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Interrelationships between water use efficiency and light use efficiency in four row crop canopies

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Abstract

Quantitative evidence of light use efficiency (LUE) controls on water use efficiency (WUE) is lacking, especially comparatively across row crops. Field research experiments (2016–2018) were set up for maize (*Zea mays* L.), soybean [*Glycine max* (L.) Merr.], sorghum [*Sorghum bicolor* (L.) Moench], and winter wheat (*Triticum aestivum* L.), under optimal growth conditions in dry sub-humid conditions. Overall, LUE was able to explain 52% of variance in WUE, and were related as WUE = 1.73 LUE, although crop-specific variation was observed. Highest sensitivity of WUE to changes in LUE was found in sorghum, followed by soybean, winter wheat, and maize. Evapotranspiration per unit light absorbed by crop canopy, which is a measure of canopy conductance (g_c) ranged from a minimum of 0.45 kg H_2O MJ^{-1} in sorghum to a maximum of 0.68 kg H_2O MJ^{-1} in maize. Slopes of WUE vs. LUE relationship were limited by energy-limited upper ceiling of latent heat of vaporization and characterized distribution of absorbed energy into latent heat of vaporization and sensible heat. Vapor pressure deficit (VPD) accounted for 41% of variability in the WUE vs. LUE relationship, and the relationship was subject to change with VPD conditions higher or lower than 0.85 kPa. Seasonal evolution of crop-specific g_c was modeled and communicated as a function of heat accumulation during the growing season. The research findings contribute to quantification of critical parameters that bridge water and light use efficiency, and better understanding of the resource use in C_3 and C_4 agricultural row crops.

1 | INTRODUCTION

The efficiency of vegetation to capture and use light and water resources determines crop dry matter production (Monteith, 1994). Among these resources, light provides the energy required for photosynthesis and water governs both leaf-scale photosynthesis by controlling stomatal behavior (Beer, Reichstein, Ciais, Farquhar, & Papale, 2007), and canopy-scale photosynthesis by controlling morphological area (Eamus, Hutley, & O'Grady, 2001).

Abbreviations: AGB, aboveground biomass; APAR, absorbed photosynthetically active radiation; E, evaporation; ET_c, crop evapotranspiration; g_c, canopy conductance; IPAR, intercepted photosynthetically active radiation; LUE, light use efficiency; OLS, ordinary least squares; PAR, photosynthetically active radiation; PAR_{in}, incoming photosynthetically active radiation; PAR_{ref}, reflected photosynthetically active radiation; PAR_{tr}, transmitted photosynthetically active radiation; PPFD, photosynthetic photon flux density; T, transpiration; VPD, vapor pressure deficit; WUE, water use efficiency.

The use-efficiencies of these resources (i.e., light use efficiency, LUE, and water use efficiency, WUE) are effective tools to report sensitivity of dry matter production to light and water supply (Beer et al., 2007; Hu et al., 2008; Ponton et al., 2006; Turner et al., 2003). The LUE and WUE in any vegetative surface can vary with environmental stress and vegetation characteristics (Farquhar, Ehleringer, & Hubick, 1989; Law et al., 2002; Schwalm et al., 2006). Both LUE and WUE have been studied in various agroecosystems via site-specific research (Hamilton, Hussain, Bhardwaj, Basso, & Robertson, 2015; Hattendorf, Redelfs, Amos, Stone, & Gwin, 1988; Kukal & Irmak, 2020a; Kukal & Irmak, 2020b) as well as across spatial and temporal domains (Kukal & Irmak, 2017; Liu, Williams, Zehnder, & Yang, 2007; Lobell & Gourdji, 2012). These efforts have increased our understanding of variability in LUE and WUE in agricultural production systems and its drivers (Shi et al., 2014) and enabled us to further enhance land productivity (Narayanan, Aiken, Prasad, Xin, & Yu, 2013).

Despite these advances, little is known about interrelationships of light and water use processes in agroecosystems. It is well established at the leaf-scale that light absorbed by the leaf influences stomatal control of transpiration (Buckley, 2019; Mott & Peak, 2011; Pieruschka, Huber, & Berry, 2010). Thus, light absorption has a substantial control on the water vapor exchange as well as carbon assimilation in plants. These investigations (Mott & Peak, 2011; Pieruschka et al., 2010) were performed in controlled greenhouse conditions for model plants (sunflower [*Helianthus annuus* L.), cockelbur [*Xanthium strumarium* L.], maize [*Zea mays* L.], barley [*Hordeum vulgare* L.), bean [*Phaseolus vulgaris* L.), oleander [*Nerium oleander* L.]). However, this dependence of water use process on light use process has not been shown to be manifested in actual (field-based) agroecosystems at canopy-scales. Moreover, resource use processes are functions of crop-specific features such as mechanism of photosynthetic pathways (i.e., C_3, C_4), canopy architecture (spherical, heliotropic), leaf angle distribution (erectophile, planophile), ground cover fraction, leaf morphology, plant densities, etc. (Kukal & Irmak, 2019). Thus, it is hypothesized that the WUE vs. LUE relationship would possibly be subject to differences among crops.

1.1 | Theoretical basis of associations between WUE and LUE

Aboveground crop biomass (dry matter) (AGB) can be defined as a function of both WUE and LUE:

$$\mathrm{AGB} = \mathrm{WUE} \times \mathrm{ETc} \tag{1}$$

Core Ideas

- Light use efficiency (LUE) was able to explain 52% of variance in water use efficiency (WUE).
- Averaged across all crops, WUE = 1.73 LUE, with substantial crop-specific variability.
- Evapotranspiration/absorbed photosynthetically active radiation ranged from 0.45 to 0.68 kg H_2O MJ^{-1} across all crops.
- Seasonal evolution of canopy conductance was communicated using heat accumulation.

$$\mathrm{AGB} = \mathrm{LUE} \times \mathrm{APAR} \tag{2}$$

where, ET_c is crop evapotranspiration and APAR is absorbed photosynthetically active radiation (PAR).

Aboveground biomass has been conventionally defined using intercepted PAR or IPAR (not APAR, as in this research), but the IPAR-based view of LUE definition is suboptimal to APAR definition, owing to improved measurement of canopy-light dynamics (Kukal & Irmak, 2020a; Lindquist, Arkebauer, Walters, Cassman, & Dobermann, 2005). Intercepted photosynthetically active radiation–based LUE does not take into account the reflected PAR from canopy and soil, unlike APAR-based definition. In Equation 1, ET_c has been considered as crop water use, despite the fact that evaporation (E) does not contribute to carbon assimilation, biomass production, yield, or other beneficial processes, and hence is non-beneficial loss of water (Irmak, 2015a, 2015b). Although ET_c is not the real representation of crop water use, it is easier to measure ET_c than transpiration (T) in field conditions. To minimize the errors resulting from this approximation, irrigation systems that allow for minimal E can be employed, such as sub-surface drip irrigation technology.

