Influence of management practices on water-related grain yield determinants

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Highlights

This review highlights the significance of management practices in enhancing water-related grain yield determinants (evapotranspiration and water use efficiency) with a particular focus on the maize crop.

Abstract

Adequate management of N supply, plant density, row spacing, and/or soil cover has proved useful to increase grain yields and/or grain yield stability across years of rainfed crops. We reviewed the impact of these management practices on grain yield water-related determinants (ET, seasonal crop evapotranspiration and $WUE_{G,\ ET,s}$, water use efficiency for grain production, indicated by the G suffix, per unit of evapotranspired water, indicated by the ET suffix, during the season, indicated by the s suffix). We highlighted a large number of conflicting results on the impact of management on ET and exposed the complexity of ET response to environmental factors. We analyzed the influence of management practices on $WUE_{G,ET,s}$ in terms of the three main processes controlling $WUE_{G,ET,s}$: (i) the proportion of transpiration in ET (T/ET), (ii) transpiration efficiency for shoot biomass production (TE_B; where B suffix indicates shoot biomass) and (iii) harvest index (HI). We directly related the impact of management practices on T/ET to the effect of these practices on crop light interception. Furthermore, we evidenced that management practices significantly influence TE_B. To optimize $WUE_{G,ET,s}$, management practices should favor soil water availability during critical periods for seed set, to benefit HI. The need for improving the performance of existing crop growth models for the prediction of water-related grain yield determinants under different management practices was also discussed.

Keywords

Crop growth model
Evapotranspiration
Light interception
Nitrogen
Plant density
Row spacing
Soil cover
Transpiration
Transpiration efficiency
Water use efficiency

Introduction

Water is one of the main resources affecting grain production and thus, the grain yield of rainfed crops is closely related to in-season rainfall (Andrade and Satorre, 2015; Aramburu Merlos et al., 2015). Many regions suitable for grain production where rainfed crops are grown show significant interannual rainfall variation (Podestá et al., 1999; Löffler et al., 2005). Water-limited environments often found in these regions (Fischer et al., 2014) account for low productivity. For instance, estimates of major grain yield reductions due to water limitations across climatic zones for the maize crop (*Zea mays*) were 49% in Argentina, 37% in the USA, and 42% in China (Global Yield Gap and Water Productivity Atlas, 2023). For soybean (*Glycine max*), major grain yield reductions were in the order of 62% in Argentina and 50% in the USA (Global Yield Gap and Water Productivity Atlas, 2023). Similar values of grain yield reductions due to water limitations were estimated for the sunflower crop (*Helianthus annus*) in Argentina (≈ 50%, Fischer et al., 2014). Adequate management of N supply, plant density, row spacing, and/or soil cover, for example, have proved useful to increase grain yields and/or grain yield stability in environments with a high risk of low water supply (Caviglia et al., 2019; Cooper et al., 2020, 2021). This manuscript reviews the impact of these management practices on the water-related determinants of grain yield and the mechanisms underlying these determinants.

Grain yield (GY) can be expressed as the product of seasonal crop evapotranspiration (ET) and water use efficiency for grain production per unit of water evapotranspired during the season ($WUE_{G,ET,s}$; Viets, 1962; Howell et al., 2001; Eq. 1 and Figure 1).

$GY = ET \times WUE_{G,ET,s}$

(Eq. 1)

Crop evapotranspiration (ET), the total use of water by the crop, results from the combination of two different processes, evaporation (E) and transpiration (T). E represents the non-productive loss of water directly from the soil, while T is the use of water by the plant and therefore it is closely related to biomass production. $WUE_{G,ET,s}$ represents the grains (indicated by the G suffix) that can be produced per each unit of water evapotranspired (indicated by the ET suffix) during the whole growing season (indicated by the s suffix; Sinclair et al., 1984).

Equation 1 has long been used as a framework for analyzing the mechanisms underlying the effects of water availability on grain yield (Passioura, 1977). The following sections focus on the influence of management practices on water-related grain yield determinants ET and $WUE_{G,ET,s}$. The first part of this review addresses the influence of management practices on ET and root system characteristics influencing water uptake. The second part of this review focuses on the influence of management practices on each process controlling $WUE_{G,ET,s}$: (i) the proportion of T in ET, (ii) the transpiration efficiency for shoot biomass production (TE_B), and (iii) the allocation of shoot biomass to reproductive structures. Finally, we review how well some of the broadly used crop growth models predict water-related grain yield determinants under different levels of N supply, plant density, or soil covers. Much of the review focuses on the maize crop, while some insights into other summer crops, in particular sunflower and soybean are also provided.

1. *Seasonal crop evapotranspiration (ET)*

ET is modulated by: (i) the atmospheric evaporative demand, (ii) crop factors, and (iii) soil water availability (Allen et al., 1998; Figure 1). The atmospheric evaporative demand is driven by solar radiation, wind speed, vapor pressure deficit, and temperature (Allen et al., 1998). In general, it is characterized by the reference ET (ETo) using the Penman-Monteith equation, which includes these meteorological variables (Allen et al., 1994) or by the vapor pressure deficit (VPD), a variable commonly used to calculate crop transpiration efficiency (Sinclair et al., 1984 and Section 2.2 of this review). The evaporative demand varies significantly across seasons and locations, being lower in humid and cold than in arid and warm environments. Crop factors influencing ET, for a given crop, include the crop cover (which can be characterized by the leaf area index, LAI, or light interception), crop roughness, rooting characteristics, and crops resistances to water transport (Al-Kaisi et al., 1989; Villalobos and Fereres, 1990; Rhoads and Bennett, 1990; Steduto and Hsiao, 1998a,b). Furthermore, the reduction of ET occurs when soil available water, also known as transpirable soil water or extractable soil water (Soltani and Sinclair, 2012), falls below a critical threshold.

Water-limited environments are those where the supply of water is insufficient to reach the maximum ET value for a particular crop. For maize crops, the thresholds values of the fraction of soil available water below which ET or T is reduced (FTSWt) range from 0.17 to 0.80 (Table 1; Sadras and Milroy, 1996; Ray and Sinclair, 1997; Ray et al., 2002; Della Maggiora et al., 2002; Gholipoor et al., 2013b; Choudhary et al., 2020; Devi and Reddy, 2020; Echarte et al., 2023). A comprehensive review conducted by Sadras and Milroy (1996) examined the FTSWt in several crops. The authors concluded that FTSWt can be influenced by factors such as evaporative demand, root distribution, soil texture, and soil bulk density. Ray and Sinclair (1998) further demonstrated that FTSWt is not influenced by pot size (Table 1). Moreover, subsequent studies have demonstrated significant differences in FTSWt among maize genotypes (Ray and Sinclair, 1997; Ray et al., 2002; Gholipoor et al., 2013b; Choudhary et al., 2020; Devi and Reddy, 2020; Echarte et al., 2023; Table 1) as well as among different levels of VPD and air temperature (Choudhary et al., 2020; Devi and Reddy, 2020; Echarte et al., 2023; Table 1). To the best of our knowledge, no studies are elucidating whether management practices can influence maize FTSWt.

In non-water-limited environments with frequent soil-wetting events, there is a weaker influence of crop cover on ET (Allen et al., 1998). This is because solar radiation that is not intercepted by a crop reaches the wet soil surface, leading to water loss through soil evaporation instead of transpiration from the crop canopy. In crops grown with adequate nutrition and without any soil water limitations, ET varied between 450 and 900 mm for maize (e.g. Brouwer y Heibloem, 1986; Howell et al., 1997; Heatherly y Ray, 2007; Facchi et al., 2013; Nagore et al., 2014; Hernández et al., 2015; Curín et al., 2020; Marek et al., 2020; Sandhu and Irmak, 2022); between 440 to 753 mm for soybean (Doorembos and Kassam, 1979; Hattendorf et al., 1988; Dardanelli et al., 1991; Payero et al., 2005; Irmak et al., 2013; Alfonso et al., 2020) and between 457 to 882 mm for sunflower (Hattendorf et al., 1988; Tyagi et al., 2000; Karam et al., 2007; Lamm et al., 2011; Tolk and Howell, 2012; Echarte et al., 2020). Differences among values of ET reported for each crop when water is non-limiting, would be explained by differences in evaporative demand of the environment, the length of plant cycle duration, or in crop management practices.

Many discrepancies about the effects of management practices on ET have been reported. Several authors have found that ET increased in response to plant density (Tambascio et al., 2002; Irmak and Djaman, 2016; Zhang et al., 2019; Hernández et al., 2020) but others did not find any consistent ET responses (e.g., Persaud and Khosla, 1999; Ogola et al., 2005). Some studies reported maize ET increments in response to N supply in non-water-limited environments (Pandey et al., 2000; Ogola et al., 2002; Abbas et al., 2005; Adamtey et al., 2010; Barbieri et al., 2012), whereas others showed no clear trend in ET response to N supply (Reddy et al., 1980; Jones et al., 1986; Fernández et al., 1996; Kim et al., 2008; Teixeira et al., 2014). Conflicting results are also found for the influence of row spacing modifications, while maintaining equal plant density, on ET. Row spacing reductions were associated with either higher ET (Sharratt and McWilliams, 2005) or lower ET in maize (Yao and Shaw, 1964b), as well as with no consistent influence on soybean ET (Mason et al., 1982; Reicosky et al., 1985). Differences found in the responses of ET highlight the importance of considering the possible interactions among different management practices, environmental factors, and the genotype (Cooper et al., 2020). For example, ET increments produced by N supply tended to be higher under no water limitations than in a water-limited environment (Hernández et al., 2015). Furthermore, since many of the factors evaluated produce non-linear responses of ET, the range at which studies were performed could account for some of the discrepancies found in the literature. For instance, ET significantly increased when plant density increased from 4 to 8 or from 4 to 12 plants m^{-2}, but above 8 plants m^{-2}, plant density did not promote further crop ET increments (Hernández et al., 2020).

