

1 **Crop modeling suggests limited transpiration would increase yield of sorghum**
2 **across drought-prone regions of the United States**

3

4 Rubí Raymundo¹, Greg Mclean², Sarah Sexton-Bowser³, and Geoffrey Morris^{1*}

5

6 ¹ Department of Soil and Crop Science, Colorado State University, Fort Collins, CO 80523 USA

7 ² Center for Crop Science, Queensland Alliance for Agriculture and Food Innovation, The
8 University of Queensland, Brisbane, Qld 4072, Australia.

9 ³ Department of Agronomy, Kansas State University, Manhattan, KS, 66506 USA

10

11 * Corresponding author: Geoff.Morris@colostate.edu

12

13 Prepared for submission to *Plant Direct*

14 **ABSTRACT**

15 Breeding sorghum for drought adaptation is pivotal to secure crop production in drought-prone
16 regions. Limited transpiration (LT) restricts water demand at high vapor pressure deficit, saving
17 water for use in critical periods later in the growing season. Here we evaluated the hypothesis
18 that LT would increase sorghum grain yield in the United States. We used a process-based crop
19 model, APSIM, which simulates interactions of genotype, environment, and management ($G \times E$
20 $\times M$). In this study, the G component includes the LT trait (G_T) and maturity group (G_M), the E
21 component entails water deficit patterns, and the M component represents different planting
22 dates. Simulations were conducted over 33 years (1986-2018) for representative locations across
23 the US sorghum belt (Kansas, Texas, and Colorado) for three planting dates and maturity groups.
24 The interaction of $G_T \times E$ indicated a higher impact of LT sorghum on grain for LD, MD, and
25 ED (8%), than on WW environments (4%). Thus significant impacts of LT can be achieved in
26 western regions of the sorghum belt. Otherwise, the lack of interaction of $G_T \times G_M \times M$
27 suggested that an LT sorghum would increase yield by around 8% across maturity groups and
28 planting dates. Although the interaction $G_M \times M$ revealed that specific combinations are better
29 suited across geographical regions. Overall, the findings suggest that breeding for LT would
30 increase sorghum yield in the drought-prone areas of the US without tradeoffs.

31

32 **Keywords:** Stress tolerance, crop growth model, crop adaptation, plant breeding, limited
33 transpiration, sorghum.

34 INTRODUCTION

35 Droughts resulting from changes in precipitation patterns threaten crop production and food
36 security in semiarid areas worldwide (Barbier, 2015). In the United States alone, crop yield loss
37 due to droughts costs ~\$9 billion per year (NOAA, 2020). In this respect, breeding for drought-
38 prone environments plays a pivotal role in maintaining crop production (Thornton et al., 2018).
39 Nevertheless, developing crops with less water demand is challenging because drought
40 adaptation traits are complex, difficult to identify, and often involve tradeoffs (Araus et al., 2012;
41 Monneveux et al., 2012). Furthermore, testing the effect of these traits under water stress
42 scenarios is limited since drought events vary over time and geographies (Pournasiri-Poshtiri et
43 al., 2018; Tang and Piechota, 2009). Thus, plant breeding programs require complementary
44 methods to test the effect of any hypothetical drought adaptation trait to design a breeding
45 pipeline (Bernardo, 2020; Cooper et al., 2002; Cooper and Messina, 2022).

46 Crop models have become standard tools to assess the impact of new technologies in
47 agriculture and can support plant breeding (Challinor et al., 2018; van Ittersum et al., 2003).
48 These models integrate ecophysiological knowledge to represent the plant-soil-atmosphere
49 system and predict the crop response to soil properties, climatic conditions and crop management
50 practices (Jones et al., 2003). Crop models equip breeding programs with the tools to develop
51 and evaluate hypotheses regarding the performance of new cultivars (G) under environmental
52 (E), and management scenarios (M) (Chenu et al., 2017; Messina et al., 2011). Several crop
53 modeling studies have evaluated theoretical expressions of crop traits linked to cultivar-specific
54 parameters for drought environment (Singh et al., 2014). The most common approach varies
55 cultivar parameters (Messina et al., 2011; Singh et al., 2014) or implements new traits (Sinclair
56 et al., 2005) to evaluate alternative ideotypes for constraint environments. This approach to crop
57 improvement advantages investment of finite resources to defined targets for genetic gain in
58 specific environments.