Equations 1 and 2 can be combined to deduce the following relationship between WUE and LUE:

$$\mathrm{WUE} = \mathrm{LUE}\left(\frac{\mathrm{ET_c}}{\mathrm{APAR}}\right)^{-1} \tag{3}$$

Equation 3 can be rewritten as:

$$\mathrm{WUE} = \mathrm{LUE}\, g_c^{-1} \tag{4}$$

where, g_c (canopy conductance) is the ratio of ET_c to APAR and has also been interpreted as a measure of canopy conductance in the past (Caviglia & Sadras, 2001; Matthews,

Harris, Williams, & Rao, 1988; Sadras, Whitfield, & Connor, 1991).

The g_c parameter has been quantified and used to some extent in the literature for diverse applications. For example, Caviglia and Sadras (2001) used g_c to investigate the impact of nitrogen supply on water and light use of wheat (*Triticum aestivum* L.). Sadras et al. (1991) investigated differences in g_c among semi-dwarf and standard height sunflower hybrids when managed under contrasting irrigation regimes. Matthews et al. (1988) quantified g_c to understand the yield response of four groundnut genotypes to drought. Rodriguez and Sadras (2007) quantified g_c for wheat in contrasting environments across a latitudinal transect in eastern Australia that varied in rainfall, rainfall seasonality, frost dates, and yield. Being a critical bridge between LUE and WUE, g_c can is suitable to distinguish and communicate the WUE vs. LUE relations between major row crops grown in homogenous conditions. Sinclair (2019) stated that crop canopy conductance has remained a major unknown in the area of modeling of water vapor exchange and its regulation by stomata.

The objective of this research was to quantify the relationships between WUE and LUE in four major row crops (that belong to C_3 and C_4 photosynthetic pathways) of the U.S. agricultural systems using high-frequency field experimental datasets. These major crops were maize, soybean [*Glycine max* (L.) Merr.], sorghum [*Sorghum bicolor* (L.) Moench], and winter wheat, managed under homogenous and optimal growing conditions of dry sub-humid Central Great Plains. Thus, the specific objectives of this research were to: (a) quantify crop-specific sensitivity of AGB to ET_c and APAR; (b) quantify crop-specific relationships between WUE and LUE; (c) investigate influences of environmental variability on the WUE vs. LUE relationship; and (d) develop seasonal patterns of g_c or ET_c per unit APAR.

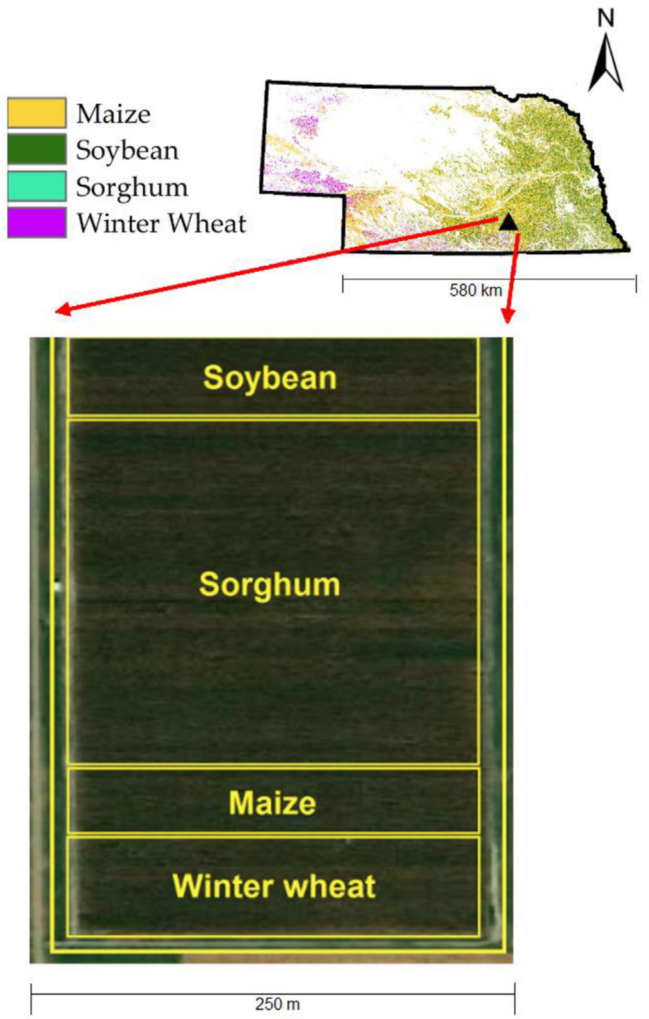

FIGURE 1 Map showing distribution of cropland in Nebraska where maize, sorghum, soybean, and winter wheat were planted in 2018 and an aerial view of the 13.5-ha subsurface drip-irrigated experimental field used in this research in the Irmak Research Laboratory research facilities

2 | MATERIALS AND METHODS

2.1 | Characteristics of the experimental site

The field research was conducted in the Irmak Research Laboratory at the University of Nebraska-Lincoln located at the South-Central Agricultural Laboratory (SCAL) (40.58° N, 98.13° W, 552 m above mean sea level) near Clay Center, NE. The experimental soil was a Hastings silt loam, well-drained upland soil (fine, montmorillonitic, mesic Udic Argiustoll) with 0.34 m^3 m^{-3} field capacity, 0.14 m^3 m^{-3} permanent wilting point, and 0.53 m^3 m^{-3} saturation point (Irmak, 2010). The total available water holding capacity of the soil profile is 240 mm 1.20 m^{-1}. The particle-size distribution is 15% sand, 65% silt, and 20% clay, with 2.5% organic matter content in the topsoil layer of 0–20 cm (Irmak, 2010). The long-term (1980–2010) average annual rainfall in the area is 680 mm, with significant annual and growing season variability in both magnitude and timing (Irmak, 2015a; Kukal & Irmak, 2016). The 13.5-ha experimental field (Figure 1) was irrigated using a subsurface drip irrigation (SDI) system. The driplines in the SDI system were installed at 40 cm depth below the soil surface with 1.52-m spacing between two adjacent driplines. The driplines were installed in the middle of the crop rows very other row. The emitter spacing was 0.45 m with a discharge rate of pressure-compensating emitters (Netafim USA) of 1 L h^{-1} (Irmak, 2010; Irmak & Djaman, 2016).