1.1. Root system and soil water uptake

The ability of the root system to absorb and supply water to meet the atmospheric evaporative demand is determined by roots distribution and depth (Connor and Hall, 1997; Amato and Ritchie, 2002; Dardanelli et al., 2004; Vadez, 2014; Gao et al., 2022). Root system characteristics vary with crop species, crop development, and soil moisture (Hoogenboom et al., 1987; Dwyer et al., 1988; Merrill et al., 2002; Sharratt and McWilliams, 2005). Roots explore soil to deeper soil layers in maize and soybean as compared to sunflower (Borg and Grimes, 1986; Bremner et al., 1986; Sadras et al., 1989; Dardanelli et al., 1997). Rapid vertical penetration and higher maximum rooting depth increase access to deeper soil water (Sponchiado et al., 1989; Turner, 2004; van Oosterom et al., 2016). However, in shallow soils or environments with mild water stress, deeper rooting is of no benefit. Higher root length density represents a higher degree of exploration within the root zone, due to a shorter distance for water movement from the soil to the root surface (Connor and Hall, 1997). This parameter decreases with depth (Sadras et al., 1989; Guan et al., 2014), and water availability may change the vertical pattern of root distribution (Connor and Hall, 1997). For maize, it was shown that root water uptake linearly increased with root length density in well-watered soils (Ma and Song, 2016) while it asymptotically increased in water-limited topsoils (Gao et al., 2022).

Many management practices affect the features of the root system. Results from Sharratt and McWilliams (2005) suggest that maize grown at narrow row spacing (less than 0.76 m) displays a more uniformly distributed root system that promotes more effective water uptake. In agreement with this, soybean sown with narrow row spacing (0.25 m) produced 49% more roots per unit of land area but with similar root length than in wide row spacing (1.0 m; Mason et al., 1982).

Several studies reported the effects of N supply on the root system. N supply increased roots biomass and promoted changes in their morphology (Wang et al, 2005; Echarte et al., 2008; Lopez et al., 2023). Oikeh et al., (1999) observed that root growth and distribution of field-grown maize was higher at a moderate N rate than at zero or high N supply. Wang et al. (2005) observed that by increasing the N supply, the total length of primary roots of maize was reduced while the total length of lateral roots increased (Wang et al., 2005). Recently, Gao et al. (2022) analyzed the effects of N supply on the maize root system architecture and water uptake and concluded that reduced N fertilization boosted root penetration and increased the root water uptake from the subsoil.

The influence of plant density on root system characteristics was also reported. Shao et al. (2018) showed that increasing maize plant density from 4 to 9 plants m^{-2} increased root biomass and produced a more uniform planting pattern, enhanced the proliferation of shallow roots, and increased the water uptake from the topsoil, from 50 days after sowing. Higher absorption of water by the crop in the top-soil layer avoids losses of water by evaporation, which in turn, contributes to a greater water use efficiency, as will be shown in Section 2. Peake et al., (2013) demonstrated that higher maize plant densities (from 2.4 to 5.5 plants m^{-2}) increased the root length density and the maximum rate of soil water extraction. In the same direction, increasing soybean plant density from 16 to 32 plants m^{-2} increased root length density by 26.7% (Liao et al., 2022). Accordingly, a substantial increment in root density in deeper soil layers was found when increasing sunflower plant density from 2.04 to 5.1 plants m^{-2} (Sadras et al., 1989). Moreover, Sadras et al. (1989) indicated that plant density did not affect the ratio between root length and leaf area, nor the lower limit of soil available water (i.e. stored water tightly held by the soil that is unavailable for the plants; Soltani and Sinclair, 2012) over the range of plant densities investigated.

Different soil cover strategies influenced root system growth. Plastic film mulching promoted significant increments in root biomass and root length at the V6 stage in maize crops (Zhang et al., 2020). In contrast, soil covered with crop residues did not affect the root distribution of maize in vegetative stages (Dwyer et al., 1996; Dal Ferro et al., 2014). Accordingly, average root length and root biomass measured at anthesis in maize were not affected by a recently established no-tillage system; however, root length density and biomass were larger in the top 5 cm and shorter in the 5–15 cm soil layer when no-till was compared with conventional tillage (Fiorini et al., 2018). Differences between the effects of plastic film and straw mulching might be explained by their effect on the soil temperature, which was increased by plastic film mulching (Zhang et al., 2020) but decreased by straw mulching (Dwyer et al., 1995).

A large body of evidence indicates that many management practices influence root system characteristics, and thus, the capacity of the crop to absorb the soil water to cope with the evaporative demand (Figure 1). The influence of these management practices on root growth dynamics is a key factor in understanding root traits' contribution to final grain yield, especially in environments where crops rely upon soil-stored water or in-season rainfall. In these environments, for instance, the rapid growth of a profuse root system might lead to faster soil water depletion and reduce soil water availability for reproductive periods. The importance of the temporal soil water uptake is discussed further in Section 2.3.

2. *Water use efficiency for grain yield production ($WUE_{G,ET,s}$).*

Equation 1 highlights the importance of increasing $WUE_{G,ET,s}$ as a way to increase and/or stabilize yields in environments with limiting water availability (Figure 1). Reported values of $WUE_{G,ET,s}$ for crops growing under variable conditions of water and/or N supply ranged from 2.8 to 39.0 kg ha^{-1} mm^{-1} for maize (e.g. Howell et al., 1998; Ogola et al., 2002; Barbieri et al., 2012; Zhang et al., 2014; Hernández et al., 2015; Tolk et al., 2016; Nagore et al., 2017), 2.1 to 15.3 kg ha^{-1} mm^{-1} for soybean (Hattendorf et al., 1988; Dardanelli et al., 1991; Copeland et al., 1993; Ram et al., 2013; Ren et al., 2017; Aydinsakir, 2018; Perozzi et al., 2020; Liao et al., 2022) and 2.5 to 9.4 kg ha^{-1} mm^{-1} for sunflower (Hattendorf et al., 1988; Zaffaroni and Schneiter, 1989; Mzezewa et al., 2011; Echarte et al., 2020). $WUE_{G,ET,s}$ depends on the availability of water, and in general, it tends to be larger in rainfed than in irrigated crops (Nagore et al., 2017). The reason for this is that in water-limited conditions, reductions in net photosynthesis are lower than reductions in transpiration (Farquhar and Sharkey, 1982; Gilbert et al., 2011; Nagore et al., 2017; Hatfield and Dold, 2019).

Several studies agree that increasing N supply, plant densities, soil cover, or shortening the distance between rows, increase $WUE_{G,ET,s}$ in well-watered environments (Yao and Shaw, 1964; Timmons et al., 1966; Al-Kaisi and Yin, 2003; Lamm et al., 2009; Barbieri et al., 2012; Hernández et al., 2015, 2020; Zhang et al., 2017; Ali et al., 2018 Alfonso et al., 2020). A recent review evaluating $WUE_{G,ET,s}$ response to mulching with different materials and tillage practices, (i.e. ridge furrow mulching, flat mulching, straw mulching, rotational tillage, no-tillage, and others) in the China Loess plateau, showed that mulching increased $WUE_{G,ET,s}$ by between 9 to 61% (Zhang et al., 2017). However, lower or no response of $WUE_{G,ET,s}$ to N supply or higher densities were found in water-limited environments (Hernández et al., 2015, 2020). $WUE_{G,ET,s}$ is a complex trait affected by the genotype (Nagore et al., 2017), many environmental factors, including water regime (i.e. distribution, intensity, and frequency of wetting events), and management practices (Cooper et al., 2023). In the following sections, the influence of management practices on $WUE_{G,ET,s}$ is analyzed in terms of the three main processes controlling $WUE_{G,ET,s}$ (i) the proportion of T in ET, (ii) the biomass production per unit of transpired water (i.e. transpiration efficiency, TE_B) and (iii) the allocation of shoot biomass to reproductive structures (i.e. harvest index, HI; Figure 1 and 2).

2.1. *Proportion of T and E in ET*

Transpiration is the component of ET that is associated with biomass production, whereas evaporation (E) represents the non-productive loss of water from the soil. The contribution of T and E to ET varies according to the soil wetness, particularly in crops with incomplete cover (Ritchie, 1972). In wet soils, E is largely controlled by solar radiation reaching the soil surface. As soils get dryer, E is better related to the moisture content and soil conductivity characteristics of the uppermost soil layer (Tanner and Jury, 1976; Gregory et al., 2000). Crop T is tightly related to light interception which largely depends on leaf area index (LAI; Ritchie, 1972; Eavis and Taylor, 1979; Villalobos and Fereres, 1990; Mc Naughton and Jarvis, 1991). Increasing LAI, in turn, decreases radiation reaching the soil surface and therefore, it decreases the E component of wet soils (Walker, 1983; Villalobos and Fereres, 1990; Eberbach and Pala, 2005; Sauer et al., 2007; Yao and Shaw, 1964). In this way, crop cover or LAI largely influences the proportions of T and E in total ET (Figure 2), with a greater influence on E in wet environments (Fischer and Turner, 1978; Gregory et al., 2000). All management practices that affect LAI and light interception have the potential to modify the contribution of T and E to ET. In this sense, plant density, row spacing, and N supply practices proved to affect LAI (Andrade et al., 2002; Timlin et al., 2014) might differentially affect ET components, with a larger impact on E in frequently wet soils.