59 Sorghum is one of the most drought-adapted crops in semiarid regions used for multiple
60 purposes, including forage, fiber, and food (Doggett and Majisu, 1968; Smith and Frederiksen,
61 2000). Most of the grain sorghum production worldwide (15%) is grown under rainfed
62 environments in the sorghum belt of the United States that runs from South Dakota to South
63 Texas (Laingen, 2015). Kansas, Texas, and Colorado lead grain sorghum production in the
64 sorghum belt with 50%, 30%, and 6%, respectively (Laingen, 2015). Across this area, water
65 limitation and high vapor pressure deficit (VPD) affect plant transpiration, making sorghum
66 production vulnerable to droughts. Although sorghum harbors drought adaptation (Abdel-Ghany
67 et al., 2020; Abreha et al., 2021), breeding for drought traits has received less attention.
68 Therefore, the full potential of sorghum production under water-limited environments in the
69 sorghum belt of the United States may not yet have been achieved.

70 Limited transpiration (LT) is a hypothetical trait that restricts water demand in periods of
71 high VPD which occurs around mid-day (Figure 1A and 1B). This mechanism shifts plant-water
72 demand, conserving water in the soil profile during the vegetative stage and for use during grain
73 filling (Figure 1) (Sinclair et al., 2005). Reducing transpiration (H_2O) due to stomatal closure in

74 hours with high VPD would penalize carbon assimilation (CO₂). Thus, causing grain yield
75 reductions under well-watered conditions but increasing the grain yield and the effective use of
76 water under moderate water-limited environments (Vadez et al., 2014). This hypothetical
77 physiological mechanism of LT has been extended into process-based models where
78 transpiration was restricted during high VPD hours (Messina et al., 2015; Sinclair et al., 2005;
79 Truong et al., 2017). Crop model simulations under rainfed conditions for sorghum and other
80 crops such as soybean, maize, lentil, chickpea, and wheat indicate a yield increase for a
81 phenotype with LT trait in areas vulnerable to water scarcity (Collins et al., 2021; Sinclair et al.,
82 2017). For sorghum, reports indicated an increase in yield production from 6 to 10% for severe
83 drought scenarios in Australia, semiarid regions of India, and the United States (Texas) (Kholová
84 et al., 2014; Sinclair et al., 2005; Truong et al., 2017).

85 Simulations for various crops (Collins et al., 2021; Guiguitant et al., 2017; Messina et al.,
86 2015) suggest that breeding for the LT trait can make a valuable economic contribution in
87 rainfed regions. Yet, its impact on grain yield in sorghum-producing regions of the United States
88 remains unknown. This study uses the APSIM-sorghum growth model to generate hypotheses of
89 the potential benefits and tradeoffs of the LT trait in grain sorghum. Under drought scenarios, we
90 expect an increase in grain yield in rainfed sorghum-producing regions for sorghum with the LT
91 trait (Figure 1). Otherwise, no impacts or detrimental effects on grain yield are expected for non-
92 stress environments. Likewise, we expect these benefits across different combinations of genetic
93 background and management practices. Results indicate that introgressing LT in grain sorghum
94 would increase yield by more than 5% in water-limited scenarios but less than 5% in well-
95 watered settings. Additionally, the LT would benefit grain yield across all combinations of
96 maturity groups and planting dates.

