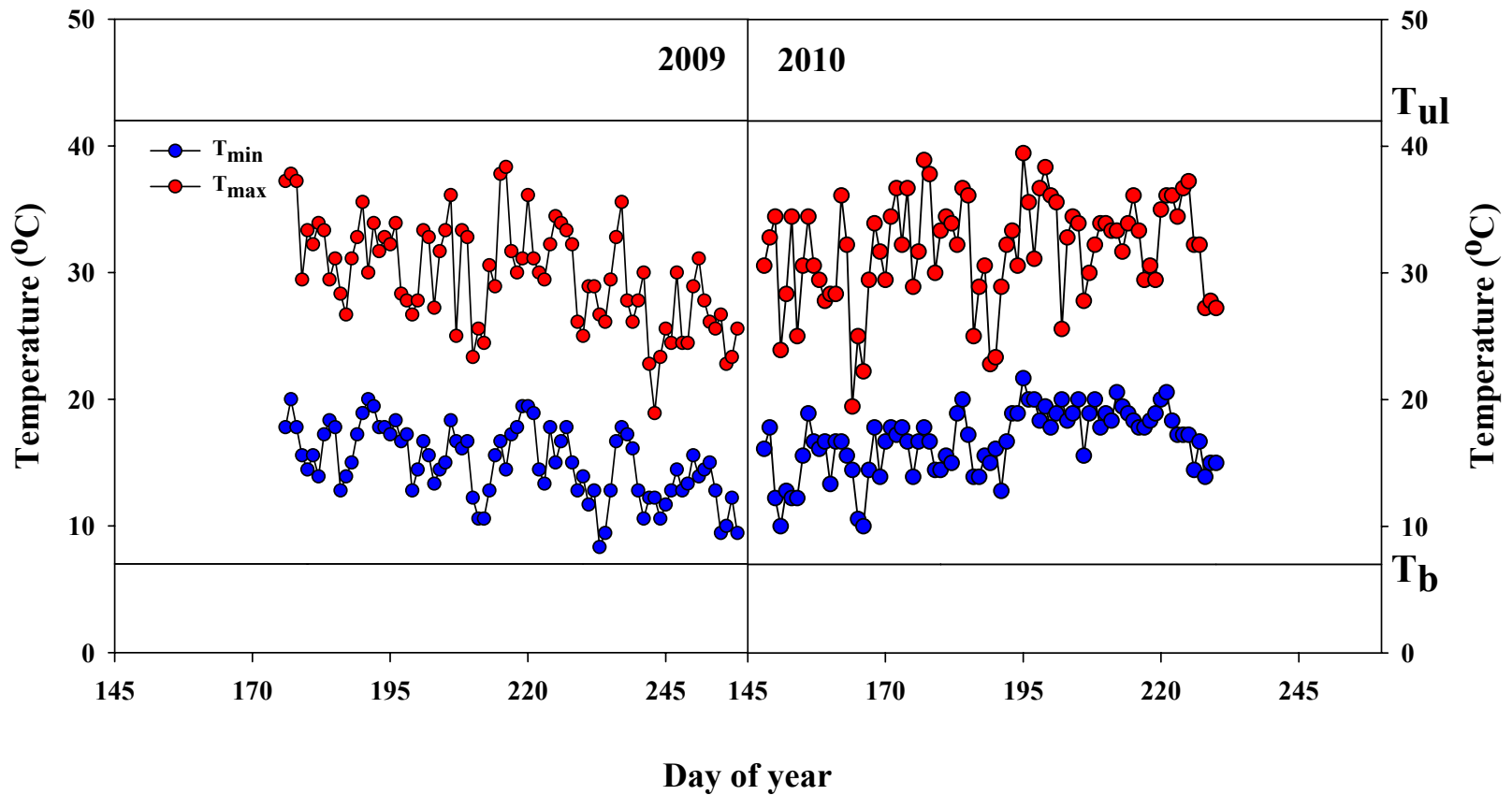


Figure 3.2. Daily maximum (T_{\max}) and minimum (T_{\min}) temperatures during the measurement period [from planting through flag leaf stage (82 days after planting)] for sorghum genotypes grown at Colby, KS in 2009 (left) and 2010 (right).

Base temperature ($T_b = 7^\circ\text{C}$) and upper temperature limit ($T_{ul} = 42^\circ\text{C}$) for sorghum leaf appearance are also indicated.

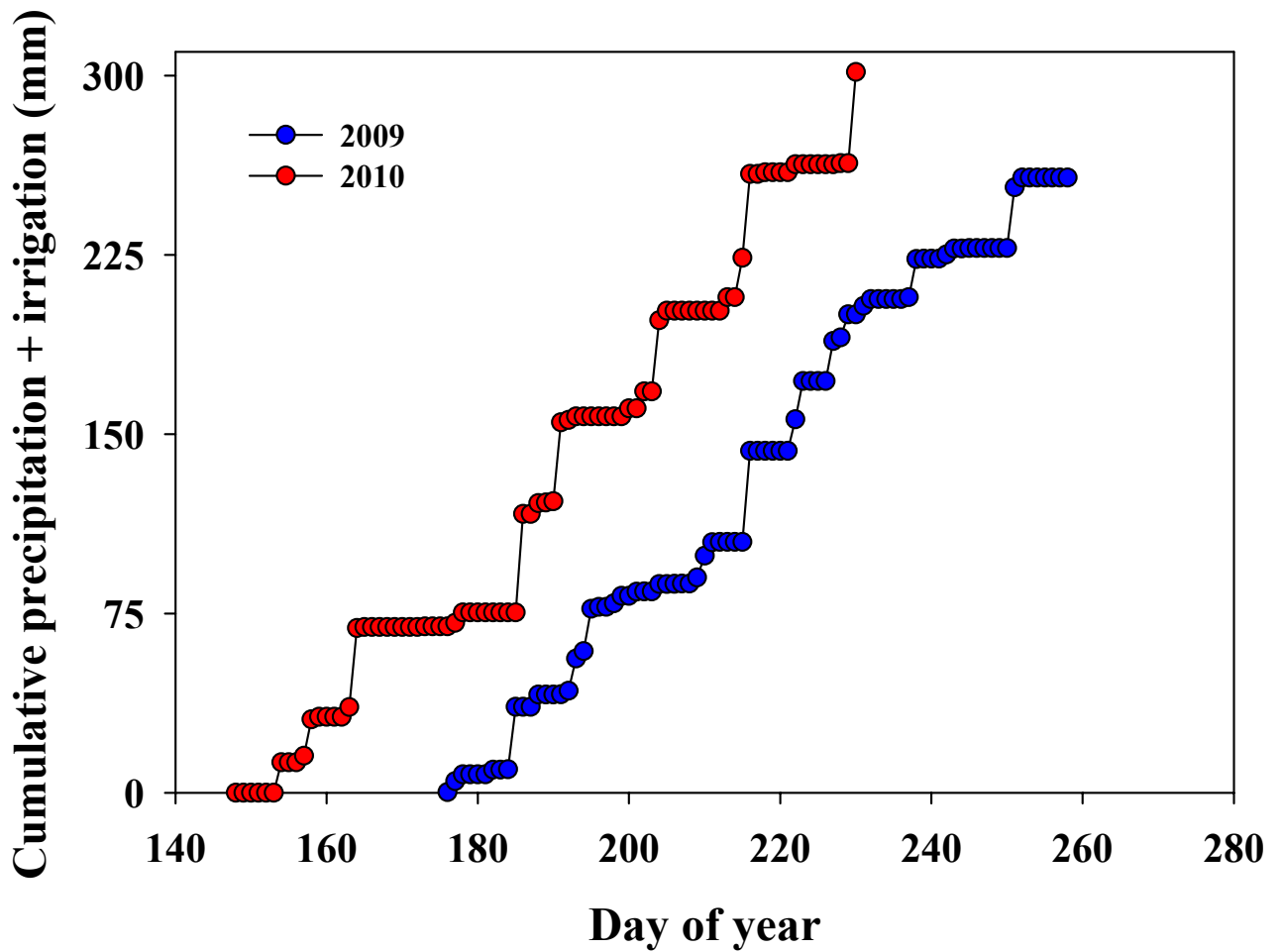


Figure 3.3. Cumulative precipitation and irrigation for the measurement period [from planting through flag leaf stage (82 days after planting)] of sorghum genotypes grown at Colby, KS in 2009 and 2010.

Measurement period started 28 days earlier in 2010 compared to 2009 due to delayed planting in 2009.