Among management practices, plant density is the one with the largest impact on LAI and hence on light interception (Hernández et al., 2015; 2020). The response of LAI to plant density is higher in crops with low vegetative plasticity, like maize than in crops with larger vegetative plasticity, like soybean or sunflower (Wells, 1991; Sadras and Hall, 1988; van Roekel and Coulter, 2011; Andrade et al., 2002, 2005). Many studies in several crops have also reported larger light interception as row spacing is reduced at a constant plant density (Kasperbauer and Karlen, 1994; Flenet et al., 1996; Barbieri et al., 2000; Sharratt and McWilliams, 2005; Drouet and Kiniry, 2008; Zhou et al., 2011). Nitrogen deficiency has also been reported to affect light interception (Teixeira et al., 2014; Hernández et al., 2015) by decreasing LAI (Muchow and Davis, 1988; Wolfe et al., 1988, Gastal and Lemaire, 2002; Boomsma et al., 2009). In agreement with the effect of higher plant density, shorter row spacing, or N supply on crop light interception, several studies have shown that these practices reduce E (Hernández et al., 2015; Rahman et al., 2017). The absence of response of E to any of these management practices reported by other authors (Yunusa et al., 1993; Sharratt and McWilliams, 2005), could be explained by the dependence of their effect on the moisture content of the upper soil layer (Ritchie, 1972; Allen et al., 1998). Hernández et al., (2020) found that increments in seasonal light interception increased the proportion of T in ET (Figure 3), contributing to the increments in $WUE_{G,ET,s}$ at higher light interception when increasing plant density (Echarte et al., 2020).

Soil water deficit reduces leaf water content, leading to reduced cell turgor, plant hydraulic conductivity, and stomatal conductance (Lambers et al., 2008). Tissue expansion processes are more responsive to water deficits than stomatal conductance (e.g., Sadras and Milroy, 1996); thus, reduced LAI restricts water loss in response to drought (Earl and Davis, 2003). Increments of LAI and iPAR (intercepted photosynthetically active radiation) in response to increments in plant density or N supply, in general, are lower in water-limited than in well-watered environments (e.g. Figure 3a). Hernández et al., (2020) found that when maize plant density increased from 4 to 8 plants m^{-2}, seasonal iPAR increased 23% in irrigated plants and 12% in rainfed plants in a water-limited environment. Since water deficiencies reduce leaf expansion (Sadras and Milroy, 1996; Tanguiling et al., 1987; Earl and Davis, 2003; Tardieu, 2013), the extent to which management practices can improve light interception is limited by water availability (Hernández et al., 2015; 2020). In addition, in water-limited environments, where the soil's upper layer is frequently dry, the contribution of management practices to reducing E (and thus increasing the proportion of T) through a decrease in radiation reaching the soil is not expected to be significant. Depending on management practice's impact on light interception and frequency of wetting events, increments in the proportion of T in ET as a function of light interception have been detected also in water-limited environments (Figure 3; Hernández et al., 2020).

Practices that do not directly influence crop light interception, like mulching, have reduced crop ET in humid environments, presumably by reducing the contribution of the E component to ET (Zhang et al., 2017; Adeboye et al., 2017;

Chen et al., 2019; Alfonso et al., 2020; Figure 2). For example, in soybean crops, the proportion of E in ET decreased from 35 to 29% when conventional tillage with no soil cover was compared to no-till management with crop residue cover (Liebhard, 2022). Alfonso et al., (2020) observed that in a humid environment, the larger the stubble biomass, the larger the reduction in soybean crop ET. In agreement, several authors reported that surfaces covered with stubble have lower E rates than bare soil surfaces (Aase and Siddoway, 1980; Enz et al., 1988; Hatfield and Prueger, 1996). Enz et al., (1988), however, noted that E was greater from bare soil than from covered soil until the bare soil is dry. But E from a stubble-covered surface is higher than that from bare dry soil because of its larger available water. Horton et al., (1996) reviewed the effects of straw mulching on a micro-environment without crops, highlighting the influence of the soil surface water on the soil surface energy balance and resultant soil temperatures. Under wet conditions, most of the incoming energy is used to evaporate water, and, temperatures of near-surface bare and mulch soils are similar. In dry conditions, the fraction of energy used for evaporation decreases more rapidly in bare than in mulched soils with a resultant rapid increase in soil temperature (Horton et al., 1996). In addition, mulching insulates the soil surface and hence increases resistance to heat and vapor transfer (Chung and Horton, 1987; Bussiere and Cellier, 1994). In this sense, reduced evaporation from stubble-covered soil has been related to reduced wind speed and lower surface temperatures (Enz et al., 1988).

In summary, a substantial body of experience shows that the proportions of ET components can be manipulated by applying different management practices. To achieve higher values of $WUE_{G,ET,s}$, strategies designed to increase T (or decrease

E) proportion in ET by promoting increments in the crop's light interception and/or decreasing the light reaching the soil surface should be considered (Figure 2).

2.2. Transpiration efficiency (TE_B)

Transpiration efficiency (TE_B) refers to the shoot biomass (indicated by the B suffix) produced per unit of transpired water (i.e. Shoot biomass/T; Tanner and Sinclair, 1983; Vadez et al., 2017). For maize grown in field experiments under different environmental conditions and management practices, TE_B values ranged between 29 to 124.1 kg ha^{-1} mm^{-1} (Table 2; Walker, 1986; Otegui et al., 1995; Pilbeam et al., 1995; Ogola et al., 2005; Suyker and Verma, 2009; Tallec et al., 2013; Teixeira et al., 2014; Kunrath et al., 2020; Hernández et al., 2021; Xie et al., 2022). Similarly, a comparable range of TE_B (33 to 93 kg ha^{-1} mm^{-1}) was reported for maize genotypes grown in lysimeter and pot experiments under different environmental conditions (Table 2). This similarity is noteworthy considering (i) different methods used to partition evapotranspiration (ET) into transpiration (T) and evaporation (E; Table 2), (ii) the known limitations of smaller pot sizes on TE_B (Ray and Sinclair, 1998; Poorter et al., 2012; Chenu et al., 2018), and (iii) the differences in resistance to water vapor transfer between leaves and the canopy scale (including leaf stomatal resistance and aerodynamic resistance within and immediately above the canopy; Jarvis and McNaughton, 1986). In comparison, TE_B values for sunflower ranged from 17.4 to 19.2 kg ha^{-1} mm^{-1} (Sadras et al., 1991), while for soybean, the values ranged from 2.96 to 27 kg ha^{-1} mm^{-1} (Suyker and Verma, 2009; Liebhard et al., 2022).

The wide range of TE_B values observed across different environments is generally attributed to variations in vapor pressure deficit (VPD, Tanner and Sinclair, 1983; Abbate et al., 2004). In general, the reports on VPD lack consistent calculation methods, making it difficult to compare results across different experiments (Abbate et al., 2004; Ghanem et al., 2020). However, within a specific field study that employed a consistent approach to calculating VPD across various locations, a reduction in VPD from 4.35 to 2.1 kPa was found to be associated with a 117% increase in TE_B (Tanner and Sinclair, 1983). Similarly, in a specific pot experiment, TE_B increased by 69% when VPD was reduced from 3.6 to 1 kPa while keeping the temperature constant (Ray and Sinclair, 2002). In this context, Tanner and Sinclair (1983) defined TE_B as the ratio between a transpiration coefficient (k) and atmospheric vapor pressure deficit (VPD; Eq. 2). This formulation explicitly considers the impact of atmospheric conditions on crop transpiration rates and, consequently, on shoot biomass production.

$$TE_B = k/VPD$$

(Eq. 2)

Where TE_B is transpiration efficiency for biomass production, k represents the transpiration coefficient, and VPD is the vapor pressure deficit weighted to account for the daily cycle of VPD.

The parameter k in Tanner and Sinclair´s equation (Eq. 2) is defined by specific and mechanistic properties of leaf canopy gas exchange in well-watered crops with complete cover (i.e. LAI ~ 4). Much of the variation in k among species results from (i) the hexose conversion to plant mass, which is higher for the synthesis of plant products rich in carbohydrates compared to those rich in proteins and lipids, and (ii) the gradient between external and internal CO_2 concentrations, which is largely determined by the photosynthesis pathway (~ 0.3 for C3 species and ~0.7 for C4 species). As maize is a C4 specie and its kernel composition is high in starch, it has one of the highest values of k among crop species (Tanner and

Sinclair, 1983). Thus, based on the definition of k, a unique value of k is determined for each crop species. For instance, maize has a constant value of approximately 9 Pa for k, while soybean has a value of 4 Pa (Tanner and Sinclair, 1983). As a result, TE_B tends to remain relatively consistent across different environments characterized by varying VPD (Tanner and Sinclair, 1983; Eq. 2). However, it should be noted that a fixed k value may not hold up for crops with low LAI (i.e. below 4) through the entire growing season, which is commonly observed in maize at low plant density (e.g. maize maximum LAI was ~ 2.5 at 4 plants m^{-2}, Hernández et al., 2021).