2.2 | Soil, crop, and irrigation management

The field experiments were conducted in the Irmak Research Laboratory advanced field research facilities at the South Central Agricultural Laboratory near Clay Center, NE, during 2016 and 2017 growing seasons for maize, soybean, and grain sorghum, and during 2016–2017, and 2017–2018 for winter wheat. The selection of these crops for this research was based on some important considerations. First, these are the four major row crops in Nebraska accounting for 86% of the total harvested Nebraska cropland (USDA-NASS, 2018b) and in the U.S. Great Plains, in general. Figure 1 presents the spatial distribution of cropland, which was dedicated to these crops in 2018 within Nebraska (USDA-NASS, 2018a). Secondly, these crops make up for most of the irrigated cropland in the state (95%), and fulfilment of the objectives of this research will have potential implications for improved irrigation water management in these crops. Third, these crops also provide an opportunity to investigate how inherent crop-specific differences such as mechanism of photosynthetic pathways (maize and sorghum are C_3 crops, soybean and wheat are C_4 crops), canopy architecture (spherical, heliotropic), leaf angle distribution (erectophile, planophile), ground cover fraction, leaf morphology, resource use (water, light, nitrogen), plant densities, etc. (Kukal & Irmak, 2019) translate to differences in LUE vs. WUE relationship.

It was ensured that soil and crop management practices were maintained as uniform as possible for all crops and represented regionally prevalent grower management. Appropriate fertilizer rates were applied to all crops based on the soil sampling determined residual nitrogen in each plot (University of Nebraska-Lincoln crop-specific nitrogen recommendation algorithms). For maize, sorghum, and soybean, monoammonium phosphate 11–52–0 at the rate of 122 kg ha^{-1} was broadcasted in the experimental field on 14 Mar. 2016, and at the rate of 244 kg ha^{-1} on 9 Feb. 2017. A second input of 32–0–0 urea ammonium nitrate (UAN) was applied in furrow at the rate of 196 and 140 kg ha^{-1} for maize and sorghum, respectively, on 23 Apr. 2016. During the 2017 growing season, the second in-furrow application of 32–0–0 UAN at the rate of 146, 173, and 173 kg ha^{-1} were applied during 19 Apr.to 25 Apr. 2017 for maize and sorghum, respectively. For winter wheat, the same applications at the rate of 224 kg ha^{-1} (11–52–0 as broadcast) and 67 kg ha^{-1} (32–0–0 as liquid foliar application) were applied on 9 Feb. and 13 Apr. 2017, and 1 Jan. and 24 Apr. 2018. Herbicide, insecticide, and fungicide were applied to all crops uniformly as required.

It was ensured that all crops never undergo water stress, and hence optimum growth conditions and high-yielding environments were maintained. This necessitated continuous monitoring of soil moisture and appropriate irrigation scheduling to maintain root zone soil–water between approximately 90% of the field capacity and 55% of total available water (maximum allowable depletion). Total precipitation received was greater in the 2017 growing season than the 2016 growing season for maize (by 23%), sorghum, and soybean (by 37%), whereas the 2016–2017 growing season was wetter than 2017–2018 for winter wheat (by 27%). These precipitation amounts were supplemented by irrigation, and the total irrigation amounts received by each crop during two growing seasons are shown in Table 1. The source of irrigation water was Ogallala aquifer, and the depth to water table at the site was 35 m. Besides nitrogen and irrigation management, it was also ensured that no stress from weed, insect, and disease pressure was imposed (Table 1).

2.3 | Experimental setup

The experimental field consists of a unitextural soil type (Hastings silt loam) and has the same topographical characteristics. The 13.5-ha research field was divided in the north–south direction into sub-areas to accommodate each crop: 2–3 ha for maize, soybean, and winter wheat, and 7.0 ha for sorghum (to ensure appropriate fetch for a flux tower installed in sorghum). Thus, the design of the experiment ensured that each crop was allocated a large plot with homogenous soil properties and characteristics. Each crop was managed to maintain optimal growing conditions to allow for maximum productivity potential, and thus no specific treatments were imposed. Since the intention was to compare the crops among each other for WUE vs. LUE relations, the goal was to robustly measure or sample critical variables for each crop and then compare the resultant relations. The large plots allowed for sampling and measuring resource use efficiency by addressing spatial variability, if any. There were no replications, however, controlling for any spatial variability within crop areas, which is the goal of replications in a traditional experimental design was accomplished. Sub-seasonal LUE and WUE data were pooled across the 2 yr for each crop to decipher relations and other parameters, to include data points from variable environmental conditions. The consistent optimal growth conditions maintained for each crop ensured that any within-crop differences detected are attributed to crop species-specific characteristics and are not management-induced.

TABLE 1 Crop-specific establishment, environmental, and management details for the field experiments conducted in this research

Detail	Unit	Growing season 2016	2017	2016	2017	2016	2017	2016–2017	2017–2018
		Maize, DKC 30-19 RIB		Sorghum, DKS 44-20		Soybean, AG 2431		Winter wheat, SY Wolf	
Sowing density	seeds ha^{-1}; kg ha^{-1} for winter wheat	84,767	84,767	280,939	280,939	371,654	371,654	101	101
Actual plant density	plants m^{-2}	8.5	8.5	28.1	28.1	37.2	37.2	278.8	278.8
Row spacing	cm	76.2	76.2	76.2	76.2	76.2	76.2	14.3	14.3
Sowing	DOY	116	114	134	129	134	129	273	290
Emergence	DOY	132	133	146	143	144	136	281	301
Harvest	DOY	231	264	277	293	272	285	198	192
Max CTU (since sowing)	°C	1,291	1,570	1,658	1,688	1,627	1,660	2,920	2,305
Max CTU (since emergence)	°C	1,231	1,503	1,606	1,609	1,596	1,608	2,803	2,179
Irrigation amount	mm	254	279.4	285.75	279.4	285.75	279.4	152.4	190.5
Precipitation received	mm	331	407	341	467	341	467	385	282

Note. CTU, cumulative thermal units; DOY, day of year.