97 **MATERIALS AND METHODS**

98 *Production system and study sites*

99 The simulation study was conducted for Kansas, Texas, and Colorado counties that have high
100 sorghum production (Figure 2A) area and are located in contrasting gradients of precipitation
101 and VPD (Table 1, Figure 2D). Across these locations annual precipitation and VPD are
102 inversely associated (Figure 1B, 1C, and 1E) with declining precipitation and increasing VPD
103 from east to west (<https://prism.oregonstate.edu/>). Annual precipitation shapes farmer crop
104 management including maturity group adoption (Ciampitti et al., 2019; Roozeboom and Fjell,
105 1998; Shroyer et al., 1998). Therefore, in these regions plant density of 17 plants m² and 6 plants
106 m² are recommended for areas with annual precipitation around 800 mm and 350 mm,
107 respectively (Shroyer et al., 1998). Similarly, full-season hybrids are planted in regions with high
108 annual precipitation while short-season hybrids are grown in regions with low precipitation
109 (Ciampitti et al., 2019; Roozeboom and Fjell, 1998).

110 *APSIM-sorghum crop model*

111 APSIM-Sorghum (Hammer et al., 2019, 2010) is a crop model that integrates the intertwined
112 interaction of G × E × M) to simulate plant development and growth on a daily basis (Holzworth

113 et al., 2014; Keating et al., 2003; Wang et al., 2002). The model requires the following input
114 data: daily weather records, soil profile characteristics, crop management, and cultivar-specific
115 parameters. Crop phenology development is estimated as the summation of thermal time for nine
116 phases from germination to physiological maturity. Daily biomass is estimated as the minimum
117 of biomass limited by solar radiation or water availability. The biomass limited by solar radiation
118 is the product of radiation use efficiency (RUE, MJ m⁻²), solar radiation (MJ m⁻²), and the fraction
119 of light intercepted. The biomass limited by water availability is the product of transpiration
120 efficiency and soil water supply. The model estimates water, temperature, and nitrogen deficit
121 factors which affect phenology and growth. To estimate the effect of LT on carbon assimilation
122 in hours with high VPD, APSIM-sorghum downscales daily temperature and solar radiation to
123 hourly time steps and estimates relative humidity (RH) on each hour (Parton and Logan, 1981).
124 Temperature and RH are used to calculate VPD on each hour (Monteith and Unsworth, 2013;
125 Murray, 1967), then the model estimates biomass as a function of hourly water supply and
126 demand. Finally, the biomass accumulation is aggregated for each daily timestep. Note, the
127 version of APSIM-sorghum used and LT modifications were made for research purposes and are
128 not in the release version.

129 ***Model inputs***

130 Daily weather data at each site, including precipitation (mm), solar radiation (MJ m⁻² day⁻¹),
131 maximum (°C), and minimum temperature (°C), were obtained from NASA Prediction of
132 Worldwide Energy Resources (POWER-<https://power.larc.nasa.gov/>) from 1986 to 2018. The
133 spatial resolution of the data are 1.0° latitude by 1.0° longitude for solar radiation and 0.5°
134 latitude by 0.5° longitude for the remaining variables. Soil profile information such as soil
135 texture (%), bulk density (g ml⁻¹), organic carbon (%), and pH was downloaded from the web
136 soil survey (<https://websoilsurvey.sc.egov.usda.gov/App/HomePage.htm>). These data were used
137 to estimate the saturation capacity (SAT), field capacity (DUL), and wilting point (LL15) for
138 each layer of the soil profile using the SBuild application of the Decision Support System for
139 Agrotechnology Transfer (DSSAT) program (Hoogenboom et al., 2019). Crop management
140 practices such as planting depth, plant population and planting dates were obtained from
141 experiments or variety trials (Larson et al., 2021; Pachta, 2007; Schnell et al., 2021).

142 ***Model testing***

143 Model testing was conducted in two steps: model calibration and model evaluation (Wallach et
144 al., 2014). In model calibration, specific parameters were iteratively adjusted to fit observations,
145 while model evaluation estimated the accuracy of the model with independent data. For model
146 testing we collected available information on field experiments for hybrid 87G57 from 1997 to
147 2007 (Figure 1D, Table S1). Model calibration was conducted with a high quality experiment
148 that accounts for information of crop management, phenology development, in-season biomass
149 components, and initial soil water (Pachta, 2007). Information of this experiment including
150 weather, soil and crop management was arranged into APSIM-Sorghum. First, a simulation was
151 conducted for the hybrid 86G56 (no calibration), which was available in the library of the model.
152 Next, cultivar parameters were modified, to eliminate the photoperiod sensitivity

153 (*photoperiod_slope* from 10 to 0), and to match the grain yield components by modifying the
154 parameter relation between biomass accumulated from floral initiation to the start of grain
155 (*dm_per_seed* from 0.00087 to 0.00099). There was no need to adjust parameters related to
156 phenology development since the model was accurate in predicting flowering time for this
157 experiment (observed: 52, and simulated: 53).