In addition to the influence of VPD on $TE_{B,}$ as described in Eq. 2, soil water conditions also play a role in the wide range of maize TE_B values shown in Table 2. Specifically, under water-limited conditions, maize exhibits higher TE_B compared to maize grown in non-water-limited environments. The increase in TE_B due to low soil water availability ranged from 21 to 34 % for field experiments (Ogola et al., 2005, Otegui et al., 1995) and from 14 to 23 % in lysimeter and pot experiments (Ray and Sinclair, 2002; Vadez et al 2021). These increments in TE_B due to low soil water availability are primarily attributed to smaller reductions in net photosynthesis compared to transpiration rates (Farquhar and Sharkey, 1982; Gilbert et al., 2011; Nagore et al., 2017; Hatfield and Dold, 2019). However, it is worth noting that reductions in TE_B have also been observed in certain experiments, with decreases ranging from 8% to 15% (Kunrath et al., 2020) and from 7% to 48% in three experiments reported by Vadez et al. (2021). These reductions are associated with severe water deficiencies that significantly suppress photosynthesis (Nagore et al., 2017).

Management practices can also influence the wide range of maize TE_B values reported in the literature (Table 2). A complementary approach used to understand the impact of management practices on TE_B, which overcomes the assumption of complete cover in Eq. 2, involves analyzing shoot biomass production as a function of both, photosynthetically active radiation (PAR, Monteith and Moss, 1977) and water resources (Sadras et al., 1991; Caviglia and Sadras, 2001). In this context, by rearranging the shoot biomass equations based on radiation or water resources, TE_B can be expressed as:

$$TE_B = RUE_B \times g_C^{-1}$$

(Eq. 3)

Where RUE_B (radiation use efficiency for shoot biomass production) represents shoot biomass per unit of intercepted PAR (iPAR), and g_C (crop conductance) represents transpired water per unit of iPAR (Matheews et al., 1988; Sadras et al., 1991; Caviglia and Sadras, 2001). Crop conductance (g_C or T/iPAR) is regulated by a series of conductance that involve (i) leaf stomatal conductance to water vapor (g_{SL}) integrated across leaves and (ii) canopy boundary layer conductance (g_B) which refers to the aerodynamic conductance within and just above the canopy; McNaughton and Jarvis, 1991; Polley et al., 2002).

When considering plant density management, higher plant densities have been associated with increases in maize TE_B in well-watered environments. Under these conditions, notable increases in TE_B have been observed, with increases ranging from 12% to 14% when plant density was increased from 4 to 8 plants m^{-2} and from 4 to 12 plants m^{-2}, respectively (Hernández et al., 2021). Similar findings were reported by Ogola et al. (2005), who observed a 20% increase in TE_B when plant density was increased from 6.6 to 13.3 plants m^{-2}, and by Walker et al. (1986), who reported a 34% increase in TE_B for plant density increments from 4.6 to 6.3 plants m^{-2}. Consistent with these results, it has been observed that higher plant densities lead to significant increases in TE_B across a range of pearl millet genotypes, without any interaction between genotype and density (Pilloni et al., 2022). However, Pilbeam et al. (1995) did not find significant maize TE_B responses to increases in plant density from 3 to 4 plants m^{-2}, which may be attributed to the limited range of crop cover explored across densities. Furthermore, Hernández et al., (2021) found that the increments in TE_B associated with increasing plant density were related to reductions in canopy-level conductance (g_C) when changing plant density (Figure 4, Eq. 3). Decreases in canopy coupling with the atmosphere (i.e. a canopy is coupled with the atmosphere when air temperature, VPD, and CO_2 concentration at the surface of the leaves are the same as ambient values, Jarvis and McNaughton, 1986) associated with higher aerodynamic resistances at higher LAI (Steduto and Hsiao, 1998) could be at the basis of the contribution of g_B to reductions in g_C. Additionally, Pilloni et al. (2022) demonstrated that plant density management modifies VPD within the canopy of pearl millet crops. In this work, high-density treatments significantly reduced the VPD and increased TE_B both in lysimeter and field conditions. Lower VPD values at higher densities could also explain the higher maize TE_B observed by Hernández et al. (2021) according to Eq. 2. Moreover, g_C and VPD are closely related since the former represents the relationship between T per unit of light intercepted and T is linearly related to VPD (Lambers et al., 2008; Gholipoor et al., 2013a). In contrast, in water-limited environments, higher plant densities were not effective in increasing water use efficiency for grain yield determination (Hernández et al., 2020).

Similarly, N supply has been shown to increase maize TE_B in well-watered conditions (Sadras et al., 1991; Caviglia and Sadras, 1991; Teixeira et al., 2014; Kunrath et al., 2020). Several studies have reported increments in maize TE_B due to

N supply, ranging from 20% to 16 % (Hernández et al., 2021, Teixeira et al., 2014; Kunrath et al., 2020, Pilbeam et al., 1995). Xie et al. (2023) demonstrated TE_B increments ranging from 49% (moderate N supply) to 95% (high N supply), while Walker (1986) reported a 6% increase in TE_B due to N supply. The magnitude of the TE_B response to N supply across studies may be influenced by the genotypes used and the initial soil N conditions in the experimental site. The effects of N supply on TE_B were primarily associated with increases in (RUE_B) (Eq. 3; Caviglia and Sadras, 1991; Teixeira et al., 2014; Hernández et al., 2021), in contrast to the influence of plant density on TE_B, which was mainly mediated by changes in crop conductance (g_C). The contribution of N supply to RUE_B has been extensively documented (Muchow and Davis, 1988; Wolf et al., 1988; Sinclair and Muchow, 1999; Teixeira et al., 2014) and is attributed to higher leaf N content per unit of leaf area, leading to increased leaf photosynthesis rates (Sinclair and Horie, 1989; Muchow and Sinclair, 1994; Vos and van der Putten, 1998; Echarte et al., 2006). However, under severe N deficiency, which significantly influences canopy architecture (Uhart and Andrade, 1995; Boomsma et al., 2009), changes in canopy-atmosphere coupling and subsequent effects on crop conductance could be expected. In water-limited environments, similar to the influence of plant density, N supply was not effective in increasing water use efficiency for grain yield determination (Hernández et al., 2015).

The wide range of reported TE_B in the literature can also be attributed to the genotypes used in each study. Only a few studies have explored TE_B across different maize genotypes (Table 2; Ray and Sinclair, 2002; Choudhary et al., 2020; van Oosteron et al., 2016, 2021; Vadez et al., 2021). Significant variations in TE_B were observed among hybrids in both non-water-limited and water-limited conditions (van Oosteron et al., 2021; Choudhary et al., 2020). An estimation of the TE_B range across genotypes under non-water-limited conditions is not possible since values for each genotype were not provided in the study by van Oosteron et al. (2021) conducted under well-watered conditions. Other studies did not observe significant differences in TE_B among maize genotypes grown in well-watered conditions (van Oosteron et al., 2016; Ray et al., 2002). In water-limited environments, maize TE_B exhibited significant variability across genotypes, with the highest TE_B being 50% greater than the lowest TE_B (Choudhary et al., 2020). During short-term soil drying experiments conducted in the vegetative period, the variability in TE_B among genotypes can be attributed to their ability to minimize reductions in transpiration rates while sustaining photosynthesis rates (Nagore et al., 2017). This ability could be associated with their capacity to minimize transpiration rates under high VPD conditions, which typically occur around midday (Gholipoor et al., 2013a; Sinclair, 2017).

In summary, a series of studies have demonstrated that management practices, such as increasing plant density and N supply, can promote substantial increments in TE_B in non-water-limited environments (Figure 1). These practices can achieve this by reducing VPD within the canopy and g_C (higher plant density) or increasing RUE_B (N supply). However, in water-limited environments, the advantages in TE_B appear to be mainly mediated by the genotype, with the little effect observed from N supply and increased plant density.

2.3. Shoot biomass partitioning to reproductive structures (Harvest index, HI)

The two previous sections addressed the processes contributing to total shoot biomass production (i.e. T and TE_B). The final grain yield is determined by the proportion of the total shoot biomass that is allocated to reproductive structures (i.e. harvest index, HI; Sinclair et al., 1990). Grain yield results from the combination of seed number and seed mass. Both grain yield components contribute to explaining the responses of grain yield and HI to variations in resource availability (Echarte and Andrade, 2003). However, variation in seed number highly accounts for the variations in grain yield across growing conditions, while individual seed mass is a much more stable trait (Egli, 1998; Otegui et al., 1995; Chapman and Edmeades, 1999; Rotundo et al., 2012; Cerrudo et al., 2013). Therefore, understanding the effects of water availability on seed number determination is central to understanding the influence of management practices on biomass partitioning to reproductive structures and final harvest index under different water availability scenarios.