2.4 | Field measurements

2.4.1 | Soil moisture flux

Soil moisture was measured every 30 min throughout the crop growing seasons via John Deere (JD) Field Connect probe (John Deere Water), which is a capacitance-based sensor. The JD probes (Figure 2d) consist of adjustable capacitors along the probe shaft, and were set at depths of 0.10, 0.20, 0.30, 0.50 and 1.00 m in this experiment (manufacturer-recommended placement). Greater sensor density at shallower depths allowed for higher spatial resolution sampling, as shallower depths are subject to greater variability from wetting events and surface processes. These capacitor placements represent soil layers of 0–0.15, 0.15–0.25, 0.25–0.40, 0.40–0.75 and 0.75–1.20 m, respectively. Probes were installed in the inter-plant spacing within the row immediately after plants emerged. Four to six probes per crop were used, proportional to the plot area. To remove any uncertainties and inaccuracies in soil moisture arising from the probes, depth-specific calibration functions against neutron scattering technique of moisture measurement were implemented. These functions were developed from extensive research data collected at the same site (Sharma, Irmak, & Kukal, 2021), from JD probes and standardized moisture measurement technique (neutron scattering).

2.4.2 | Continuous light measurement setup

Under this approach, light interactions were measured using permanently installed sensors (Figure 2a–c) in each crop canopy (Kukal & Irmak, 2020a). All variables were observed every minute and recorded every 15 min as averages continuously during the entire growing season each year. In each crop, one set of sensors, each measuring the following fluxes were installed. Three variables were observed under this approach include:

1. Incoming PAR flux (PAR_{in}). This is the uninterrupted incoming PAR that is received at the Earth's surface. This was measured using a point quantum sensor (Apogee Instruments Inc.), which measures PAR portion of the electromagnetic spectrum (400–700 nm) and was mounted at the top of the canopy. Since the incoming PAR is not a function of vegetative surface, this measurement was made at a single point at the research field.
2. Transmitted PAR flux (PAR_{tr}). This is a time-variant portion of the PAR_{in} that gets transmitted through the

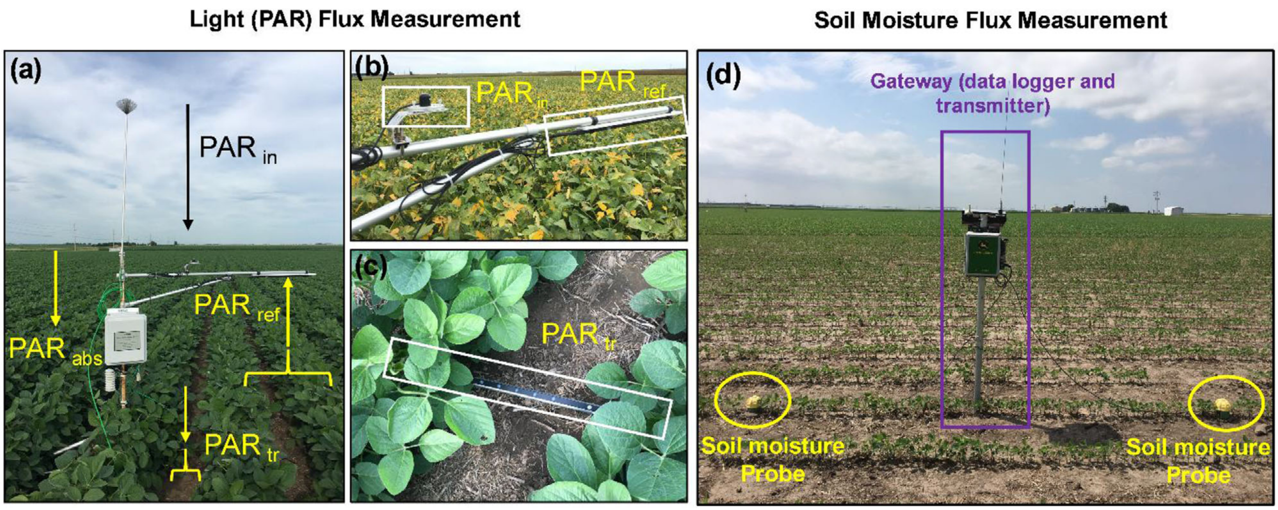

FIGURE 2 The continuous photosynthetically active radiation (PAR) balance system monitoring light interactions in soybean canopy in the Irmak Research Laboratory. Identical setups were used in all crop canopies. The three constituent pictures show (a) various PAR flux components and their directions; (b) point quantum flux and inverted line quantum flux sensor mounted over the canopy to measure incoming PAR (PAR_{in}) (downwelling), and reflected PAR (PAR_{ref}) (upwelling), respectively; (c) a line quantum sensor at the soil surface level beneath the canopy to measure transmitted PAR (PAR_{tr}) (downwelling); (d) the continuous soil moisture flux measurement using capacitance probe with sensors at depths of 0.10, 0.20, 0.30, 0.50, and 1.00 m. Four to six probes were installed in each crop canopy

canopy and reaches the surface (soil). Since this component is subject to spatial variability in the inter-row spacing because of the complex shading effects of the canopy, using a point quantum sensor would have resulted in erroneous and non-representative measurements. Thus, a line quantum sensor was mounted at the ground level in the inter-row spacing in a diagonal orientation. A line quantum sensor (Apogee Instruments Inc.) spatially averages the outputs of six individual PAR sensors placed linearly across the inter-row space. Each crop canopy was subjected to independent measurement of PAR_{tr}, unlike PAR_{in}.

3. Reflected PAR flux (PAR_{ref}). This is a time-variant portion of PAR_{in} that gets reflected from the canopy and/or the soil back to the surroundings. This component is also subject to spatial variation because of canopy non-uniformity, and hence, a line quantum sensor was used in an inverted fashion, aligned to monitor the top portion of the canopy. Similar to PAR_{tr}, PAR_{ref} was measured independently in each crop canopy.

These variables were measured in units of quantum flux or photosynthetic photon flux density (PPFD) (μmol m^{-1} s^{-1}), and the conversion of quantum flux to units of energy require detailed solar spectral data, which are expensive and difficult to collect. However, a conversion value of 4.57 μmol J^{-1} was used, which is a conservative estimate under diverse atmospheric conditions, as it is centered at 550 nm across the PAR range (Jacovides, Timbios, Asimakopoulos, & Steven, 1997; Lindquist et al., 2005; McCartney, 1978; McCree, 1972; Tollenaar & Aguilera, 1992). All sensors were frequently maintained to be clean from any unwanted foreign material covering the optical sensor such as soil particles, plant material, residue, etc.

2.4.3 | Aboveground dry matter

Four quadrats, each of 1-m^2 area were destructively sampled in each crop every 1–1.5 wk for AGB determination. To avoid any edge effects, each sampling was conducted at least 4–5 m from previously sampled areas. Sampling was limited to a dedicated and representative section in each crop to minimize random gaps that can confound crop yield assessments from the grain yield monitor (Kukal & Irmak, 2019). The samples were dried at 60 °C until constant weight attainment and weighed dry matter.