158 Model evaluation was conducted with variety trial experiments conducted in Garden
159 City, Colby, and Hays (Kansas). These experiments have information of planting date, plant
160 density, flowering time, and grain yield. Environment (daily weather data, soil profile) and crop
161 management practices for these simulations were arranged into APSIM-Sorghum. Each year the
162 crop was simulated to be planted under optimal soil moisture (70% soil available water), and
163 non-nitrogen limitations at plant density of 6–14 plants m⁻². Grain yield was expressed assuming
164 12.5% of moisture content. Model accuracy was analyzed using the root mean square error
165 (RMSE), which indicates the distance from a perfect prediction (Wallach et al., 2014).

166 **Model application**

167 Parameters for hybrid 87G57 corresponded to a commercial short-season sorghum hybrid with
168 15 leaves and a non-LT trait. The number of tillers was kept constant for all phenotypes.
169 Parameters controlling growth and development, *tt_endjuv_to_init*, *Tpla_prod_coef*, and
170 *Tpla_inflection*, were adjusted to simulate mid-season and late-season sorghum hybrids, each
171 with 17 and 19 leaves, respectively. The number of tillers was kept constant (0.3) for all maturity
172 groups. The model defines a phenotype with an LT trait by assigning the parameter *limited*
173 *maximum transpiration* to any value from 0.2 to 0.9 mm h⁻¹ (Table S1). Note a phenotype with a
174 LT trait of 0.9 mm h⁻¹ represents a genotype that restricts the transpiration by 10%. For
175 simulations across all locations, the LT trait was imposed as 0.9 mm h⁻¹. Simulations for
176 sorghum with LT and non-LT traits started every year on the first of January with initial soil
177 moisture of 60%. In these simulations, the crop was automatically planted at three time intervals,
178 early-May, mid-May, and early-June, a row distance of 76 cm, planting depth of two cm, and
179 fertilized to fully meet plant nitrogen demand. Simulations were conducted every year from 1986
180 to 2018. We analyzed the grain yield, transpiration, and soil moisture for both sorghum
181 phenotypes (non-LT and LT).

182 We conducted a sensitivity analysis in a representative location to identify initial
183 conditions' effect on grain yield changes resulting from the LT trait. Therefore, simulations
184 started with initial soil moisture of 20%, 30%, 40%, 50%, 60%, 70%, 80%, and 90% while
185 maintaining the LT trait at 0.9 mm h⁻¹. Otherwise, to determine yield gains resulting from
186 hypothetical genetic variability, we created simulations and varied the LT parameter from 0.2 to
187 0.9 mm h⁻¹ while maintaining the initial soil moisture at 60%. As previously outlined, these
188 simulations started each year on the first day of January under similar maturity groups and
189 management practices. Absolute and relative change in harvested grain yield for the phenotype
190 with LT trait was calculated for each simulation and averaged over environments.

191 ***Statistical analysis and interpretation***

192 Statistical analyses of model outputs were performed in the R statistical environment utilizing
193 mixed linear models and the *lmer* library (Bates et al., 2015). The analysis quantified the size of
194 fixed effects on grain yield. Factors with fixed effects were trait (G_T), maturity group (G_M),
195 planting date (M), water stress environments (E), and their interaction while factors with random
196 effects were years nested on each location.