There is a period during the reproductive growth of the plants when the seed set is most sensitive to resource limitations and thus, the physiological status of the crops during this period largely influences the seed number (Edmeades and Daynard, 1979; Tollenaar et al., 1992; Andrade et al., 1993, 2002b). This period is recognized as the critical period for seed number determination and occurs around flowering in maize and sunflower (Earley et al., 1967; Hall et al., 1981; Aluko and Fisher, 1988; Cantagallo et al., 1997; Cerrudo et al., 2013), and from flowering to beginning or middle seed filling in soybean (Jian and Egli, 1995; Egli, 1998; Monzon et al., 2021). Several studies have used the plant or crop growth rate (PGRcp or CGRcp, respectively) to characterize the physiological status of plants or crops during the critical period for seed number determination (Williams et al., 1968; Villalobos et al., 1992; Jian and Egli, 1995; Andrade et al., 1999). Although other mechanisms can concurrently regulate seed set (e.g. direct effects of water and nitrogen deficiencies on kernel abortion, stress-induced changes in hormones), PGRcp or CGRcp are regarded as indicators of the amount of carbon available for the plant or crop growth and can be used as acceptable predictors of seed set

(Andrade et al., 2002b). The relationship between seed number per plant and PGRcp is curvilinear for maize and sunflower and almost linear for soybean (Vega et al., 2001; Echarte et al., 2004). A particular feature of the seed number per plant – PGRcp relationship in maize, is a significant PGRcp threshold for seed set, which reflects the abrupt decrease in dry matter partitioning to the ear at low resource availability (Vega et al., 2001; Echarte et al., 2004). In contrast, no significant PGRcp threshold for the seed set was evident for soybean (Vega et al., 2001). Therefore, severely low resource availability can lead to a high proportion of plants growing at rates close to or below the threshold for seed set and thus, result in sharp HI reductions in maize but not in soybean (Andrade et al., 1999; Vega et al., 2000; Echarte and Andrade, 2003; Carciochi et al., 2019).

In well-watered environments, high plant densities or N supply increase light interception during the critical period for seed set and maximize CGRcp (Uhart and Andrade, 1995; Andrade et al., 1999; Hernández et al., 2020; Figure 5), contributing to higher seed number set and in turn, to larger maize grain yield (Figure 6). Thus, N supply avoids HI reductions due to N deficiency (Uhart and Andrade, 1995; Figure 2). However, high plant densities also promote higher competition for resources among plants, leading to lower seed number response to further CGRcp increments (Andrade et al., 1999). Therefore, lower HI at high than at low stand density are commonly obtained (Tollenaar et al., 1989; Echarte et al., 2000; Kiniry and Echarte, 2005; Hernández et al., 2020). The effect of plant density on HI depends on the maize hybrid characteristics (i.e. with more or less reproductive plasticity; Sarlangue et al., 2007). Hence, in non-water-limited environments, positive effects of higher plant densities on increasing $WUE_{G,ET,s}$ are mostly mediated by increments in biomass production due to higher T/ET and TE_B, and not in HI. Increments in grain yield in response to narrow rows were closely related to the improvement in light interception during the critical period for seed set (Andrade et al., 2002). However, major benefits of reducing row spacing on HI in environments not limited by water during critical periods, are expected in crops that would not achieve full light interception during critical periods for seed set (e.g. short season and/or erect leaf cultivars, or crops subjected to defoliation or nutritional stresses during vegetative periods; Barbieri et al., 2000). For instance, Barbieri et al. (2012) demonstrated that maize HI increased in response to reduced row spacing only in N-deficient crops.

Harvest index response to water availability is largely influenced by the intensity and moment of water deficiency occurrence. It has been shown that maize HI is quite stable under moderate water stress but it sharply drops under severe water stress around silking (Sinclair et al., 1990). Low water availability during the critical period for seed set limits ET (Nagore et al., 2017) and, in turn, reduces CGRcp and seed set (Andrade et al., 2002a; Echarte and Tollenaar, 2006; Nagore et al., 2017). In this type of environment, N supply or higher densities fall short to increase maize grain yield (Figure 6; Hernández et al., 2015; 2020). Increments in plant density in this condition did not increase CGRcp (Figure 5). Thus, in environments with a high probability of water deficit during the critical period for seed set, it is crucial to apply management practices that promote water conservation during vegetative periods, so that water is available during critical reproductive stages. Plant density is one of the most frequently manipulated management practices when farmers try to cope with limited water availability. In this sense, low stand densities not only reduce plant-to-plant competition and avoid PGRcp decrease close to threshold values for seed set (Echarte et al., 2004; Hernández et al., 2020) but also decrease soil water uptake during the vegetative period and thus, contribute to higher water availability during the critical period for seed set (Echarte et al., 2020). Accordingly, wide rows would also contribute to a conservative use of water during the vegetative period. In agreement with this, Barbieri et al. (2012) showed that soil water depletion during the initial stages of maize growth was higher for narrow than for wide row spacing. Higher soil water depletion and ET early in the season under narrow compared with wider row spacing were also reported for soybean (Taylor, 1980; Reickosky et al., 1982; Nagore et al., 2020; Perozzi et al., 2020) and for sunflower crop (Vijayalakshmi et al., 1975). A higher soil water depletion under narrow row spacing during initial growth stages could be related to (i) a more uniform and deeper root system (Section 1.1 of this review, Raper and Barber, 1970; Sadras et al., 1989, Sharratt and McWilliams, 2005), and (ii) larger increments in T than reductions in E from the soil. In a severely water-limited environment during vegetative stages and for most of the critical period for seed set, narrow rows decreased soybean grain yield (Mujica et al., 2020), probably associated with a more rapid depletion of soil water availability that limited shoot biomass production during critical stages.

In summary, management practices meant to promote higher $WUE_{G,ET,s}$ should be adjusted to the environment and consider not only the available resources but the dynamics of crop growth and the moment when those resources are more necessary for crop growth. In other words, special attention on granting resource availability during critical periods for grain yield determination should be paid. Thus, management practices are key determinants of effective water use for grain production in non-water-limited environments as well as to avoid large grain yield reductions under low soil water availability (Figure 1, 2). Future technological solutions should focus on combining genotype improvements with management practices to maximize crop productivity. As highlighted by Cooper et al. (2020, 2023), such an integrated approach could be the key to unlocking the full potential of modern maize genotypes in targeted environments.

3. Modeling efforts for predicting water-related grain yield determinants

Crop growth models can largely guide management practices that optimize grain production in each environment (e.g. Monzón et al., 2007; Mercau et al. al., 2014; Rattalino Edreira, et al 2018; Rotili et al., 2019). Likewise, crop growth models can expedite the design of crop improvement strategies that integrate genetic gains from breeding and crop management strategies that reduce yield gaps for targeted environments (Cooper et al., 2016, 2020, 2023). In this sense, modeling approaches have made possible the determination of risks or probabilities of certain results based on the use of several years of meteorological data (e.g. Bassu et al., 2014; Yakoub et al., 2017; Monzón et al., 2018). Many available crop growth simulation models were extensively used for guiding crop management (e.g. plant density, soil cover, planting date). Examples of these models are DSSAT (Hoogenboom et al., 2010; Jones et al., 1998), APSIM (Keating et al., 2003), AquaCrop – FAO (Steduto et al., 2009) and CropSyst (Stockle et al., 2003). However, to be used as a tool for designing management solutions for water limitations, a model should be solid in predicting the water-related grain yield determinants (ET, $WUE_{G,ET,s}$), and in particular in those environments that are limited by water. The major interest of this section is to review current knowledge on how well some crop growth models perform for the prediction of water-related grain yield determinants (i.e. ET, $WUE_{G,ET,s}$) and/or soil water content which contributes to ET and $WUE_{G,ET,s}$ accurate predictions, under varying levels of N supply, density or soil cover. For details about different approaches in simulating soil water balance refer to Jara and Stockle (1999) for CERES-maize and CropSyst, Keating et al. (2003) for APSIM, and Steduto et al. (2009) for AquaCrop. This section was narrowed to discuss the performance of different simulation models for the maize crop in particular since extending the revision to soybean and sunflower would imply an amount of information that would qualify for a separate review.

The performance of simulation models for the prediction of water-related grain yield determinants has been much less evaluated than the performance for the prediction of biomass or grain yield. It is noteworthy that in many studies, the validation of the models is limited to the prediction of grain yields in environments with non or moderate water stress, and is assumed to be valid for simulating outputs related to ET, $WUE_{G,ET,s}$ and/or soil water content in any condition of water availability. Basso et al. (2016) stated that the CERES-Maize model performance for the prediction of water-related grain yield determinants was evaluated in a few studies (9 studies for evapotranspiration, and 17 studies for soil water content). These authors noted that the validation of seasonal ET simulation of CERES maize presented errors ranging from 2.3 to 12%, with larger errors under water stress conditions (Anothai et al., 2013 and other references in the review by Basso et al, 2016). Some studies suggested that large errors for maize ET prediction, in particular in water-limited environments, could be reduced by changing the parameter that partitions ET between crop T and soil E (López-Cedrón et al., 2008; Dejonge et al., 2012; Attia et al., 2021). In agreement with previous findings, more recent evaluations of the CERES maize performance indicated good accuracy of the model in simulating soil water content in fully irrigated conditions or under moderate water stress (Wang et al., 2021; Amiri et al., 2022) but with increasing water stress, the accuracy decreased (Amiri et al., 2022; Song and Jin, 2020). CropSyst model showed an advantage over CERES-maize in predicting soil water content as water stress conditions increased (Jara and Stockle, 1999). Umair et al. (2017) presented ET overestimations of 21% and underestimations of 9% with CropSyst for irrigated maize in the arid-semiarid conditions of North China and concluded that CropSyst gave an acceptable simulation. AquaCrop model was able to simulate general trends in soil water content, maize ET and/or maize $WUE_{G,ET,s}$ (Hsiao et al., 2009; Ahmadi et al., 2015; Shirazi et al., 2021), across a range of locations with contrasting environments, but failed in severe water stress environments (Heng et al., 2009; Katerji et al., 2013). Comparison between observed and predicted soil water content with the APSIM model indicated that soil water dynamics were well simulated during the maize growing season at different water regimes (Archontoulis et al., 2014; Magaia et al., 2017; Chen et al., 2021; Santos et al., 2020; Ebrahimi et al., 2022). As well, accurate ET predictions under a wide range of irrigation treatments in the North China Plain were achieved with the APSIM model (Sun et al., 2015). Further, Guo et al. (2021) showed a close relationship between measured soil E with micro-lysimeters and soil E simulated by the APSIM model, beneath a maize crop canopy in a humid area. Fewer reports, however, examined predicted and observed values of ET, $WUE_{G,ET,s}$ or soil water content under varying N supply, plant density, or soil cover.