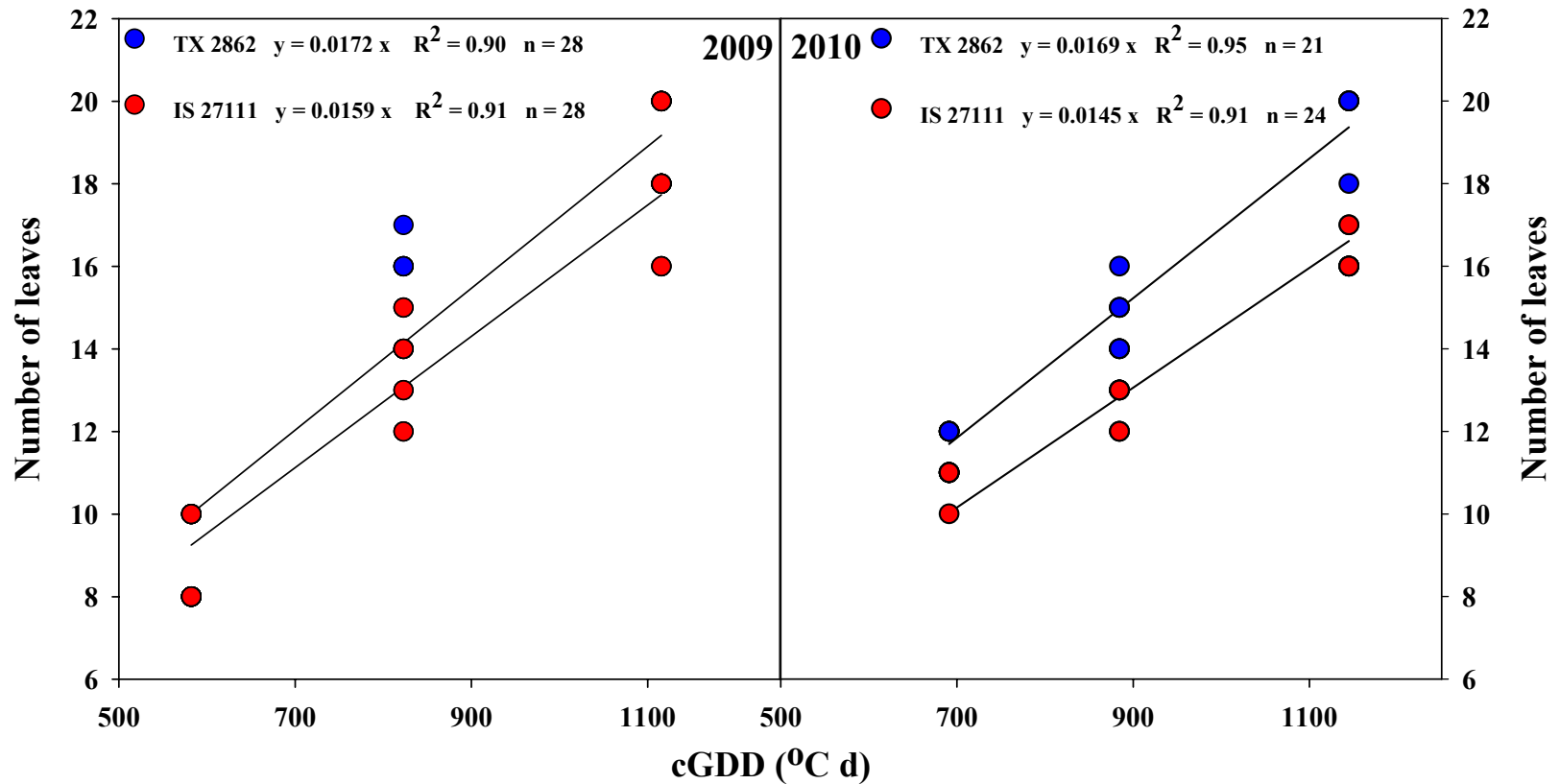


Figure 3.4. Sorghum leaf production in response to accumulation of thermal time [cumulative growing degree days (cGDD)] in 2009 (left) and 2010 (right).

Phyllochron was estimated as the inverse of the slope of observed leaf appearance regressed on cGDD with a suppressed intercept (since intercept was not significantly different from zero). GDD accumulated from the day of planting.

Genotypes with largest and lowest values for phyllochron (IS 27111 and TX 2862 respectively) are shown in the graphs.

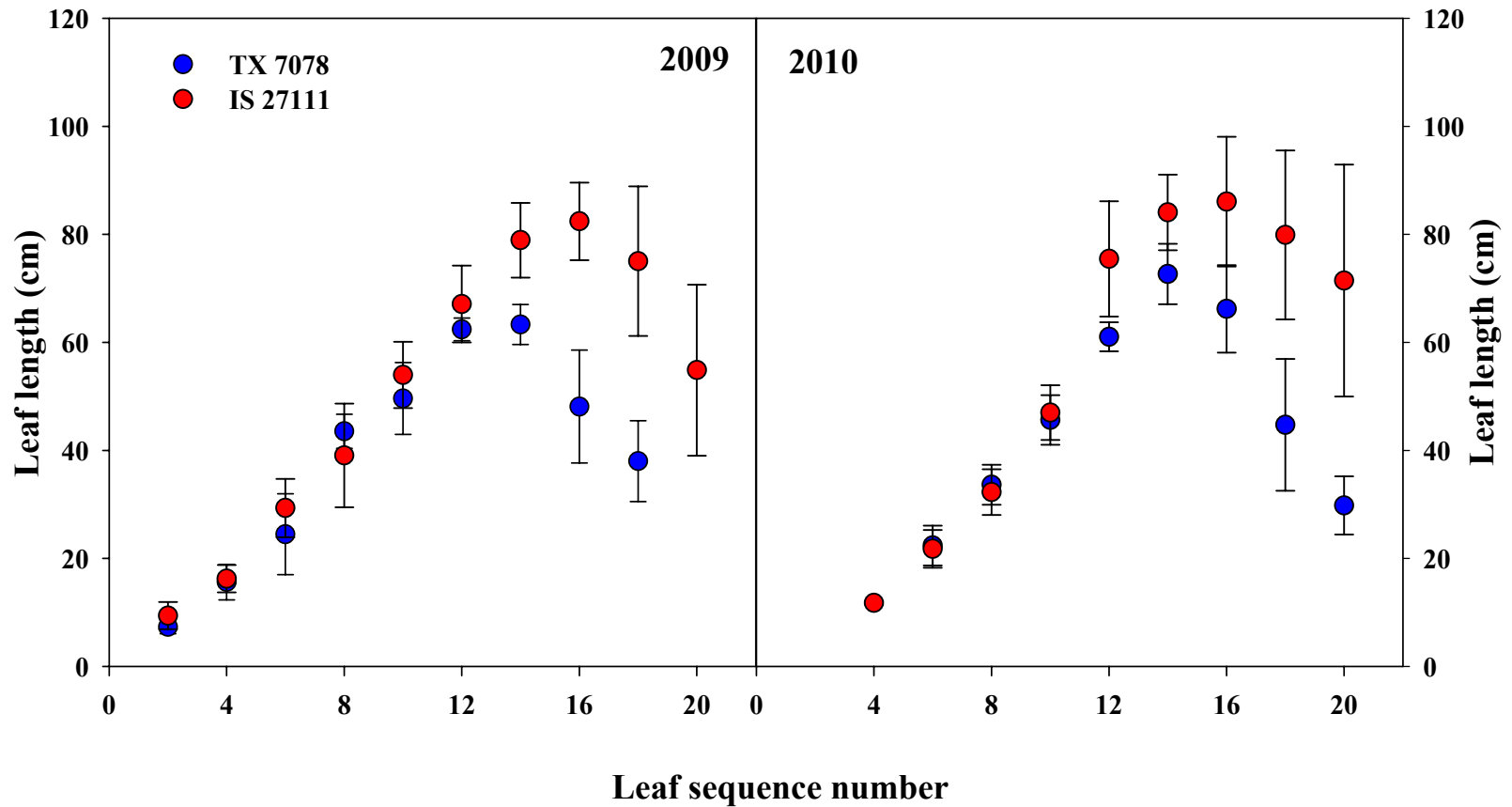


Figure 3.5. Length (mean \pm standard deviation) of different even numbered mature leaves for sorghum genotypes grown at Colby, KS in 2009 (left) and 2010 (right).

Genotype with longest leaves (IS 27111) and shortest leaves (TX 7078) are shown in the graphs. Leaf sequence number refers to the leaf position on the culm.