197

$$198 \text{ yield} = G_T + G_M + M + E + G_T \times G_M \times M \times E + (1|\text{location}/\text{years})$$

199

200 Tukey's test was performed when the F value was below an $\alpha < 0.05$ significance threshold. In
201 this study, the water stress environment (E) was determined for non-LT sorghum which resulted
202 from seasonal trajectory of daily water stress simulated for each season. This time series
203 information was analyzed via a hierarchical classification using the *cluster* (Maechler et al.,
204 2022) library and the *clara* (Clustering Large Applications clara) method (Kaufman and
205 Rousseeuw, 1990). The number of clusters was determined via the silhouette method
206 (Kassambara, 2017), a measure of similarity for each data point relative to the assigned cluster
207 and other clusters. The final water stress patterns resulted as the median of water stress on each
208 cluster.

209 **RESULTS**

210 ***Accuracy of model for grain yield prediction***

211 To determine the model accuracy for flowering time and grain yield, we compared the observed
212 data versus the information simulated by the model. For a growing season with hybrid 87G67 in
213 Manhattan, Kansas (Figure 3A, 3B, 3C, and 3D), the model reproduced the trajectory of dry
214 weight for total biomass, stem, and panicle with an RMSE of 1.1, 0.4, and 0.7 Mg ha⁻¹,
215 respectively. However, a substantial underestimation occurred for dry leaf weight. In this
216 experiment, the observed grain yield was 4.8 Mg ha⁻¹, and the results after calibration were 5.4
217 Mg ha⁻¹. For experiments in Kansas from 1997 to 2007 in Garden City, Hays, Colby, and
218 Manhattan, the model showed satisfactory predictions for days to anthesis with an RMSE of 5
219 days (Figure 3E) and grain yield with an RMSE of 2 Mg ha⁻¹ (Figure 3F). Despite the lack of
220 experimental field data for model testing in Texas and Colorado, a comparison of statistical (2.2
221 to 6.6 Mg ha⁻¹) versus simulated grain yield (1.5 to 6 Mg ha⁻¹) resulted in a RMSE of 1.1 Mg ha⁻¹
222 (Figure 3G).

223 ***Variation of grain yield across $G_M \times M$ scenarios in the absence of LT***

224 To determine the best G_M and M combination for grain yield in precipitation gradients, we
225 conducted simulations for short-, medium- and full-season sorghums planted in early May (May
226 01), mid May (May 15) and early June (June 15). Note, around 3% of the simulations were
227 removed for the analysis because they did not complete the vegetative stage (hereafter referred to
228 as "failed seasons") and the yield was close to zero. This occurred under extreme drought events
229 (Rippey, 2015). For instance, in Colorado in 2012, the annual precipitation was less than 207

230 mm, and the rainfall during the simulated growing period was less than 130 mm. The number of
231 failed seasons for full-season sorghum either planted early or late was higher in Colorado
232 suggesting that short season varieties outperform any maturity group under low rainfall, while
233 the frequency of failed seasons in Texas was higher in early planting dates (Figure S2).

234 Grain yield for simulated sorghum with a non-LT trait for different maturity groups and
235 planting dates in Kansas, Texas, and Colorado, are indicated in Figure 4. An average across G_M
236 and M indicated that grain yield varied from 1.7 to 6.5 Mg ha⁻¹ (Figure 4A), with higher and
237 lower yields in eastern and western regions, respectively. Interannual variability for grain yield
238 ranged from 30 to 50% (Figure 4A). The model predicted higher yields in Colorado and Kansas
239 when all maturity groups were planted in early May, followed by planting dates in mid-May and
240 early June. In most Texas locations, the model predicted a higher yield for planting dates in early
241 June (Figure 4B). The seasonal rainfall during each simulated season influenced the performance
242 of different maturity groups for grain yield (Figure S1A). On planting dates in June,
243 discrepancies among maturity groups occurred under high precipitation; nevertheless, as the
244 amount of rainfall during the growing season decreases, these differences become negligible (<
245 1%; Figure S1B). By contrast, differences in maturity groups for grain yield across precipitation
246 gradients in early May are insignificant ($p > 0.05$) (Figure S1B).