After carefully calibrating water-related grain yield determinants under varying N supply levels, Dokohaky et al. (2016) showed that CERES-maize and a hybrid model (CERES-maize + SWAP model, an agrohydrological model; Van Dam et al., 2008) generally under-predicted the total soil water content for all N supply levels (see Table 6 in Dokohaky et al., 2016). These authors concluded that both models displayed a general tendency to extract more water than was expected from the soil profile. Kaur and Arora (2018), instead, reported consistent under-estimation of maize water use at different irrigation and N regimes, with CERES-maize. By contrast, soil moisture simulations with the APSIM model under varying N supply and water regimes were acceptable (Magaia et al., 2017). Accordingly, predicted maize $WUE_{G,ET,s}$ values with the AquaCrop model under varying water regimes and N supply levels closely matched the observed values (Abendinpour et al., 2012).

Ren et al. (2016) evaluated the performance of the APSIM model for estimating total soil water content in 260 cm soil layers during the season, for a range of maize plant densities between 5.2 to 9.8 plants m^{-2}. These authors included changes in the root water uptake parameter (kl, Peake et al., 2008, 2013) and concluded that the improved calibration of the APSIM model yielded reliable simulations of soil water content at different plant densities. The performance of the AquaCrop model for estimating ET and soil water content under different plant densities ranging from 5.9 to 8.9 plants m^{-2} was evaluated by Sandhu and Irmak (2019). The authors noted that despite adopting careful parameterization and calibration, the AquaCrop model consistently underestimated soil water content and overestimated seasonal ET. Accordingly, the CERES maize model underestimated the soil water content during the maize growing season and was not able to identify differential soil water depletion among plant densities in the range between 5.2 and 9.8 plants m^{-2} (Zhang et al., 2022).

The evaluation of water-related grain yield determinants simulated with CropSyst under no-till with straw mulching and conventional tillage indicated good predictions in general but a large deviation of modeled from observed data of soil moisture in the first 15cm during a dry period (Sommer et al., 2010). Similarly, Monzon et al. (2012) concluded that CropSyst simulated particularly well the cumulative seasonal ET under no-till with straw mulching and conventional tillage, although seasonal ET overprediction was consistently evident at low ET values (≈200 mm) under both tillage managements. Simulated maize daily ET with mulch with the AquaCrop model presented higher accuracy in well-watered than in water stress treatments (Ran et al., 2017). Recently, Feng et al., (2022) indicated that simulated values of soil water content were underestimated and ET was generally higher than the one observed in the field for mulched drip-irrigated maize. APSIM model validation showed appropriate simulated vs. observed data relationship for soil moisture at different soil layers for maize grown under no-till with straw mulch and under conventional management, in wet environments (Yang et al., 2018; Dutta et al., 2020).

In summary, current knowledge on the performance of the most widely used crop growth models for predicting water-related maize grain yield determinants (ET, $WUE_{G,ET,s}$) warns about the errors in the simulations of water-related components, especially in water-limited environments. This section also draws attention to the need for adjustments in model parameters that consider different levels of N supply, plant densities, or soil cover to reduce errors in simulations of soil water content, ET, and $WUE_{G,ET,s}$. Improving the prediction of water-related grain yield determinants can ultimately improve accuracy for guiding farmers in their management decisions when willing to grow maize under rainfed conditions.

4. *Concluding remarks*

We have reviewed the impact of some management practices, particularly N supply, plant density, row spacing, and soil cover, on water-related processes contributing to grain yield determination. The major focus was on maize but some insights for sunflower and soybean were also provided.

The first part of this review addressed the influence of management practices on crop evapotranspiration (ET) and root water uptake. A large number of conflicting results available in the literature regarding the response of ET to management practices explored evidence of the complexity of such responses, and highlight the importance of considering processes underlying ET, interactions of factors, and non-linear response of ET to these factors. Most ET responses are mediated by root system development and architecture and thus understanding the effects of management practices on root system characteristics is a key factor to promote adequate soil water uptake that allows to cope with evaporative demand and also to avoid or reduce water deficiencies in reproductive periods, especially in environments where crops rely upon soil stored water.

The second part of this review examined the influence of management practices on the water use efficiency for grain yield production ($WUE_{G,ET,s}$); and analyzed in particular how management practices influence each of the three main processes determining $WUE_{G,ET,s}$: (i) the proportion of T in ET, (ii) the transpiration efficiency for shoot biomass production (TE_B) and (iii) the allocation of shoot biomass to reproductive structures (i.e. harvest index, HI). The major focus of reviewed research literature was on the influence of management practices on increasing transpiration (or reducing evaporation) proportion in the total ET. When analyzing the influence of management practices on the proportion of T in ET, a distinction can be made between those that promote changes in crop light interception (i.e. N supply, plant density, and row spacing) and those with no apparent direct effect on crop light interception (i.e. soil cover). For the formers, this review analyzed the expected impact of management practice in terms of the magnitude of its effect on crop light interception. For the latter, a large body of evidence shows that soil cover reduces E component, mainly in frequently wet environments. However, we found some gaps in knowledge regarding the influence of soil cover on the crop environment at the canopy level. For example: can reflection from the soil cover significantly affect crop light interception?, can the soil cover influence VPD experienced by the canopy? Addressing this issue gains relevance in light of the influences of environmental changes at the canopy level on TE_B. In this sense, the analysis of the effects of management practices on TE_B was addressed following two different approaches, i.e. TE_B = k/VPD or RUE_B x g_C^{-1}. We showed that management practices that affect crop light interception can influence TE_B by modifying any of its determinants and we highlighted that a fixed k value (Eq. 2) might not be valid for crops with low LAI during the whole growing season. The revision of the influence of management practices on partitioning to reproductive structures was focused on seed number, the grain yield component that better reflects grain yield variability across environments. Here we emphasized the importance of adjusting the management practice to the environment, to favor water resource availability during critical periods for grain yield determination. Overall, this review highlights the key role of management practices in optimizing effective water use and enhancing grain yields under contrasting soil water availability. Moving forward, future technological advancements should prioritize the integration of genotype improvements with effective management strategies to maximize crop productivity in targeted environments.

Although many crop growth models that predict both grain yield and water-related grain yield determinants are available, few studies have validated the water-related component predictions of these models. And even fewer of them evaluated the performance of these models for predicting the influence of management practices on water-related grain yield determinants. Some of the most broadly used models present errors in predicting water-related components that are larger in water-limited than in non-water-limited environments, exposing the need for improvements of existing models. Future joint efforts of researchers running field experimentation and modelers to validate and or improve the estimates of water-related components could help to develop reliable tools to guide farmers' management decisions based on the probability of occurrence of drought risks in long series of years.

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Table 1: Threshold of fraction of transpirable soil water for the decline in transpiration rates (FTSWt) minimum (min), maximum (max) and mean, for maize plants grown in pot experiments (Exp.) including different treatments (genotypes, g or vapor pressure deficit levels, vpd), at different VPD (kPa) and daytime temperature (°C, when provided), in several studies (source) after Sadras and Milroy´s review.

Exp. #	Treatments	VPD	Temp	FTSWt			Source
		kPa	°C	min	max	mean	
1	g	1.2	29	0.34	0.59	0.47	Choudhary et al., 2020
2	g	4.3	38	0.49	0.64	0.56	
1	g		30	0.37	0.60	0.48	Gholipoor et al., 2013
2	g		> 30	0.35	0.51	0.42	
1	g			0.38	0.60	0.51	Ray and Sinclair, 1997
2	g			0.36	0.44	0.39	
3	g			0.38	0.41	0.39	
1	vpd	1.2	26			0.42	Devi and Reddy, 2020
		2.3	30			0.48	
		3.5	34			0.51	
1	g	1.9	32	0.22	0.42	0.29	Echarte et al., 2023
2	g	3.8	38	0.36	0.46	0.42	
1	g, vpd	1.0	33	0.36	0.38	0.37	Ray et al., 2002
		1.1	33	0.33	0.37	0.35	
		2.9	33	0.33	0.35	0.34	
		3.6	33	0.31	0.38	0.35	

All the experiments were conducted during the early vegetative stages initiating at the 4 to 5 leaves stage.

Table 2: Transpiration efficiency for shoot biomass production (TE_B, shoot biomass per unit of transpired water, kg ha^{-1} mm^{-1}) minimum (min), maximum (max), and at non-limiting condition (oc) in three types of experiments (field, modeling, and lysimeter or pots) for maize grown under different treatments, estimated during different periods and using different methodologies for partitioning evaporation from ET, for measuring soil water content (SW) and for estimating ET or T, in studies (Source) that partitioned the components of ET (E and T).