2.5 | Computation of absorbed light (PAR_{abs})

The fate of PAR_{in} can take three possible outcomes, depending on the surface characteristics. These possible outcomes, described in Equation 5, when summed, should be equal to PAR_{in}, similar to a mass or energy balance:

$$PAR_{in} = PAR_{tr} + PAR_{abs} + PAR_{ref} \quad (5)$$

where PAR_{in}, PAR_{tr}, and PAR_{ref} have been described previously, and PAR_{abs} is the quantity of light absorbed by the canopy to be used in photosynthesis. This component of the light balance is also time-variant. It is calculated as a residual from Equation 5 when all the other components are measured using approach outlined in section 2.4.2. The 15-min PAR_{abs} was summed within each window between AGB samplings to compute LUE within each of these periods.

2.6 | Computation of crop evapotranspiration

Crop evapotranspiration was calculated individually for each crop using a soil water balance equation (represented by Equation 6). Crop-specific soil moisture data, irrigation data, crop phenology data, soil characteristics, and daily weather data were used as inputs to the model, with parameterization and methods adopted from ASCE guidelines (Irmak, 2015a, 2015b; Jensen and Allen, 2016)

$$P + I + U + R_{on} = R_{off} \pm \Delta SW + D + ET_c \quad (6)$$

where P is rainfall (mm), I is irrigation applied (mm), U is upward soil moisture flux (mm), R_{on} is surface run-on within the field (mm), R_{off} is surface runoff from the field (mm), ΔSW is the change in soil moisture storage in the root zone (mm) between beginning and end of the growing season, and D is deep percolation (mm) below the crop root zone. Deep percolation was estimated using a computer program-driven daily soil–water balance (Bryant, Benson, Kiniry, Williams, & Lacewell, 1992; Payero, Tarkalson, Irmak, Davison, & Petersen, 2009). The daily soil–water balance equation for deep percolation is:

$$D_j = \mathrm{Max}(P_j - R_j - I_j - ET_{cj} - CD_{j-1}, 0) \quad (7)$$

where D_j is deep percolation on day j, CD_{j-1} is root zone cumulative soil–water depletion depth at the end of day j–1, P_j is precipitation, R_j is precipitation and/or irrigation runoff from the soil surface on day j (mm), I_j is irrigation depth on day j (mm), and ET_{cj} is crop evapotranspiration on day j (mm) estimated by the two-step approach. Surface runoff was estimated from each crop using USDA Natural Resources Conservation Service (NRCS) curve number method (USDA-SCS 1985). A curve number ($C = 75$) was used to represent the silt loam soil at the site and the known land use, slope, and the conservation tillage. It was assumed that U and R_{on} are negligible, and hence, the soil–water balance equation is reduced to Equation 8. Crop-specific I, R, D, and ΔSW were used to calculate crop-specific ET_c at each of the 4–6 soil moisture probes in each crop area. The ET_c quantities calculated at individual probes were averaged to report mean ET_c for each crop.

$$ET_c = P + I - R - D \pm \Delta SW \quad (8)$$

The crop-specific ET_c was computed for several periods (5–10 d) within each crop's growing season (Kukal & Irmak, 2020b) that for the most cases, coincided with the AGB inter-sampling windows. Due to wetting events causing abrupt changes in soil moisture, it was not always possible to maintain consistency between the ET_c calculation periods and AGB sampling periods.

2.7 | WUE and LUE estimation

Water use efficiency was estimated as the slope of the linear regression (ordinary least squares or OLS) between independent pairwise data of AGB and ET_c sampled at successive points during the growing season for each crop. Similarly, LUE was estimated as the slope of the linear regression between independent pairwise data of AGB and APAR sampled at the same successive points during the growing season for each crop. It is important to note that contrary to the literature, independent (incremental) data for AGB, ET_c, and APAR were used, rather than cumulated data, as recommended by Kukal and Irmak (2020c).

3 | RESULTS AND DISCUSSION

3.1 | LUE and WUE in C_3 and C_4 crops

Crop-specific LUE and WUE (biomass-based) estimates were quantified from sub-seasonal AGB, APAR and ET_c data collected during two crop growing seasons. Figures 3a and 3b present linear regressions used to estimate LUE and WUE as slope coefficients, respectively. The maximum LUE was demonstrated by maize (4.72 g MJ^{-1}), followed by sorghum (3.87 g mJ^{-1}), soybean (2.44 g MJ^{-1}), and winter wheat (2.06 g MJ^{-1}). On the other hand, the maximum WUE was demonstrated by sorghum (2.89 kg m^{-3}), followed by winter wheat (2.44 kg m^{-3}), soybean (2.02 kg m^{-3}), and maize (1.32 kg m^{-3}). By these observations, it is inferred that various crops are not equally efficient in using both light and water for biomass production. The method used for computing LUE and WUE can have impacts on these inferences. Recently, Kukal and Irmak (2020c) demonstrated the weaknesses associated with the conventionally employed cumulated data approach for LUE and WUE estimation and presented an alternative independent data approach to

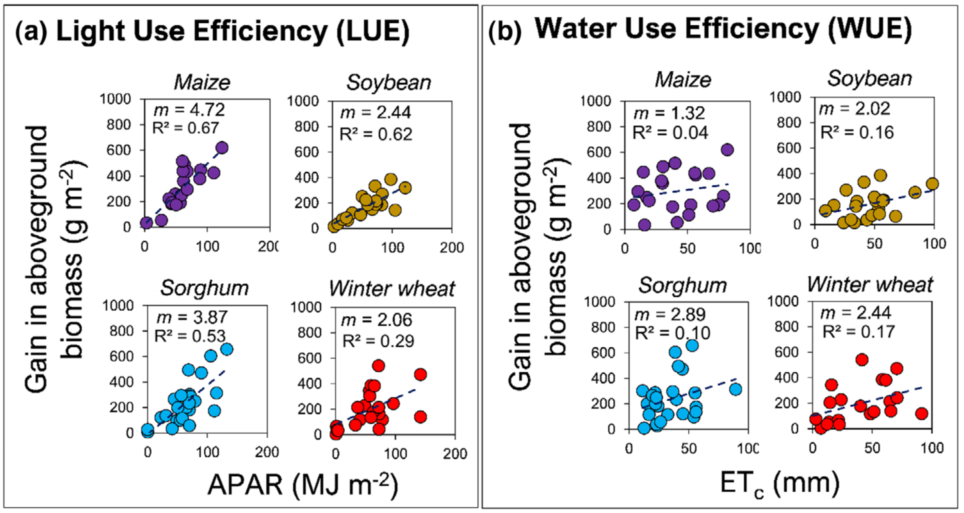

FIGURE 3 Estimation of (a) light use efficiency (LUE) and (b) water use efficiency (WUE) in maize, soybean, sorghum, and winter wheat. Light use efficiency was estimated as the slope of gain in aboveground biomass during sub-seasonal intervals and the light (photosynthetically active radiation) absorbed during the corresponding intervals. Similarly, WUE was estimated as slope of gain in aboveground biomass during sub-seasonal intervals and the crop water use (ET_c) during the corresponding intervals. Each sub-figure is accompanied by the slope (m) and coefficient of determination (R^2) of linear regression functions