247 ***Effect of LT on the best combination of maturity group and planting date across sites***

248 Due to $G \times M \times E$ interactions, the effect of non-LT vs. LT trait (G_T) may depend on agronomic
249 options, such as maturity group (G_M) of the hybrid and planting date (M). To identify the best
250 combination ($G_M \times M$) at each site (E), we obtained the maximum yield for LT sorghum. The
251 model indicated similar combinations for non-LT and LT sorghums (Figure 4C–D). In Colorado
252 and Kansas, higher yields resulted when seasons for all maturity groups started on the first of
253 May. In Colorado, short-season sorghum performed better in northern regions, while medium-
254 season sorghum in southern regions. Full-season sorghum yielded higher across Kansas, except
255 in Colby, where medium-season sorghum outperformed any other combination. In Texas, the
256 model indicated full-season sorghum planted on the first of June as the best combination, with
257 some exceptions in the northern regions (i.e. Hansford). Overall, sorghum with LT across all
258 locations is expected to increase grain yields from 0 to 15% (Figure 4E). Note, the relative
259 change is lower than 3% in regions with high precipitation and this change increases as declining
260 precipitation amplifies water deficit scenarios in western regions of the study site.

261 ***Water deficit environments are more recurrent in the West***

262 To evaluate the value of LT in target population environments, we determined water stress
263 patterns by clustering simulated time series information on water supply and demand (waterSD).
264 The classification indicated four water deficit environments: well-watered or light stress at grain
265 filling (WW), late drought (LD), mid-season drought (MD), and early drought (ED) (Figure 5A).
266 WW and LD predominated in eastern regions of Kansas and Texas, while MD and ED
267 predominated in eastern Colorado and western Texas (Figure 5B). The analysis revealed a strong
268 correlation between seasonal precipitation and water deficit patterns; although it was non-

269 significant ($r = 0.9$, $p < 0.06$). On average, WW, LD, MD, and ED, showed seasonal
270 precipitation of 400 mm, 300 mm, 244 mm, and 230 mm, respectively.

271 ***The effects of $L \times G_T \times G_M \times M \times E$***

272 To determine significant interaction of $G_T \times G_M \times M \times E$, we used a mixed model to compare
273 variances across the mean (Table S3). We conducted this analysis for dependent variables at the
274 end of the growing season (grain yield, transpiration and water productivity) and flowering time
275 (biomass, transpiration, and soil water content). All individual fixed effects (G_T , G_M , E , and M)
276 had high significance ($p < 1 \times 10^{-4}$, Table S3), and a post hoc analysis suggested that factors on
277 each fixed effect belonged to different groups (Table S3). For instance, sorghum's LT trait
278 increased grain yield by 5%. Full-season sorghum yielded 21% and 10% higher than early and
279 mid-season sorghum. WW favored grain production; while lower yields correspond to ED.
280 Likewise, earlier planting dates outperformed sorghum planted either in mid-May or early-June.

281 All dependent variables exhibited high significance ($p < 1 \times 10^{-5}$) in two-way interaction
282 for three combinations: $G_T \times E$, $E \times M$, and $G_M \times E$ (Table S3). The significant interaction for G_T
283 $\times E$, and the pairwise comparison for grain yield (Figure 5C), water productivity (Figure 5D),
284 biomass at flowering (Figure 5C), and soil moisture at flowering (Figure 5H) indicated that the
285 LT trait outperformed the non-LT trait in all environments. Note, grain yield for a LT sorghum in
286 a WW environment was lower (4%) than in LD, MD, and ED environments (8%). However, the
287 pairwise comparison for total transpiration and transpiration at flowering confirmed the
288 significance for the interaction $G_T \times E$. For instance, the non-LT trait exhibited higher total
289 transpiration in WW, while the LT trait improved it in MD and ED (Figure 5C). At flowering
290 time, LT increased transpiration in WW, LD, and MD, but both traits exhibited similar
291 transpiration in ED (Figure 5C). Only for biomass at flowering time and water productivity the
292 interaction $G_T \times M$ had high significance.