Exp. type	Exp.	Treatments[£]	TE_B (Kg ha^{-1} mm^{-1})			Period[€]	Evaporation[§]	SW[Ŧ] and ET or T[Ƀ] estimate	Source
			min	max	oc[*]				
Field	1	W (ws, ww) and N (L, N)	54.0	66.0	64.4	Seasonal	ML	NP, SWB	Hernández et al., 2021, 2015
	2		54.0	75.0	65.0				
	1	W (ws, ww) and D (4, 8, 12)	57.0	81.8	64.5	Seasonal	ML	NP, SWB	Hernández et al., 2021, 2020
	2		56.0	64.3	61.0				
	1	W (ws, ww) and D (7, 13)	47.5	60.6	55.4	Seasonal	ML	NP, SWB	Ogola et al., 2005
	1	W (ws, ww)	48.3	56.9	56.9	Seasonal	x-intercept	NP, SWB	Kunrath et al., 2020
	2	W (ww, ws), LN	56.5	52.0		to silage			
	3	N (L, N)	32.5	45.2	45.2	Seasonal			
	1	Locations, ww	46.0	54.0	50.0[#]	Seasonal	model	NP, SWB[¥]	Tanner and Sinclair, 1983
	2		42.0	55.0	48.5[#]				
	3		37.0	46.0	41.5[#]				
	4		20.0	26.0	23.0[#]				
	5		29.0	47.0	38.0				
	1	N (L,N), ww	95.6	107.9	107.9	Seasonal	model	NP, SWB	Pilbeam et al., 1995
	2	N (L,N), ww	60.7	76.3	76.3				
	3	D (4.4, 3), ww	110.5	124.1	124.1				
	4	ws	60.5						
	1	ww			52.0[#]	Seasonal	model	Eddy covariance	Suyker and Verma, 2009
	1	N (L, N), ww	31.0	60.0	54.8	Seasonal	sc	Gravimetry, SWB	Xie et al., 2022
	1	ww			74.3	to silage	model	Eddy covariance	Tallec et al., 2013
	1	W (ws, ww)	49.0	74.0	49.0	RP	model	NP, SWB	Otegui et al., 1995
	2	W (ws, ww)	60.0	83.0	60.0				

	3	W (ws, ww)	59.0	77.0	59.0				
	4	W (ws, ww)	50.0	65.0	50.0				
	1	D (4, 6), ww	55.5	85.8	82.2	RP	ML	NP, SWB	Walker, 1986
	2	N (L, N), ww	66.0	94.4	84.8		sc		
Modeling	1			$54.0^{¢}$		Seasonal		Modeling	Grassini et al., 2009
Lysimeter and Pot	1	g, ws	65.0	87.0		ev	sc (9 l)	WC	Choudhary et al., 2020
	2	g, ws	62.0	93.0					
	1	W (ws, ww) and vpd and g	67.0	84.1	67.8	ev	sc (2.2 l)	WC	Ray et al., 2002
			65.6	82.3	66.2				
			44.8	56.7	45.6				
			38.9	49.4	40.1				
	1	ww, pot size			41.9	ev	sc (2.3 l)	WC	Ray and Sinclair, 1998
					50.5		sc (4.1 l)		
					56.3		sc (9.1 l)		
					54.2		sc (16.2 l)		
	1	g, ww			$90.7^{\#}$	to silking	sc (51 l)	WC	van Oosteron et al., 2016
	2	g, ww			$83.5^{\#}$				
	3	g, ww			$81.4^{\#}$				
	1	g, ww			85.8	to silking	sc (50 l)	WC	van Oosteron et al., 2021
	2	g, ww			61.8				
	1	Sg	43.8	46.3	45.1	Seasonal	sc (2.5 l)	WC	Reddy et al., 2015
	1	W (ww, ws) and g	33.0	63.0	33.0	Seasonal	Sc (67 l)	WC	Vadez et al., 2021
	2	W (ww,ws) and g	74.0	91.5	80.0				
	3	St and g, ww	48.0	70.0	60.3				
	4	St and g, ww	30.0	$31.5^{¢}$					

[*] Non-limiting conditions (oc) refer to plants or crops grown with adequate nutrition and in well-watered conditions, and under adequate density management in the case of the field experiments.

[£] Treatments include water regimes, W (water stress, ws and or well-watered, ww); density levels, D (plants m^{-2}); N supply, N (non or low N supply, LN or adequate N supply, N); genotypes, g; VPD levels, vpd; spatial geometry, Sg and soil types, St.

[€] Periods include seasonal, from around sowing to silage (to silage) or to silking (to silking), during the early vegetative period, ev (which generally starts 30 days after sowing), and during the reproductive period, RP.

[§] Approaches for estimating the evaporation component of ET include micro-lysimeters (ML), x-intercept of the relationship between biomass and ET, modeling, minimization with soil surface cover (sc). The volume of the pots and lysimeters is provided between brackets (liters).

[₸] Methods for measuring SW include neutron probe (NP) and gravimetry.

[฿] Approaches for estimating ET or T include soil water balances (SWB), Eddy covariance, modeling, and lysimeter or pot weight change adjusted for the water applied (WC).

[¢] Estimated with boundary limit function.

[#] TE_B includes root biomass.

[¥] From Stewart et al. 1977.

[¢] Abnormally low values.

Figure Legends

Figure 1: Schematic representation of water-related determinants of grain yield (ET, evapotranspiration and $WUE_{G,ET,s}$, water use efficiency for grain yield) and their controlling factors and processes influenced by management practices. N supply, plant density, row spacing, and soil cover affect ET through their effects on the root system (Section 1.1) and crop and soil cover (Section 1). Additionally, effects of management practices on crop and soil cover affect $WUE_{G,ET,s}$ by affecting the proportion of transpiration (T) in the total ET (T/ET; Section 2.1), transpiration efficiency for shoot biomass production (TE_B, Section 2.2) and harvest index (HI, Section 2.3). The dashed line represents the direct effects of N supply on TE_B and kernel setting. The environment, characterized by soil available water (SAW) and the major drivers of evaporative demand (vapor pressure deficit [VPD] or also characterized by reference evapotranspiration; Section 1), along with genotype effects, influence the response of the water-related grain yield determinants to management.

Figure 2: Schematic representation of processes affected by management practices (N supply, plant density, soil cover) that influence the controlling factors of $WUE_{G,ET,s}$: the proportion of transpiration (T) in the total evapotranspiration (**T/ET**), transpiration efficiency for shoot biomass production (**TE_B**), and harvest index (**HI**). In well-watered environments, soil cover influences T/ET by affecting the soil energy balance (EB). Higher plant densities increase leaf area index (LAI) which promotes higher photosynthetically active radiation interception (iPAR), and in turn, higher T/ET and TE_B mediated by reductions in vapor pressure deficit (VPD) and crop conductance (g_C). In addition, higher plant densities maximize crop growth rate during the critical period (CGRcp) but may promote higher competition for resources among plants, leading to lower seed number response to further CGRcp increments (i.e. higher plant density, in general, reduce HI). N supply increases iPAR and radiation use efficiency for biomass production (RUE_B). Higher iPAR promotes higher T/ET and along with RUE_B increases CGRcp and in turn, HI. Under severe N deficiency, which significantly influences canopy architecture, higher TE_B due to lowering gc could be expected (dashed line from iPAR to TE_B due to N supply).

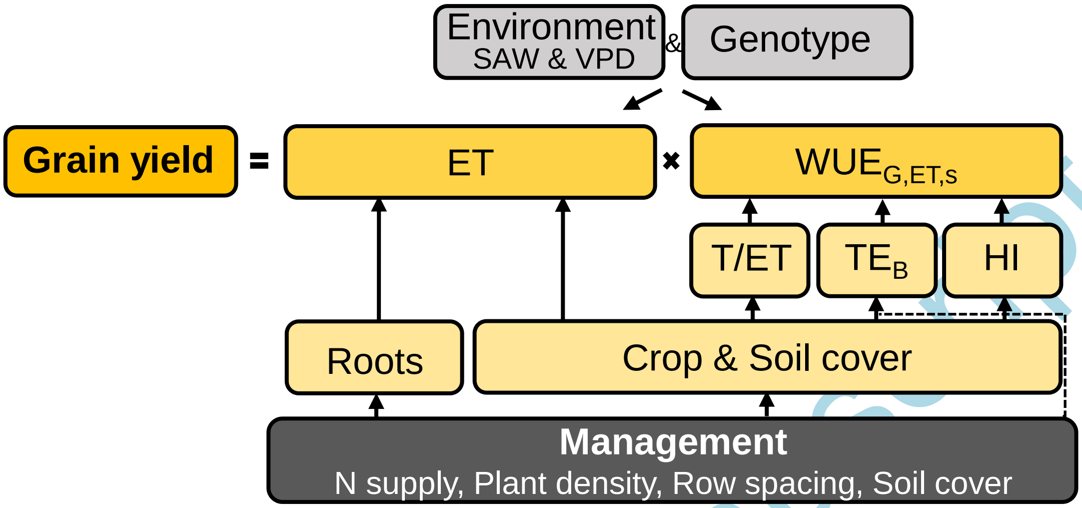
Figure 3: (A) Seasonal intercepted photosynthetically active radiation (iPAR, MJ m^{-2}) as a function of plant density (plants m^{-2}) and (B) Seasonal T/ET ratio as a function of iPAR (MJ m^{-2}), for maize grown in irrigated (I) and Rainfed (R) treatments during Season 1 (S1) and Season 2 (S2). From Hernández et al., 2020.

Figure 4: Crop conductance (g_C, mm MJ^{-1}) as a function of plant density for maize crops grown in well-watered conditions, during two seasons (S1 and S2). Means followed by a common letter are not significantly different among plant densities, at $p < 0.05$, within each season. Adapted from Hernández et al., 2021.