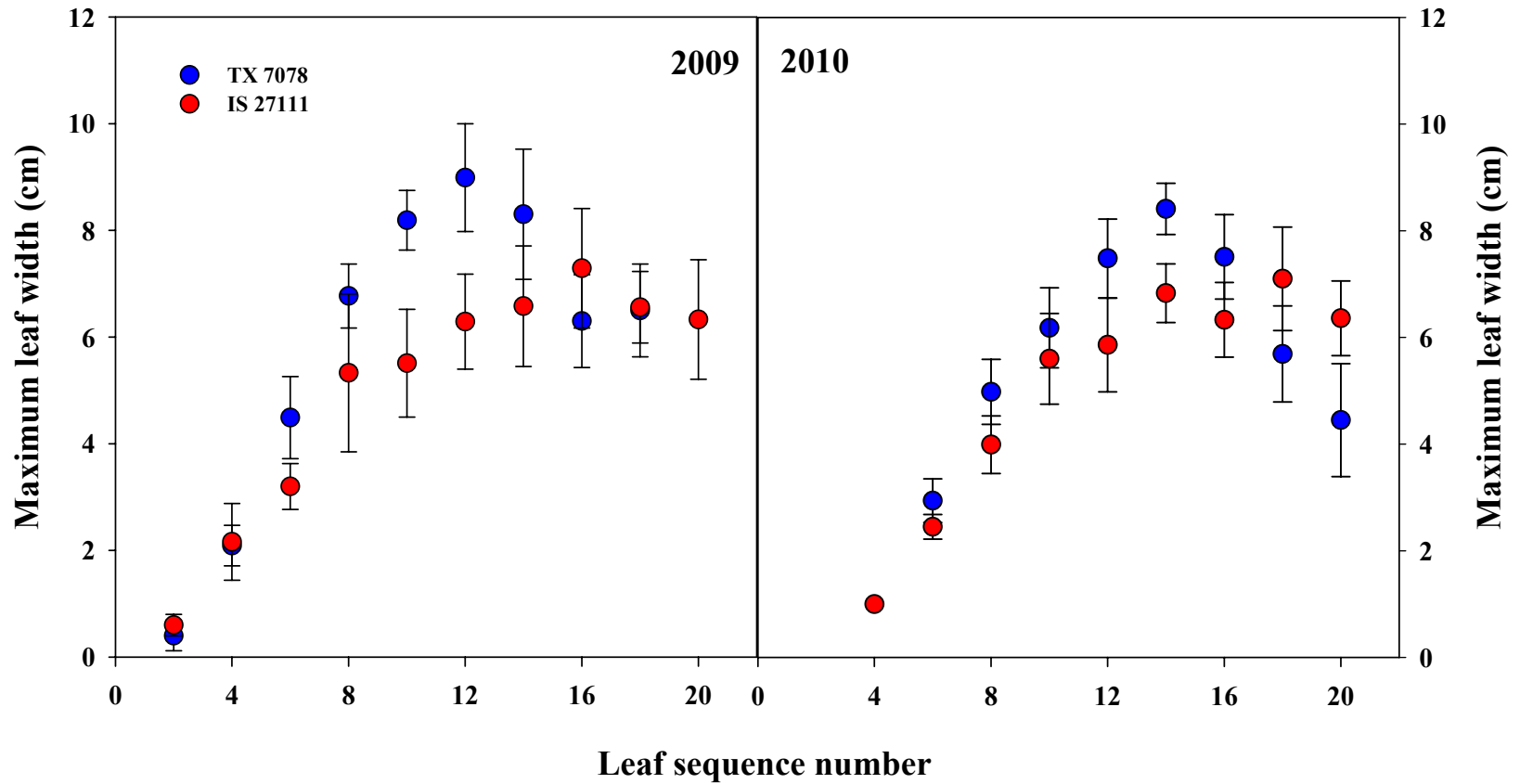


Figure 3.6. Maximum width (mean \pm standard deviation) of different even numbered mature leaves for sorghum genotypes grown at Colby, KS in 2009 (left) and 2010 (right).

Genotype with narrow leaves (IS 27111) and wide leaves (TX 7078) are shown in the graphs. Leaf sequence number refers to the leaf position on the culm.

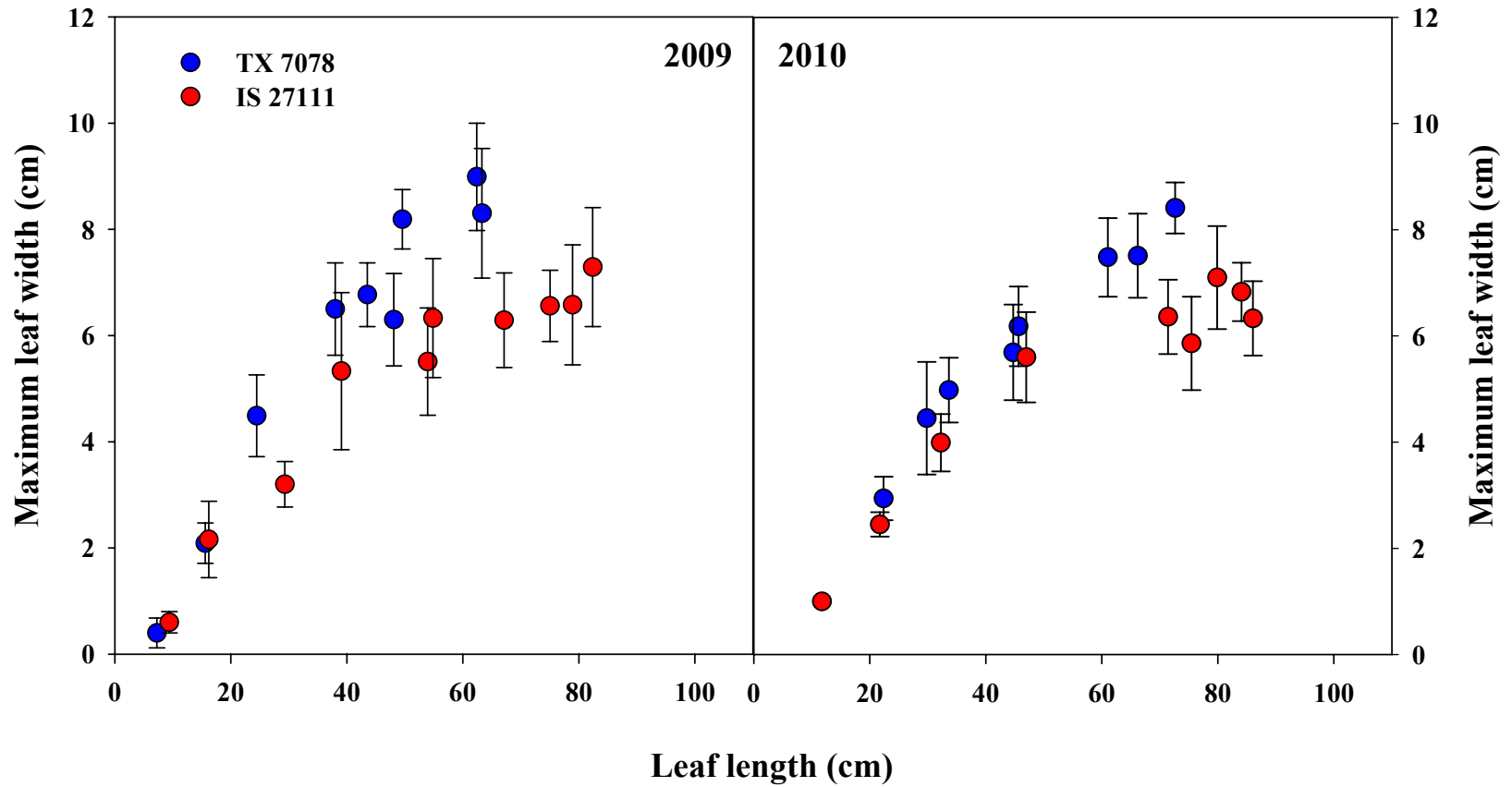


Figure 3.7. Maximum width of mature leaves as a function of leaf length for sorghum genotypes grown at Colby, KS in 2009 (left) and 2010 (right).

Genotype with long, narrow leaves (IS 27111) and short, wide leaves (TX 7078) are shown in the graphs.