overcome these weaknesses. The independent data estimation method used here provides an opportunity to observe true linkage between biomass production and resource (light and water) use in crops. The resulting LUE and WUE values derived here represent the sensitivity of biomass production to light and water used, respectively, unlike the statistical artefacts produced from cumulated data method (Kukal & Irmak, 2020c). Thus, the approach used here is more relevant and realistic in quantifying LUE and WUE as compared with conventionally employed cumulated data approach.

Overall, APAR was a more significant driver of gain in AGB relative to ET_c, as mean (across all crops) R^2 from AGB gain vs. APAR (.53) was 349% higher than that from AGB gain vs. ET_c (.12). Three primary factors are likely to explain the observation of greater relative importance of light than water for biomass production. First, since crop productivity was not constrained by any inputs, crop performance was near-full potential and hence, driven largely by light interception and absorption. Secondly, resolution of soil–water balance is more challenging than that of light balance, due to additional uncertainties in estimates of surface runoff, deep percolation, and soil–water storage, thus potentially confounding ET_c. Third, the analyses rely on ET_c, which includes transpiration and soil–water evaporation, to represent crop water use, although non-beneficial evaporation component does not contribute to carbon assimilation. To be specific, the greater relative importance of APAR than ET_c was highest in maize (1,575%), followed by sorghum (430%), soybean (288%), and winter wheat (71%). The inter-crop differences in relative importance of APAR and ET_c possibly stem from dissimilar crop characteristics, contributing to dynamics of resource use processes. Specifically, these underlying crop characteristics can primarily include photosynthetic pathway mechanisms (C_3, C_4), phylogenetic affinity (monocots, dicots), physiologic growth (Table 1), canopy architecture and geometry (spherical, heliotropic), leaf angle distribution (erectophile, planophile), ground cover fraction, plant density (Table 1), leaf morphology, etc. (Kukal & Irmak, 2019).

3.2 | Associations of WUE and LUE

Sub-seasonal LUE and WUE values were investigated for inter-relationships for each crop individually (Figure 4a). It was found that LUE explained at least 54% (sorghum) of the variance in the WUE, which was as high as 70% in winter wheat. Sensitivity of WUE to LUE was the highest in sorghum (2.22 MJ kg^{-1} H_2O), followed by soybean and winter wheat (1.57 MJ kg^{-1} H_2O) and maize (1.46 MJ kg^{-1} H_2O). When all the crops are considered in a pooled OLS linear regression analysis (Figure 4b), LUE was able to explain 52% of variance in WUE, and the slope of the relationship was 1.73 MJ kg^{-1} H_2O. All the crop-specific WUE vs. LUE relationships were statistically significant at the 99% confidence interval ($p < .01$), except for soybean, which was significant at the 95% confidence interval ($p < .05$). Also, the pooled relationship demonstrated statistical significance at the 99% confidence interval ($p < .01$).

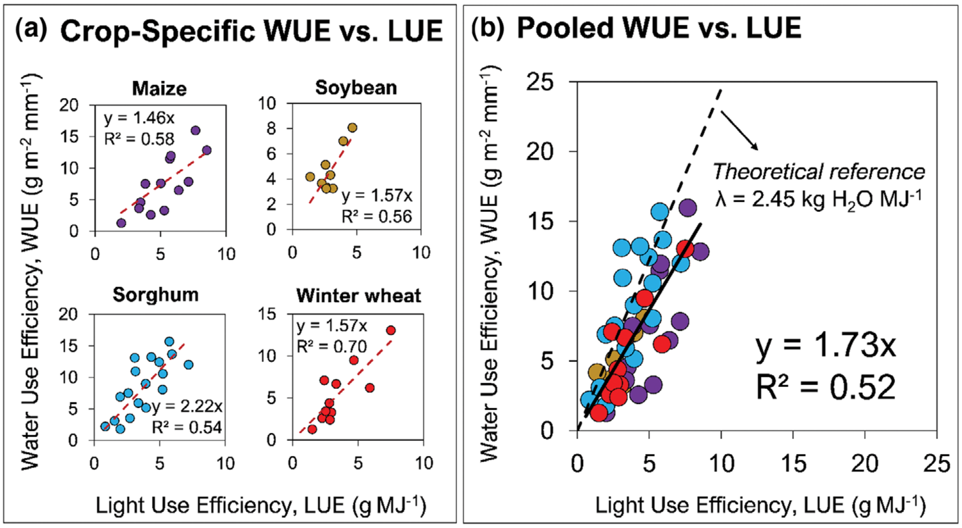

FIGURE 4 (a) Crop-specific relationships between water use efficiency (WUE) and light use efficiency (LUE) in maize, soybean, sorghum, and winter wheat; (b) pooled WUE vs. LUE relationship quantified from pairwise WUE and LUE data from all crops. The broken line in (b) represents the theoretical, energy-limited upper limit determined by the inverse of λ (2.45 MJ m^{-2} mm^{-1} or 2.45 MJ kg^{-1} H_2O)

The WUE vs. LUE relationships are also in agreement with the theoretical, energy-limited upper limit determined by the latent heat of vaporization ($\lambda = 0.408$ kg H_2O MJ^{-1}). In other words, the slopes of these relationships are analogous to the inverse of λ (2.45 MJ m^{-2} mm^{-1} or 2.45 MJ kg^{-1} H_2O). It is evident that none of the crops' sensitivity of WUE to LUE was beyond this energy-limited ceiling. The magnitudes of these slopes can be interpreted as the proportion of absorbed light/PAR energy that is dissipated as latent heat of vaporization. Inversely, the remainder of this proportion contributes in part to increasing the sensible heat. For example, in maize, 60% (calculated as the ratio of 1.46 and 2.45 MJ kg^{-1} H_2O) and 40% (100% minus 54%) of the absorbed radiation can be described as latent heat and sensible heat, respectively. The slopes of these relationships can also be used to infer seasonal mean magnitudes of g_c (as reciprocal of slope). The highest g_c was shown by maize (0.68 kg H_2O MJ^{-1}), followed by soybean and winter wheat (both 0.64 kg H_2O MJ^{-1}) and sorghum (0.45 kg H_2O MJ^{-1}). In the literature, no information exists on the g_c parameter for the included crops. The closest g_c values found are that of spring wheat in Argentina (Caviglia & Sadras, 2001), which ranged from 0.25 to 0.29 under various nitrogen rates. Thus, the findings of this research provide invaluable data and information to the scientific literature in terms of seasonal magnitudes of g_c for crops investigated in the same environment and management conditions under optimal growing conditions.