Figure 5: Maize crop growth rate during the critical period for kernel number determination (CGRcp, g m^{-2} d^{-1}) in response to increments in plant density for irrigated

maize (I) and rainfed maize (R) with water limitations during the critical period for kernel determination. Adapted from Hernández et al., 2020.

Figure 6: Maize grain yield in response to (A) seasonal crop evapotranspiration (mm) for maize with no N supply (No N) and with N supply (N supply; from Hernández et al., 2015) and (B) plant density (plants m^{-2}) for irrigated maize (I) and rainfed maize grown in a dry environment during the critical period for kernel set (R; adapted from Hernández et al., 2020).



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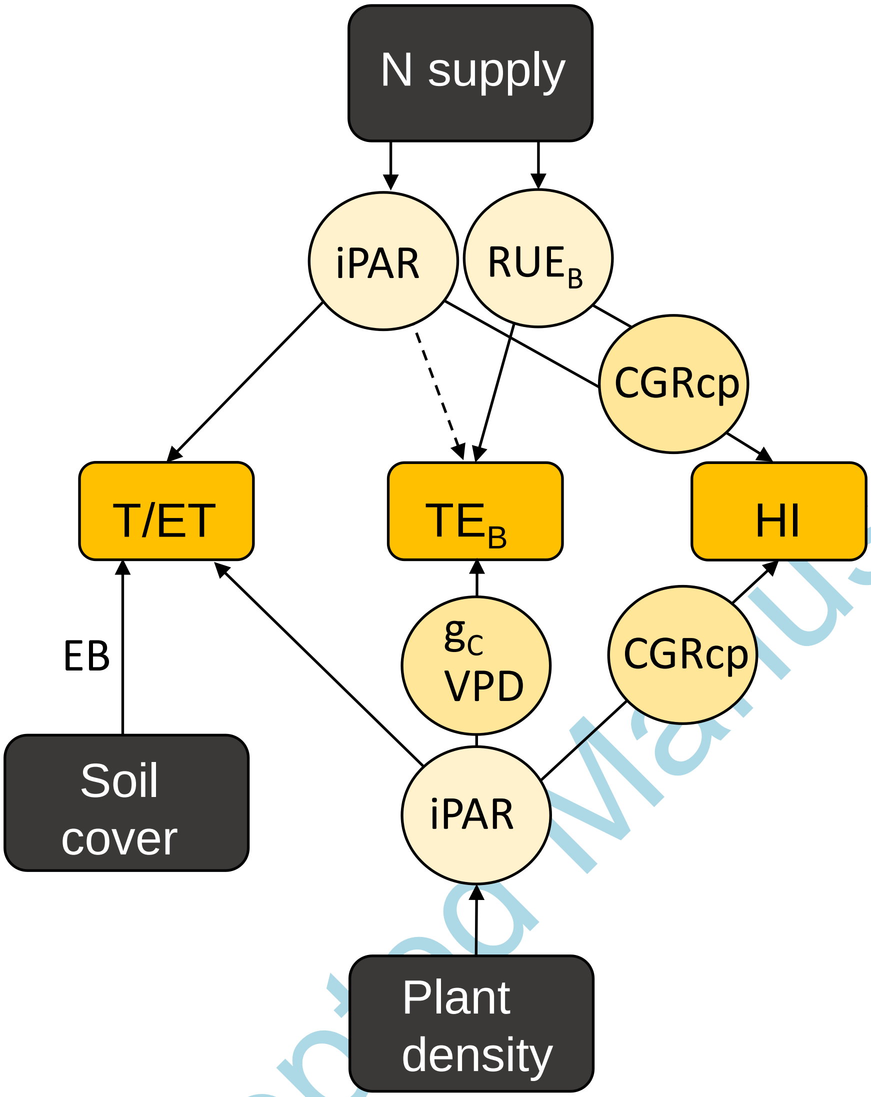

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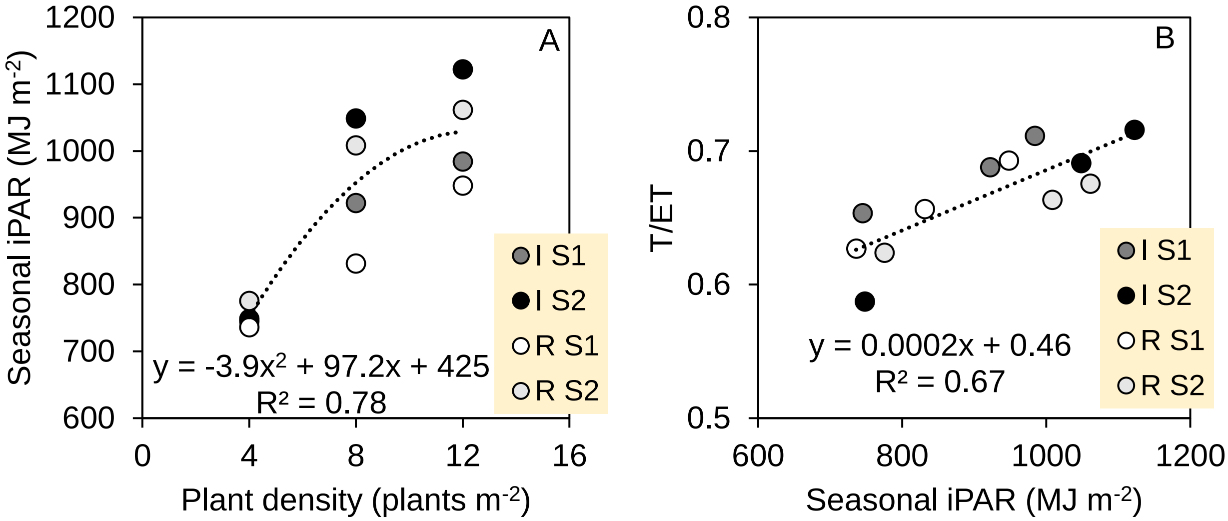

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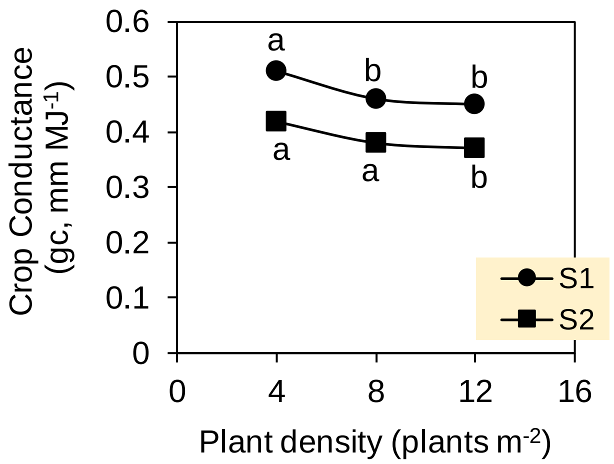

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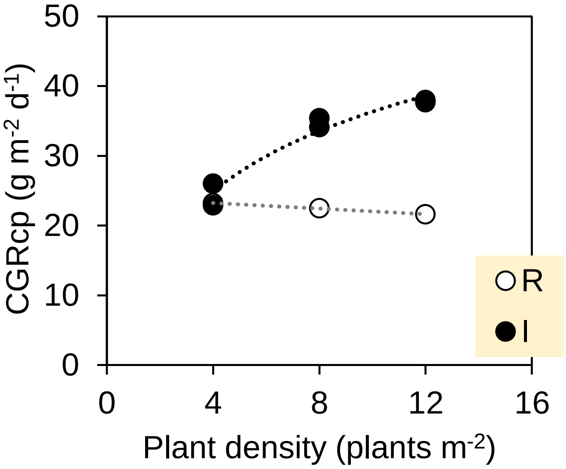

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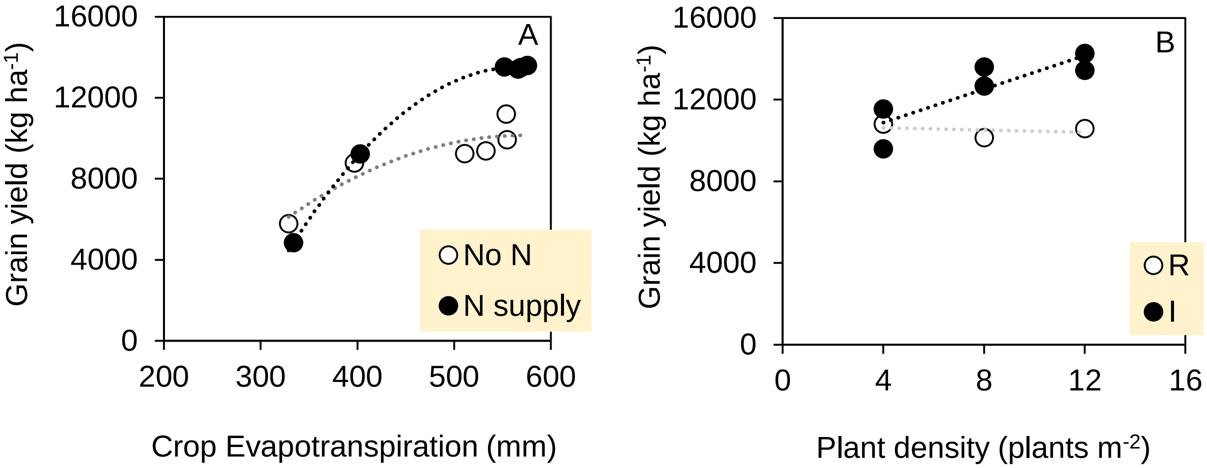

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