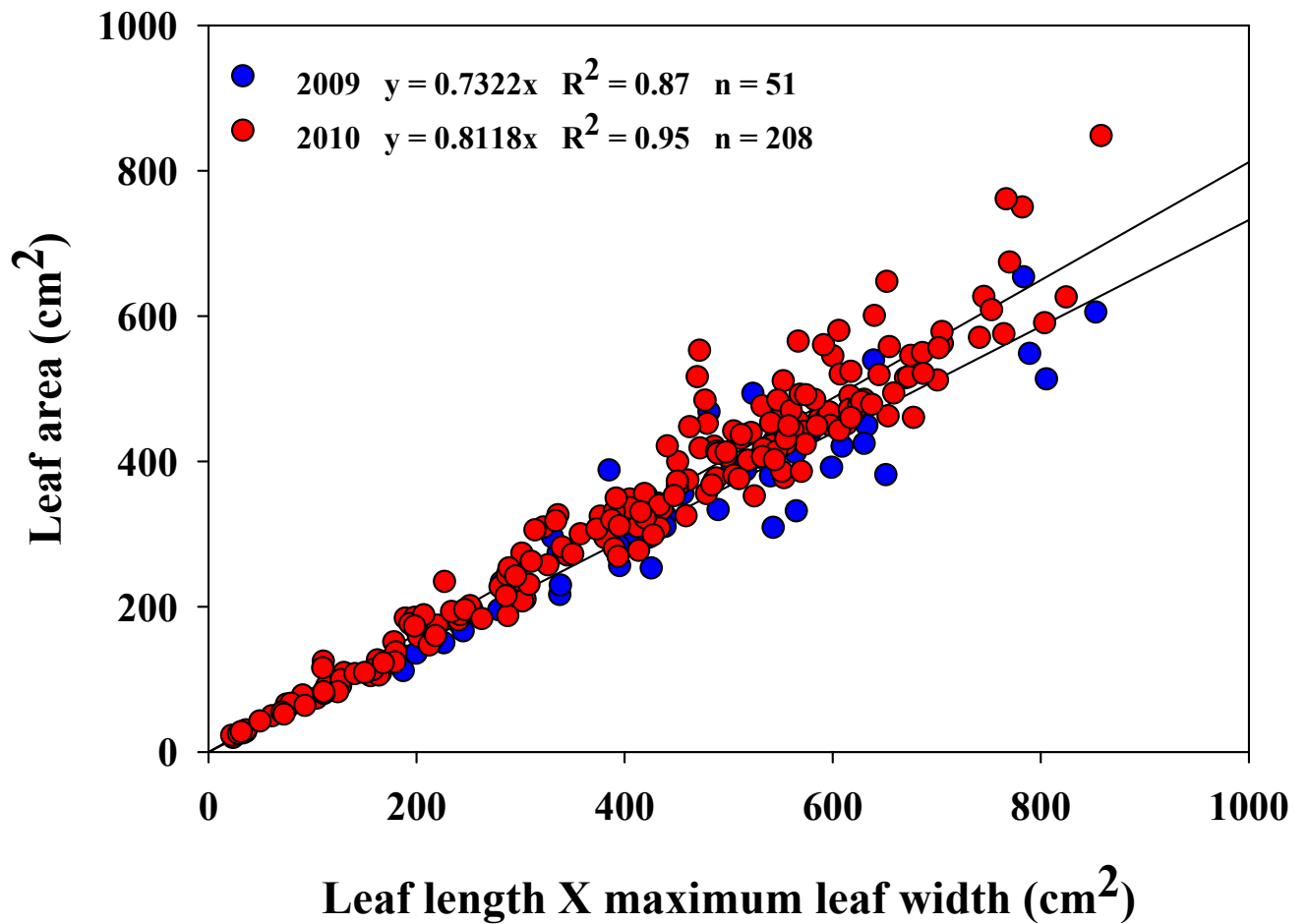


Figure 3.8. Depiction of leaf shape factor in sorghum.

Shape factor was derived as the slope of the regression of observed area of mature leaves on product of observed values of length and maximum width of mature leaves with a suppressed intercept (since intercept was not different from zero). Each symbol in the graph corresponds to a particular leaf.

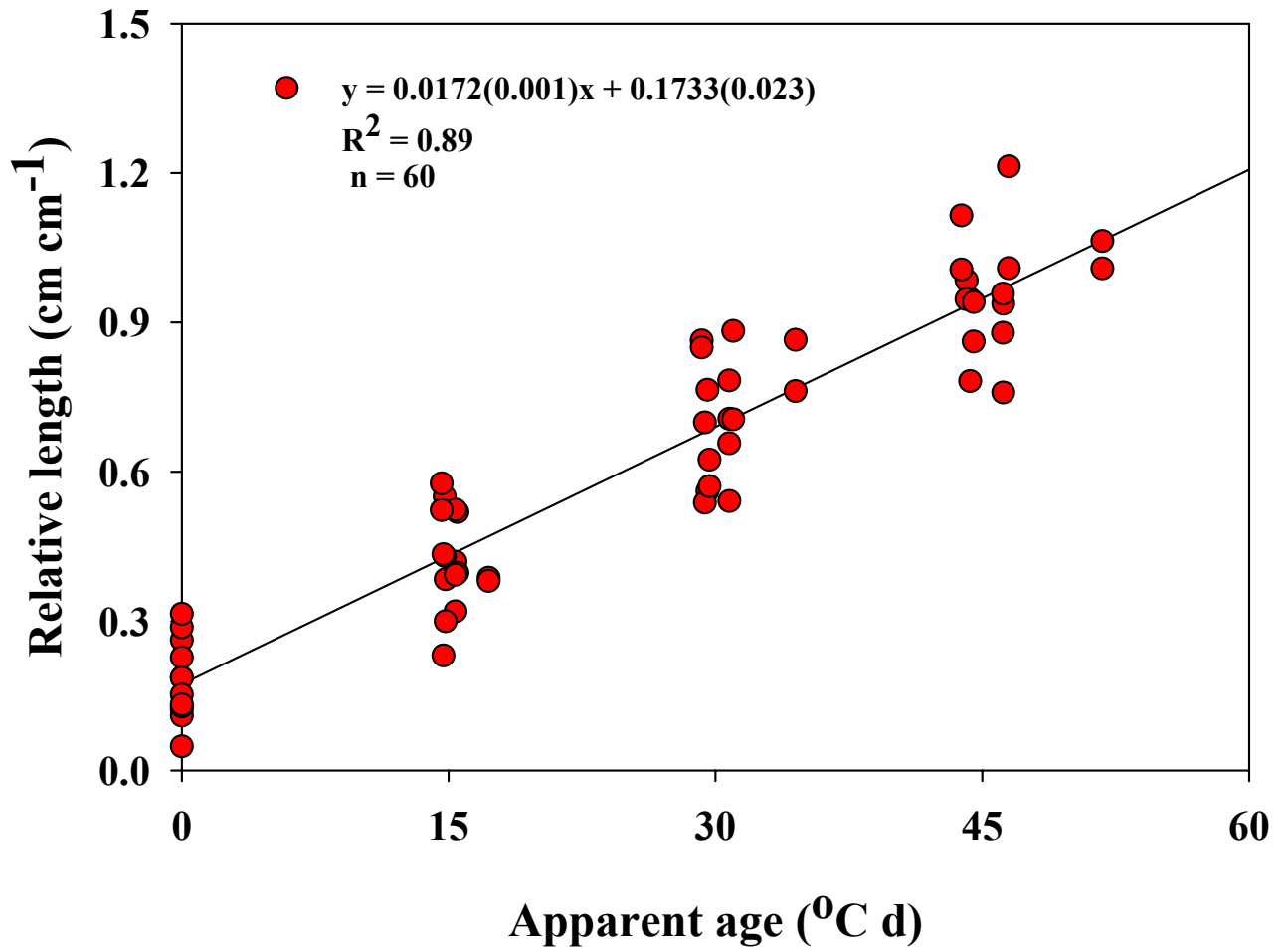


Figure 3.9. Relative length of expanding leaves as a function of their apparent age for sorghum grown at Colby, KS in 2010.

Relative length (Equation 13) is the ratio of length of the portion of expanding leaf lamina that had unwound from the whorl to the expected length of that leaf at ligule formation. Apparent age (°C d, Equation 9) of expanding leaves denotes the thermal time elapsed from their tip appearance. Each symbol in the graph corresponds to a particular leaf. The equation reports the slope (\pm SE) and the intercept (\pm SE) of the regression of relative length on apparent age of expanding leaves.