Fairly investigating WUE vs. LUE relations necessitates that AGB, ET_c, and APAR are monitored simultaneously during sub-seasonal periods, and treating them as independent data points. However, almost the entirety of the literature has been resorting to cumulate these variables over the growing season to compute LUE and WUE. This is, in part, due to extreme difficulties in simultaneously and continuously measuring all three variables during the entire growing season. However, this cumulating operation renders the data unfit to be possibly utilized for opportunities such as investigating WUE vs. LUE relationships that require preservation of inter-sampling variability in data (Arkebauer, Weiss, Sinclair, & Blum, 1994; Demetriades-Shah, Fuchs, Kanemasu, & Flitcroft, 1992, 1994; Kukal & Irmak, 2020c; Lindquist et al., 2005; Malet, Pécaut, & Bruchou, 1997; Monteith, 1994). For example, Narayanan et al. (2013) used cumulated values of AGB, intercepted IPAR, and water use observed in sorghum for WUE and LUE estimation and developing WUE vs. LUE relations. Malet et al. (1997) and Kukal and Irmak (2020c) showed that using cumulated data for these objectives (Narayanan et al., 2013) results in statistical artefacts that, if relied upon, provide ambiguous and problematic interpretation of WUE vs. LUE relations. This dependence on weak arithmetic methods for LUE and WUE estimation explains the scarce research into WUE vs. LUE relations. To avoid these weaknesses and in order to accurately quantify the WUE vs. LUE relationships, independent data have to be used (as in Figure 3), as recently demonstrated by Kukal and Irmak (2020c). The consideration of within-season variability allows for observation and quantification of relationships between water and light use processes during several sub-seasonal sampling periods.

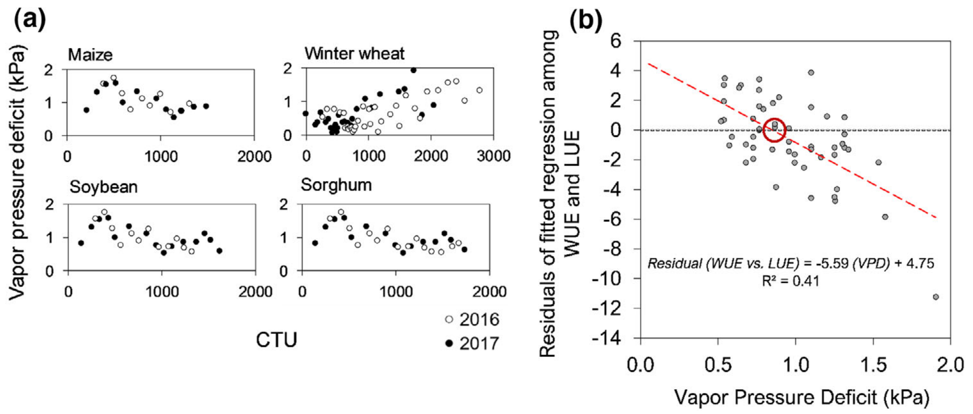

FIGURE 5 (a) Within-growing season variability observed in vapor pressure deficit (VPD) for each crop during the two growing seasons (open and solid circles); (b) residuals of the fitted linear regression in Figure 4b as a function of vapor pressure deficit (VPD) recorded during the corresponding sub-seasonal periods. The linear fit intersects the $y = 0$ line at 0.85 kPa

3.3 | Environmental control on WUE vs. LUE relationship

Although relationships between sub-seasonal WUE vs. LUE were developed, it should be realized that not all variance in WUE was explained by variance in LUE (note R^2 values in Figure 4a). A typical growing season is subject to variability in environmental conditions that alter the tradeoffs between resource use and carbon assimilation. A suitable indicator of environmental regimes that govern stomatal behavior and thus biomass production and resource use is vapor pressure deficit (VPD). The within-season environmental variability is evident from Figure 5a, which presents the VPD measured at the site during each of the sampling periods for WUE measurement for all crops during both growing seasons. For the summer crops, the VPD increased initially in the growing season to a maximum value of 1.75 kPa, and then started decreasing until physiological maturity (0.5–0.6 kPa) with substantial variability. For winter wheat, VPD decreased from around 0.5 kPa to a minimal value (< 0.05 kPa) during pre-dormant and dormant periods, and thereon increased during post-dormant period.

Given the substantial environmental variability, there is sufficient reason to hypothesize that the WUE vs. LUE relationship can be affected. To investigate this, residuals from the linear fit between WUE and LUE (in Figure 5b) were computed as WUE – 1.73 LUE. These residuals were regressed against the corresponding VPD during the inter-sampling periods (Figure 3b). Vapor pressure deficit accounted for 41% of the scattering in the 1.73 × LUE vs. WUE relationship. The linear fit was statistically significant at 99% confidence interval ($p < .01$) and the trendline intersected the $y = 0$ line at 0.85 kPa. This implies that environments with VPD higher (lower) than 0.85 kPa had lower (greater) WUE than expected from the relationship determined from Figure 5b. Thus, it was established that the WUE vs. LUE relationship is subject to environmental controls and quantify the critical VPD for the relationship to hold true. Rodriguez and Sadras (2007) conducted similar analyses for wheat in eastern Australia and found that this cutoff VPD point was 1.16 kPa, corresponding to the relation of WUE = 2.1 LUE. One methodology-dependent reason for difference in WUE vs. LUE relationship is that they used intercepted light-based LUE (LUE_i), whereas this research relied on absorbed light-based LUE (LUE_a). It has been shown previously by Kukal and Irmak (2020a) that LUE_a can be 5–7% greater than LUE_i, depending on the temporal scale of measurements. The differences in LUE_a and LUE_i are a function of crop growth stage, with differences being greater earlier in the growing season, and then abruptly declining to lower magnitudes thereon (Kukal & Irmak, 2020a).