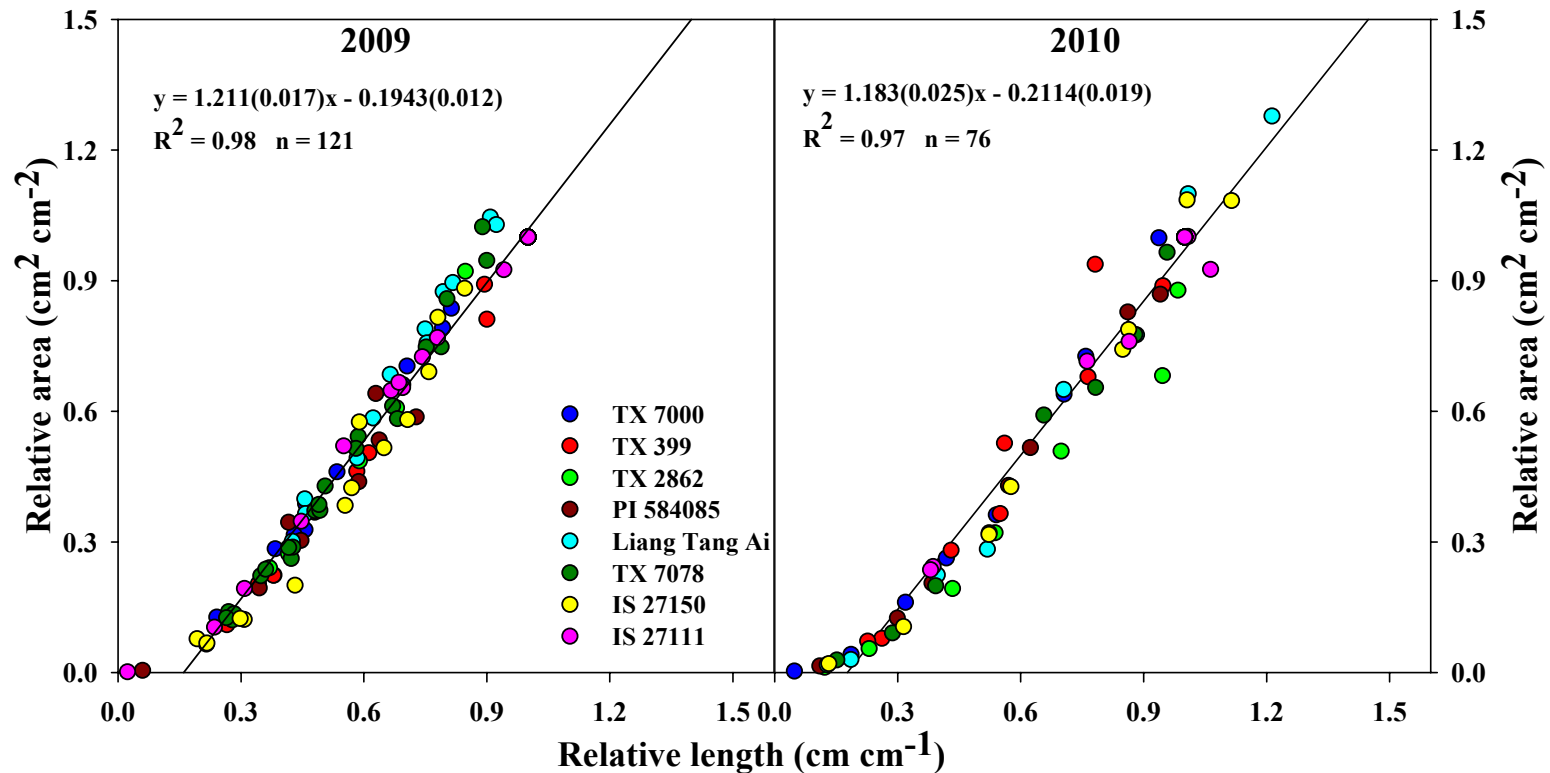


Figure 3.10. Relative area of expanding leaves expressed as a function of their relative length for sorghum grown at Colby, KS in 2009 (left) and 2010 (right).

Relative length or relative area (Equation 14) indicate the ratio of length or area (respectively) of the portion of expanding leaf lamina which had unwound from the whorl to the expected length or area (respectively) of that leaf at ligule formation. The equation reports the slope (\pm SE) and the intercept (\pm SE) of the regression of relative area on relative length of expanding leaves in 2009 and 2010.

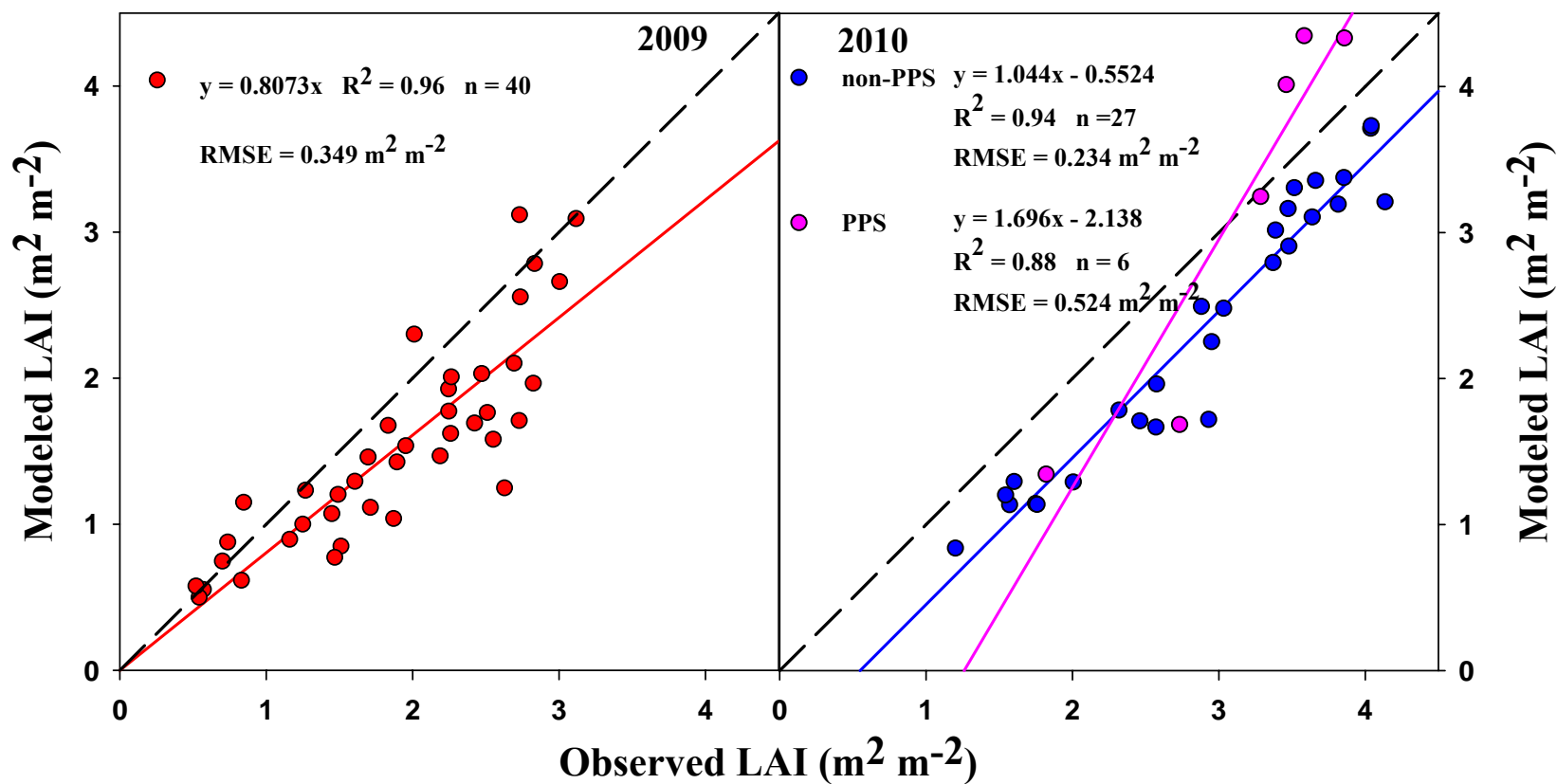


Figure 3.11. Modeled vs. observed leaf area index (LAI) in sorghum.

The dotted line is 1:1 line and the solid line is fitted regression line. Slope of the fitted regression line was different for photoperiod sensitive (PPS) and photoperiod insensitive (non-PPS) genotypes in 2010 while this difference was absent in 2009. Intercept of the fitted regression line was not significantly different from zero in 2009.

Table 3.1. Observed plant population (mean \pm standard deviation) of sorghum genotypes grown at Colby, Kansas in 2009 and 2010.

| Genotypes | Photoperiod sensitivity | Average plant population (plants m ⁻²) | |
|---------------|-------------------------|--|-------------|
| | | 2009 | 2010 |
| TX 7000 | Normal | 6.06 (0.85) | 6.6 (1.2) |
| TX 2862 | Normal | 4.17 (0.64) | 6.84 (1.0) |
| PI 584085 | Normal | 3.47 (0.93) | – |
| Liang Tang Ai | Normal | 5.68 (1.3) | 7.72 (1.5) |
| TX 7078 | Normal | 5.14 (1.5) | 5.91 (0.47) |
| TX 399 | Late flowering | 3.90 (0.90) | 5.54 (0.40) |
| IS 27150 | Late flowering | 6.47 (1.2) | 7.36 (1.5) |
| IS 27111 | PPS | 5.68 (0.92) | 9.08 (1.4) |

Observations on plant populations were made on 14 days after planting (DAP) in 2009 and 33 DAP in 2010. Plant counts included only main culm.

Table 3.2. Slope ($P^{-1} \pm$ standard error) of regression of total leaf number (TLN; measured through 16–20 leaves) of different sorghum genotypes grown in well watered condition, regressed on observed cumulative growing degree days (cGDD) with a suppressed intercept (since intercept was not significantly different from zero).

| Genotype | Year | P^{-1} ($^{\circ}\text{C d}$) ⁻¹ | P^* ($^{\circ}\text{C d}$) |
|---------------|------|--|-----------------------------------|
| TX 7000 | 2009 | 0.01609 (0.00028) | 62 |
| | 2010 | 0.01624 (0.00025) | 62 |
| TX 2862 | 2009 | 0.01718 (0.00031) | 58 |
| | 2010 | 0.01700 (0.00018) | 59 |
| PI 584085 | 2009 | 0.01657 (0.00025) | 60 |
| | 2010 | 0.01685 (0.00028) | 59 |
| Liang Tang Ai | 2009 | 0.01539 (0.00034) | 65 |
| | 2010 | 0.01613 (0.00017) | 62 |
| TX 7078 | 2009 | 0.01517 (0.00032) | 66 |
| | 2010 | 0.01625 (0.00020) | 62 |
| TX 399 | 2009 | 0.01707 (0.00027) | 59 |
| | 2010 | 0.01692 (0.00015) | 59 |
| IS 27150 | 2009 | 0.01607 (0.00034) | 62 |
| | 2010 | 0.01711 (0.00028) | 58 |
| IS 27111 | 2009 | 0.01527 (0.00024) | 65 |
| | 2010 | 0.01450 (0.00015) | 69 |

*Phyllochron (P) was estimated as the inverse of P^{-1} .

Table 3.3. Estimates of fitted coefficients (\pm standard error) for the prediction equations of length and maximum width of mature leaves for sorghum genotypes, grown at Colby, KS in 2009 and 2010.

a. Estimates of fitted coefficients for the prediction equation (Equation 4) of length of mature leaves (L) using leaf sequence number (LN) as predictive variable

| Coefficient | Year | Estimate (\pm standard error) | | | | | | | |
|-------------|------|----------------------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
| | | TX 7000 | TX 2862 | PI 584085 | Liang Tang Ai | TX 7078 | TX 399 | IS 27150 | IS 27111 |
| a_1 | 2009 | -0.0440 (0.0037) | -0.0334 (0.0026) | -0.0462 (0.0026) | -0.0543 (0.0044) | -0.0526 (0.0046) | -0.0252 (0.0023) | -0.033 (0.0030) | -0.0408 (0.0023) |
| | 2010 | -0.0309 (0.0013) | -0.0309 (0.0013) | -0.0309 (0.0013) | -0.0309 (0.0013) | -0.0309 (0.0013) | -0.0309 (0.0013) | -0.0309 (0.0013) | -0.0309 (0.0013) |
| b_1 | 2009 | 0.9813 (0.0680) | 0.7866 (0.0529) | 1.045 (0.053) | 1.059 (0.0786) | 1.038 (0.0803) | 0.6637 (0.0477) | 0.7966 (0.0595) | 0.9533 (0.0486) |
| | 2010 | 0.7774 (0.0293) | 0.7774 (0.0293) | 0.7774 (0.0293) | 0.7774 (0.0293) | 0.7774 (0.0293) | 0.7774 (0.0293) | 0.7774 (0.0293) | 0.7774 (0.0293) |
| c_1 | 2009 | - | - | - | - | - | - | - | - |
| | 2010 | - | - | - | - | - | - | - | - |
| d_1 | 2009 | 3.1421 (2.814) | 6.137 (2.622) | -1.022 (2.622) | 4.042 (3.083) | 1.555 (2.937) | 4.412 (2.543) | 9.154 (2.829) | 2.392 (2.667) |
| | 2010 | -0.364 (2.587) | 3.095 (2.359) | 4.397 (2.840) | -4.132 (2.587) | -4.991 (2.778) | 2.125 (2.396) | 0.6185 (2.545) | 7.236 (2.387) |

The coefficient for the linear term (c_1) in the relationship between L and LN (Equation 4) was not significantly different from zero in 2009 and 2010. Therefore, L was parameterized in the model by a third order linear function of LN as $L = a_1(LN)^3 + b_1(LN)^2 + d_1$.

b. Estimates of fitted coefficients for the prediction equation (Equation 5) of maximum width (W) of mature leaves using leaf length (L) as predictive variable

| Coefficient | Year | Estimate (\pm standard error) | | | | | | | |
|-------------|------|----------------------------------|----------------------|----------------------|----------------------|----------------------|----------------------|----------------------|----------------------|
| | | TX 7000 | TX 2862 | PI 584085 | Liang Tang Ai | TX 7078 | TX 399 | IS 27150 | IS 27111 |
| a_w | 2009 | – | – | – | – | – | – | – | – |
| | 2010 | 0.000011 (5.4E–6) | 0.000011 (5.4E–6) | 0.000011 (5.4E–6) | 0.000011 (5.4E–6) | 0.000011 (5.4E–6) | 0.000011 (5.4E–6) | 0.000011 (5.4E–6) | 0.000011 (5.4E–6) |
| b_w | 2009 | –0.0012 (0.0001) | –0.0016 (0.0001) | –0.0012 (0.0001) | –0.0009 (0.0002) | –0.0012 (0.0002) | –0.0011 (0.0001) | –0.0013 (0.0001) | –0.0015 (0.0001) |
| | 2010 | –0.0028 (0.0008) | –0.0028 (0.0008) | –0.0028 (0.0008) | –0.0028 (0.0008) | –0.0028 (0.0008) | –0.0028 (0.0008) | –0.0028 (0.0008) | –0.0028 (0.0008) |
| c_w | 2009 | 0.2177 (0.0113) | 0.2177 (0.0113) | 0.2177 (0.0113) | 0.2177 (0.0113) | 0.2177 (0.0113) | 0.2177 (0.0113) | 0.2177 (0.0113) | 0.2177 (0.0113) |
| | 2010 | 0.2758 (0.0375) | 0.2758 (0.0375) | 0.2758 (0.0375) | 0.2758 (0.0375) | 0.2758 (0.0375) | 0.2758 (0.0375) | 0.2758 (0.0375) | 0.2758 (0.0375) |
| d_w | 2009 | –0.7664 (0.3688) | –1.253 (0.3578) | –1.370 (0.3698) | –1.470 (0.3662) | –0.3473 (0.3626) | –0.5095 (0.3536) | –1.687 (0.3986) | –1.353 (0.3684) |
| | 2010 | –1.459 (0.5158) | –2.027 (0.5103) | –1.146 (0.5345) | –0.7515 (0.5241) | –1.5575 (0.5418) | –0.9091 (0.5134) | –2.162 (0.5266) | –2.881 (0.5341) |

The coefficient for the cubic term (a_w) in the relationship between W and L (Equation 5) was not significantly different from zero in 2009. Therefore, W was parameterized in the model by a second order linear function of L in 2009 as $W = b_w(L)^2 + c_w(L) + d_w$, and a third order linear function of L in 2010 as $W = a_w(L)^3 + b_w(L)^2 + c_w(L) + d_w$.

Table 3.4. Estimates of fitted coefficients (\pm standard error) for the relationship of relative area (RAx) and relative length (RLx) of expanding leaves (Equation 14) for sorghum genotypes in 2009.

| Parameter | Genotypes | | | | | | | |
|-----------|--------------------|--------------------|--------------------|--------------------|--------------------|--------------------|--------------------|--------------------|
| | TX 7000 | TX 2862 | PI 584085 | Liang Tang Ai | TX 7078 | TX 399 | IS 27150 | IS 27111 |
| Slope | 1.203 (0.046) | 1.250 (0.064) | 1.124 (0.043) | 1.262 (0.058) | 1.253 (0.033) | 1.220 (0.043) | 1.243 (0.039) | 1.099 (0.040) |
| intercept | -0.1820 (0.031) | -0.2312 (0.049) | -0.1522 (0.028) | -0.1909 (0.045) | -0.2209 (0.022) | -0.2252 (0.030) | -0.2406 (0.027) | -0.1012 (0.029) |

RLx or RAx (Equation 14) of expanding leaves indicate the ratio of length or area (respectively) of the portion of expanding leaf lamina which had unwound from the whorl to the expected length or area (respectively) of that leaf at ligule formation. RAx linearly related to RLx such as $RAx = c_q(RLx) + d_q$, where c_q is the slope and d_q is the intercept. The model that fits specific slope and intercept for different genotypes had an R^2 of 0.984, root mean square error (RMSE) of $0.044 \text{ m}^2 \text{ m}^{-2}$ and coefficient of variation (CV) of 7.48 in 2009. Fitting common coefficients for all genotypes [$RAx = 1.211 \pm 0.017(RLx) - 0.194 \pm 0.012$] changed R^2 , RMSE and CV to 0.978, $0.049 \text{ m}^2 \text{ m}^{-2}$ and 8.35 respectively.

Table 3.5. Linear regression equations, number of observations (n), coefficient of determination (R^2), standard error (SE), root mean square error (RMSE), percentage RMSE (RMSE %), mean absolute error (MAE) and percent bias (PBIAS) of modeled vs. observed values of sorghum leaf area index (LAI) from emergence to maximum leaf production at Colby, KS in 2009 and 2010.

| Year | Equation* | n | R^2 | SE (slope) | SE (intercept) | RMSE ($m^2 m^{-2}$) | RMSE (%) | MAE ($m^2 m^{-2}$) | PBIAS (%) |
|----------------|-----------------------|----|-------|---------------|-------------------|--------------------------|-------------|-------------------------|--------------|
| 2009 | $y = 0.8073x$ | 40 | 0.96 | 0.027 | – | 0.349 | 18.5 | –35.0 | –18.6 |
| 2010 (non PPS) | $y = 1.044x - 0.5524$ | 27 | 0.94 | 0.051 | 0.154 | 0.234 | 8.14 | –53.9 | –18.8 |
| 2010 (PPS) | $y = 1.696x - 2.138$ | 6 | 0.88 | 0.317 | 1.01 | 0.524 | 16.8 | 3.72 | 1.19 |

y = modeled LAI and x = observed LAI

Intercept was not significantly different from zero in the regression of modeled LAI on observed LAI in 2009. Fitting an intercept in the above mentioned relationship changed the regression equations to $y = 0.7665(\pm 0.074)x + 0.0890(\pm 0.150)$ in 2009.