3.4 | Evapotranspiration per unit of light absorbed

Since water and light use was monitored continuously during the two growing seasons in all crops, the seasonal patterns of g_c (i.e., ET/APAR) were studied. Crop-specific g_c values were calculated for each constituent sampling period and were presented against cumulative thermal units (CTU) (Figure 6a). The seasonal patterns in g_c were explained by logarithmic functions that indicate that heat accumulation (represented by CTU) explains 53 to 72% of the variance in sub-seasonal g_c. The coefficients of the logarithmic equation characterize the nature of these patterns. Although the general patterns are common across all crops studied, it is interesting to note that the coefficients are fairly contrasting among crops. This underscores the differential patterns of water use by different crops

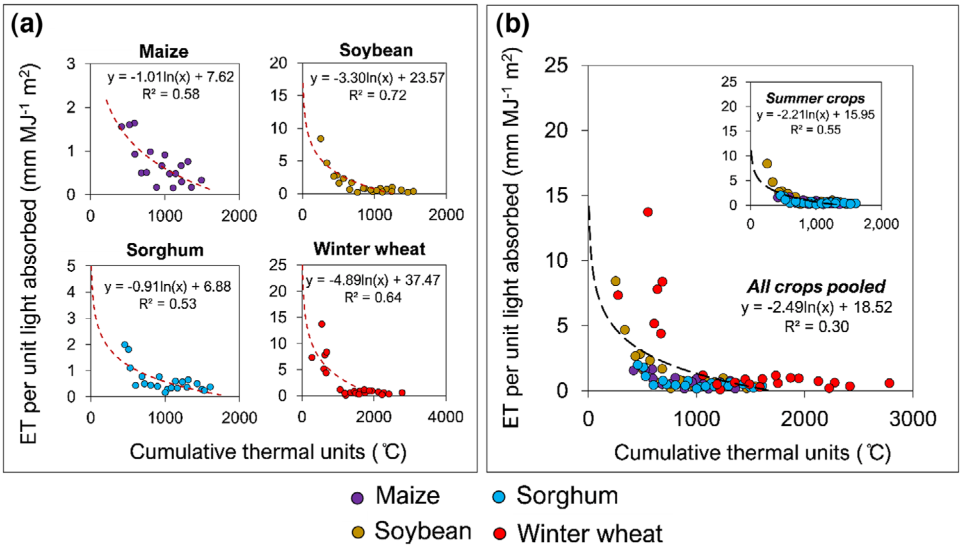

FIGURE 6 (a) Crop-specific seasonal patterns of evapotranspiration (ET_c) per unit light (photosynthetically active radiation) absorbed by the canopy (APAR) against cumulative thermal units. (b) ET_c/APAR seasonal patterns against cumulative thermal units pooled across all crops. Inset shows ET_c/APAR seasonal patterns against cumulative thermal units pooled across only summer crops. ET_c/APAR is also interpreted as a measure of canopy conductance. Seasonal patterns were explained by a logarithmic function. Each sub-figure is accompanied by the equation and coefficient of determination (R^2) of the logarithmic functions

under the same levels of absorbed light. In Figure 6b, sub-seasonal g_c data points were pooled across all crops, and a common logarithmic function was fit. Moreover, summer crops were pooled separately, which led to a better fit of the function (R^2 increased from .30 to .55). Highly contrasting environmental conditions during the winter wheat growing season as well as existence of two distinct growth periods (pre-dormancy and post-dormancy) makes its g_c magnitudes dissimilar to that of rest of the summer crops.

The empirical functions presented here can be utilized to reproduce generalized or crop-specific patterns in similar environments. Among ET_c and APAR, ET_c is relatively challenging to measure/estimate due to higher uncertainty of measuring soil–water balance components and greater observation infrastructure/costs (requiring precipitation, irrigation, multi-depth soil moisture, meteorological variables, soil and crop characteristics), relative to light balance components (only requiring PAR measurements). Empirically determined ET_c/APAR functions provide an opportunity to use ease of canopy APAR measurements to their advantage and estimate ET_c from APAR data and its seasonal evolution.

4 | CONCLUSIONS

The relationships between WUE and LUE in agricultural crops and the crop-specificity of these relationships are currently unknown/unaddressed at the canopy scale in major U.S. agroecosystems. Through extensive high-resolution field-based measurements of plant dry matter, and sampling high-frequency light and water fluxes, empirical evidence of association between light and water use processes in maize, soybean, sorghum, and winter wheat was presented. Careful and data-based irrigation and nitrogen management allowed for optimum growth conditions for maximum potential productivity representative of the U.S. Great Plains region. It was found that, on an average basis across all crops, LUE was able to explain 52% of variance in WUE, and the relationship between the two was determined as WUE = 1.73 × LUE. The relationship demonstrated high variability among various crops, with the sensitivity of WUE to unit increase in LUE being highest in sorghum (2.22 MJ kg^{-1} H_2O), followed by soybean and winter wheat (1.57 MJ kg^{-1} H_2O) and maize (1.46 MJ kg^{-1} H_2O). This research presents comparative canopy conductance (g_c) values across major regional crops, which were lacking in the region previously. The highest g_c was shown by maize (0.68 kg H_2O MJ^{-1}), followed by soybean and winter wheat (both 0.64 kg H_2O MJ^{-1}), and sorghum (0.45 kg H_2O MJ^{-1}). Water use efficiency vs. LUE relationships obeyed the energy-limited upper ceiling determined by the latent heat of water vapor ($\lambda = 0.408$ kg H_2O MJ^{-1}) and can be used to determine the proportion of absorbed energy dissipated as latent heat of vaporization and sensible heat. It was also found that VPD accounted for 41% variability in the WUE vs. LUE relationship, and the relationship is subject to change in environments with VPD higher/lower than 0.85 kPa. Finally, empirical functions that relate the

seasonal evolution of g_c (or ET_c/APAR) to heat accumulation (represented by cumulative thermal units) during the growing season were presented for each crop. These findings provide valuable contributions to the scientific literature in quantifying the dynamics involved in WUE and LUE inter-relationships and g_c for major cropping systems. The findings have potential implications in better understanding crop productivity vs. crop resource use dynamics under optimal growing conditions. These findings also add to the evidence of light (or radiation) controls on water use in actual production-scale field crops, which previously has only been limited to model plants under controlled conditions.

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AUTHOR CONTRIBUTIONS

MK and SI conceptualized the study. MK conducted field data collection under close supervision of SI. SI obtained all resources needed for the study and SI's research team helped with the field research. MK and SI contributed to discussions and interpretation of the results. MK compiled datasets and created figures/tables in close consultation and discussions with SI. MK and SI worked on completing the manuscript. SI obtained grant funding for the research.

CONFLICT OF INTEREST

The authors declare no competing interests.

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