Table 3.6. Calibration requirements of the leaf area index estimation model.

| Coefficient | Indication | Equation in which it is used | Method of estimation |
|----------------------|----------------------------|------------------------------|---|
| T_b | base temperature | Equation 1 | Already reported value from literature |
| T_{ul} | upper limit of temperature | Equation 1 | Already reported value from literature |
| P_i | phyllochron | Equation 7, 9 | Inverse slope of regression of observed TLN ¹ on cGDD ² |
| F | leaf shape factor | Equation 3, 6, 10 | Slope of regression of observed A_m ³ on the product of observed values of L ⁴ and W ⁵ |
| a_l, b_l, c_l, d_l | fitted coefficients | Equation 4 | Analysis of covariance using observed values of L and LN ⁶ |
| a_w, b_w, c_w, d_w | fitted coefficients | Equation 5 | Analysis of covariance using observed values of W and L |
| c_g, d_g | fitted coefficients | Equation 13 | Analysis of covariance using derived values of $ALGx$ ⁷ and RLx ⁸ |
| c_q, d_q | fitted coefficients | Equation 14 | Analysis of covariance using derived values of RLx and RAx ⁹ |
| PLN | plant population | Equation 18 | Field observation |

1. TLN – total number of leaves on the plant, 2. cGDD – cumulative growing degree days, 3. A_m – Area of mature leaves, 4. L – length of mature leaves, 5. W – maximum width of mature leaves, 6. LN – leaf sequence number, 7. $ALGx$ – apparent leaf age of expanding leaves, 8. RLx – relative length of expanding leaves, 9. RAx – relative area of expanding leaves. Terms are defined when introduced in the text.

Table 3.7. Angle (from the vertical) and length of linear segment (from leaf collar to the point where the linearity of leaf lamina ends) of top mature leaf (TML, top fully expanded leaf with a ligule), the expanding leaf that will be at one node above the TML (TML+1) and the fully expanded leaf one node below TML (TML-1) of sorghum grown in green house, Colby, KS in 2009 and 2010.

| Leaf | Angle (degree) | | Length (cm) | |
|-------|-----------------|-----------------|--------------------|---------------------|
| | 2009 | 2010 | 2009 | 2010 |
| TML | 13 ^b | 30 ^b | 6.81 ^{ab} | 25.66 ^{ab} |
| TML+1 | 13 ^b | 27 ^b | 10.5 ^a | 30.37 ^a |
| TML-1 | 26 ^a | 37 ^a | 4.88 ^b | 19.75 ^b |
| LSD | 9 | 6 | 3.98 | 6.61 |

Details of this study are given as additional information (Appendix B)

Appendix A - Appendix Tables

Table A.1. Slope, standard error of slope (SE), coefficient of determination (R^2), root mean square error (RMSE) and total number of observations (n) for the first order linear relationship between above-ground biomass and stem volume (Reported in chapter 2) for different sorghum genotypes.

| Parameter | Genotypes | | | | | | | |
|-----------|------------|------------|--------------|---------------------|------------|--------|-------------|-------------|
| | TX 7000 | TX 2862 | PI 584085 | Liang Tang Ai | TX 7078 | TX 399 | IS 27150 | IS 27111 |
| slope | 0.286 | 0.356 | 0.296 | 0.235 | 0.314 | 0.291 | 0.434 | 0.351 |
| SE | 0.009 | 0.012 | 0.004 | 0.008 | 0.012 | 0.008 | 0.014 | 0.011 |
| R^2 | 0.96 | 0.95 | 0.91 | 0.94 | 0.93 | 0.96 | 0.95 | 0.95 |
| RMSE | 7.62 | 7.19 | 10.5 | 10.3 | 8.79 | 7.06 | 8.97 | 6.13 |
| n | 52 | 51 | 363 | 51 | 51 | 52 | 53 | 53 |

Intercept was not significant for the relationship between above-ground biomass and stem volume. Since information needed to calibrate allometric relationship between above ground dry matter and stem volume was absent for the genotype PI 584085, data collected on other genotypes were pooled to derive an equation for genotype PI 584085.

Table A.2. Analysis of variance for observed variables of interest (presented in Table 2.2.) for sorghum genotypes differing in water use efficiency and grown in well watered and limited irrigation conditions at Colby, KS in 2009.

| Source of variation | df | F value for type III tests of fixed effects | | | | |
|---------------------|----|---|------------------|------------|-----------|------------|
| | | Stem ht [†] | Internode length | Biomass | Water use | CIPAR |
| Genotype | 7 | 134.45 ***** | 127.44 ***** | 11.99***** | 3.5** | 12.51***** |
| Irrigation | 1 | — | — | 0.17 | 8.93** | 1.3 |
| Irrigation*Genotype | 7 | — | — | 0.95 | 0.29 | 0.54 |

* indicates significance at $P < 0.1$

** indicates significance at $P < 0.05$

*** indicates significance at $P < 0.01$

**** indicates significance at $P < 0.001$

***** indicates significance at $P < 0.0001$

† Observations on plant height were recorded only for well watered plots.

Table A.3. Analysis of variance for observed variables of interest (presented in Table 2.2.) for sorghum genotypes differing in water use efficiency and grown in well watered condition at Colby, KS in 2010.

| Source of variation | df | F value for type III tests of fixed effects | | | | |
|---------------------|----|---|------------------|---------|-----------|------------|
| | | Stem ht | Internode length | Biomass | Water use | CIPAR |
| Genotype | 6 | 940.7 ***** | 479.85 ***** | 3.65* | 1.39 | 12.39***** |

* indicates significance at $P < 0.1$

** indicates significance at $P < 0.05$

*** indicates significance at $P < 0.01$,

**** indicates significance at $P < 0.001$,

***** indicates significance at $P < 0.0001$

Table A.4. Analysis of covariance for modeling biomass as linear functions of days after planting (DAP; reported in Chapter 2).

| Source of variation | F value (df) | | | |
|-----------------------------|---------------------------|----------------------------|-----------------------------|---------------------------|
| | Full model | | Reduced model | |
| | 2009 | 2010 | 2009 | 2010 |
| Genotype | 0.77 (8) [†] | 2.18 (7) ^{†**} | 5.84 (8) ^{*****} | 2.18 (7) ^{**} |
| DAP | 0.05 (1) | 16.89 (1) ^{*****} | – | – |
| DAP ² | 12.53 (1) ^{****} | 33.74 (1) ^{*****} | – | – |
| DAP ³ | – | 16.63 (1) ^{*****} | – | – |
| DAP * Genotype | 0.88 (7) | 1.38 (6) | – | 3.72 (7) ^{****} |
| DAP ² * Genotype | 1.19 (7) | 1.64 (6) | 143.17 (8) ^{*****} | 6.62 (7) ^{*****} |
| DAP ³ * Genotype | – | 1.64 (6) | – | 7.02 (7) ^{*****} |

[†] Including entry and specifying no intercept in the model statement results in 8 degrees of freedom for genotype in 2009 and 7 degrees of freedom in 2010.

Table A.5. Analysis of covariance for modeling leaf area index as linear functions of days after planting (DAP; reported in Chapter 2).

| Source of variation | F value (df) | | | |
|-----------------------------|-----------------|-----------------|-----------------|----------------|
| | Full model | | Reduced model | |
| | 2009 | 2010 | 2009 | 2010 |
| Genotype | 5.13 (8) ***** | 19.74 (7)** | 25.97 (8)***** | 20.38 (7)***** |
| DAP | 22.93 (1) ***** | 150.85 (1)***** | | |
| DAP ² | 13.19 (1)***** | 102.05 (1)***** | | |
| DAP ³ | 4.04 (1)** | 9.70 (1)***** | | |
| DAP * Genotype | 2.03 (7) | 0.56 (6) | 46.64 (8) ***** | 67.65 (7)***** |
| DAP ² * Genotype | 1.95 (7) | 0.54 (6) | 30.78 (8)***** | 68.44 (7)***** |
| DAP ³ * Genotype | 1.82 (7) | 0.49 (6) | | |

Table A.6. Analysis of covariance for modeling cumulative water use as linear functions of days after planting (DAP; Reported in Chapter 2).

| Source of variation | F value (df) | | | |
|-----------------------------|-----------------|----------------|------------------|---------------|
| | Full model | | Reduced model | |
| | 2009 | 2010 | 2009 | 2010 |
| Genotype | 11.39 (8) ***** | 4.63 (7)***** | 113.78 (8)***** | 10.9 (7)***** |
| DAP | 36.28 (1) ***** | 46.98 (1)***** | | |
| DAP ² | 0.28 (1) | 72.23 (1)***** | | |
| DAP ³ | 3.72 (1) | 7.84 (1)*** | | |
| DAP * Genotype | 1.48 (7) | 0.65 (6) | 163.47 (8) ***** | 7.88 (7)***** |
| DAP ² * Genotype | 1.43 (7) | 0.54 (6) | 32.14 (8)***** | 0.37 (7)***** |
| DAP ³ * Genotype | 1.33 (7) | 0.46 (6) | | |

Table A.7. Analysis of variance for observed variables of interest (reported in chapter 3) for sorghum genotypes differing in canopy architecture, grown at Colby, KS in 2009 and 2010.

a. Leaf length as dependent variable

| Source of variation | F value (df) | | | |
|-------------------------------------|-----------------------|----------------|-----------------|-----------------|
| | Full model | | Reduced model | |
| | 2009 | 2010 | 2009 | 2010 |
| Genotype | 1.22 (8) [†] | 0.66 (8) | 2.90 (8) ** | 4.37 (8) **** |
| Leaf number | 0.67 (1) | 1.41 (1) | – | – |
| Leaf number ² | 74.22 (1) **** | 34.90 (1) **** | – | 702.30 (1) **** |
| Leaf number ³ | 145.47 (1) **** | 82.60 (1) **** | – | 578.69 (1) **** |
| Leaf number * Genotype | 1.31 (7) | 0.58 (7) | – | – |
| Leaf number ² * Genotype | 2.13 (7) * | 0.85 (7) | 241.21 (8) **** | – |
| Leaf number ³ * Genotype | 3.33 (7) *** | 1.57 (7) | 182.47 (8) **** | – |

[†] Including entry and specifying no intercept in the model statement results in 8 degrees of freedom for genotype.

b. Maximum leaf width as dependent variable

| Source of variation | F value (df) | | | |
|-------------------------------------|----------------|----------------|-----------------|----------------|
| | Full model | | Reduced model | |
| | 2009 | 2010 | 2009 | 2010 |
| Genotype | 1.03 (8) | 4.11 (8) **** | 4.31 (8) **** | 20.42 (8) **** |
| Leaf length | 33.80 (1) **** | 38.18 (1) **** | 368.75 (1) **** | 54.13 (1) **** |
| Leaf length ² | 2.03 (1) | 17.00 (1) **** | | 11.59 (1) *** |
| Leaf length ³ | 0.64 (1) | 3.36 (1) * | | 3.92 (1) * |
| Leaf length * Genotype | 0.80 (7) | 0.91 (7) | | |
| Leaf length ² * Genotype | 1.15 (7) | 0.81 (7) | 27.12 (8) **** | |
| Leaf length ³ * Genotype | 1.38 (7) | 0.84 (7) | | |

c. Phyllochron as dependent variable

| Source of variation | F value (df) | |
|-------------------------|------------------|----------------|
| | 2009 | 2010 |
| Genotype | 2.07 (7) | 72.21 (7) **** |
| Cumulative GDD | 2160.32 (1) **** | 18.76 (1) **** |
| Cumulative GDD*genotype | 3.68 (7) *** | 66.75 (7) **** |

d. Leaf shape factor as dependent variable

| Source of variation | F value (df) | |
|--------------------------------|---------------|-------------|
| | 2009 | 2010 |
| Genotype | 0.59 (7) | 0.65 (7) |
| Leaf number | 0.07 (1) | 3.82 (1) |
| Leaf number*genotype | 1.09 (7) | 0.62 (7) |
| Area of rectangle | 34.25 (1) *** | 4.78 (1) ** |
| Area of rectangle* genotype | 0.55 (7) | 0.65 (7) |
| Area of rectangle* Leaf number | 0.06 (1) | 0.77 (1) |

e. Relative length of expanding leaf as dependent variable

| Source of variation | F value (df) | |
|------------------------------|--------------|----------------|
| | 2009 | 2010 |
| Genotype | – | 1.09 (7) |
| Apparent age | – | 48.49 (1) **** |
| Apparent age*genotype | – | 0.66 (7) |
| Apparent age square | – | 0.47 (1) |
| Apparent age square*genotype | – | 0.63 (7) |

f. Relative leaf area as dependent variable

| Source of variation | F value (df) | | | |
|---------------------------|--------------|----------|---------|----------|
| | 2009 | | 2010 | |
| Genotype | 2.70 | (7) * | 0.21 | (7) |
| Relative length | 5329.27 | (1) **** | 2031.99 | (1) **** |
| Relative length *genotype | 2.18 | (7) * | 0.39 | (7) |

g. Modeled leaf area index (LAI) as dependent variable

| Source of variation | F value (df) | | | |
|-----------------------|----------------|-----------------|--------------|--------------|
| | 2009 | | 2010 | |
| | All genotypes | All genotypes | Non PPS | PPS |
| Genotype | 0.24 (7) | 1.11 (6) | 0.35 (5) | – |
| Observed LAI | 95.91 (1) **** | 233.51 (1) **** | 291 (1) **** | 28.70 (1) ** |
| Observed LAI*genotype | 0.67 (7) | 1.96 (6) | 0.37 (5) | – |

h. Modeled leaf area index (LAI) as dependent variable [A check for differences in slope of regression of modeled LAI on observed LAI, between photoperiod sensitive (PPS) and insensitive (nonPPS) genotypes]

| Source of variation | F value (df) | | | |
|---------------------------------------|--------------|---------|--------|---------|
| | 2009 | | 2010 | |
| Photoperiod sensitivity | 0.36 | (1) | 7.11 | (1)** |
| Observed LAI | 40.08 | (1)**** | 207.91 | (1)**** |
| Observed LAI* Photoperiod sensitivity | 0.20 | (1) | 13.65 | (1)*** |

i. Angle and length of linear segment of leaves as dependent variables

| Source of variation | F value (df) | | | |
|------------------------|--------------|-------------|------------|------------|
| | Angle | | length | |
| | 2009 | 2010 | 2009 | 2010 |
| Genotype | 0.89 (7) | 2.04 (6) | 0.73 (7) | 3.23 (6) * |
| Leaf position | 5.70 (2) ** | 4.94 (2) ** | 4.08 (2) * | 4.49 (2) * |
| Genotype*leaf position | 1.29 (14) | 1.76 (12) | 0.32 (14) | 0.35 (12) |

*indicates significance at $P < 0.05$,

** indicates significance at $P < 0.01$,

*** indicates significance at $P < 0.001$,

**** indicates significance at $P < 0.0001$

TableA.8. Example for stepwise reduction of a full model into a reduced model utilizing analysis of covariance in PROC MIXED, SAS 9.1.3.

Dependent variable – leaf length (length of different even numbered leaves on a plant for sorghum genotypes grown at Colby, Kansas in 2009)

Class variables – genotype and replication

Covariates – leaf sequence number, leaf sequence number², leaf sequence number³

Step 1. Full model

| Source of variation | F value (df) |
|-------------------------------------|----------------|
| Genotype | 0.66 (8) |
| Leaf number | 1.41 (1) |
| Leaf number ² | 34.90 (1) **** |
| Leaf number ³ | 82.60 (1) **** |
| Leaf number * Genotype | 0.58 (7) |
| Leaf number ² * Genotype | 0.85 (7) |
| Leaf number ³ * Genotype | 1.57 (7) |

† Including entry and specifying no intercept in the model statement results in 8 df for genotype.

Step 2. Reduced model – 1

| Source of variation | F value (df) |
|--------------------------|----------------|
| Genotype | 4.62 (8) **** |
| Leaf number | 3.09 (1) |
| Leaf number ² | 7.36 (1) ** |
| Leaf number ³ | 29.71 (1) **** |

Step 3. Reduced model – 2

| Source of variation | F value (df) |
|--------------------------|-----------------|
| Genotype | 4.37 (8) **** |
| Leaf number ² | 702.30 (1) **** |
| Leaf number ³ | 578.9 (1) **** |

Appendix B - Additional information on procedure for leaf angle measurements.

Observations were made on green house plants under water and nutrient sufficient conditions at approximately 12 leaf stage in 2009 and 8 leaf stage in 2010. Orientation of top mature leaf (TML), the leaf which is at one node below the TML (TML-1) and the expanding leaf which will be at node above the TML (TML+1) was examined. Angle and length of the initial segment of leaf lamina (from ligule to the point where the vertical orientation of leaf lamina ends) were examined. Potted plants were kept against a big graph paper (50 cm X 50 cm) pasted on the wall. The soil level in the pots coincided with the X axis. Coordinates of ligule [$C_1 = (x_1, y_1)$] and end of vertical portion of leaf lamina [$C_2 = (x_2, y_2)$] were recorded for all the three leaves. Assuming radial symmetry of leaves around the culm, C_1 was converted to (0,0); C_2 was adjusted accordingly. Slope was calculated as $\Delta x/\Delta y$. Angle (from the vertical) was calculated as tan inverse of the absolute value of slope. Length of leaf segments was calculated using the distance formula of coordinate geometry ($\sqrt{[(x_2 - x_1)^2 + (y_2 - y_1)^2]}$). Pots were arranged in completely randomized design. Angle and length were compared among TML, TML-1 and TML+1 using analysis of covariance using Proc GLM in SAS 9.1.3. Pair wise comparisons were done using LSD at 0.05 probability level.