293 Transpiration at flowering exhibited a three-way interaction for $G_T \times G_M \times E$ ($p < 0.01$).
294 The pairwise comparison indicated a lack of differences between LT and non-LT genotypes for
295 each maturity group in WW (Figure S4A, S4B, and S4C). By contrast, the LT trait increased
296 transpiration in WW, LD, and MD for each maturity group (Figure S4A, S4B, and S4C). Grain
297 yield, transpiration, and soil water at flowering time and biomass at the flowering time exhibited
298 the following three interactions as significant: $G_M \times E \times M$ ($p < 0.02$). Pairwise comparisons
299 among these interactions revealed differences for each maturity group and planting dates in
300 environments WW and LD, but these differences become smaller in MD and ED (Figure S4A,
301 S4B, and S4C). In these environments, for all maturity groups, grain yield for planting dates in
302 early May and mid-May were similar, but these differed ($p < 0.01$) from the early June planting.

303 ***Sensitivity of initial soil moisture on LT and variability of LT in different environments***

304 To test the effect of initial water content on the LT trait, we designed simulations and created
305 eight scenarios of initial soil moisture (from 20% to 90%) while maintaining the LT parameter at
306 0.9 mm h^{-1} . We conducted these simulations in Hays (Kansas), which presented the four
307 environment classes identified in this study (Figure 2D and 5B). Nevertheless, regardless of the
308 initial water content scenario, the model pointed out a yield increase for sorghum with LT, which

309 is more pronounced under low soil moisture (i.e. 20% and 30%). Overall, model predictions
310 indicated that initial soil moisture changes do not affect LT's positive effect, although the
311 uncertainty of these changes increased under low soil moisture (Figure 6A).

312 To test the hypothetical genetic variability of LT on grain yield, we created simulations
313 for LT sorghum with a limited maximum transpiration rate from 0.2 mm h^{-1} to 0.9 mm h^{-1} , while
314 maintaining the initial soil moisture at 60%. We conducted these simulations in a central site of
315 the sorghum belt in Kansas (Hays), representing the four water deficit patterns identified in this
316 study. Model predictions indicated that grain yield increases in all environments when LT is
317 lower than 0.9 mm h^{-1} (Figure 6B), with a greater benefit under drought scenarios. For instance,
318 on average, an LT sorghum with a limited maximum transpiration rate of 0.2 mm h^{-1} increased
319 the grain yield by 15%, 45%, 70%, and 74% in WW, LD, MD, and ED, respectively. By
320 contrast, an LT sorghum with 0.8 mm h^{-1} increased the grain yield by 7%, 8%, 10%, and 11% in
321 WW, LD, MD, and ED, respectively. Note that the uncertainty of predictions, represented by the
322 standard deviation, became larger at LT lower than 0.9 mm h^{-1} . In LD, the model predicted a
323 yield increase between 25 to 79% for sorghum with an LT of 0.2 mm h^{-1} . Otherwise, this
324 increase ranged from 6 to 16% for sorghum with an LT of 0.8 mm h^{-1}

325 **DISCUSSION**

326 *LT for the US sorghum belt: Is it worth pursuing?*

327 The decision to include a trait within a breeding program clearly depends on the impact of this
328 trait on final grain yield. Breeding programs require that a candidate trait can contribute at least a
329 5% yield increase to be included in a breeding portfolio. Findings of this study revealed the LT
330 trait can potentially increase grain yield from 3% to 13% in the sorghum belt in the United States
331 (Figure 4E). Therefore, LT is a candidate trait for developing hybrids with improved water-
332 resiliency for western regions of the sorghum belt (Figure 5B).

333 Although our simulation does not present a full geospatial analysis (Messina et al., 2015),
334 our study shows results for contrasting sites across gradients of VPD and precipitation. Site-
335 specific simulations allowed for handling detailed information on additional variables (Collins et
336 al., 2021) in any growing period, such as soil moisture, transpiration, and biomass (Figure 5C).
337 Otherwise, grid geospatial simulation studies rarely provide information other than yield
338 (Guiguitant et al., 2017; Messina et al., 2015). Despite our study disregarded spatial variability
339 on initial soil moisture, the model reproduced the observed yield (RMSE 1.1 Mg ha^{-1} , Figure).
340 Likewise, a sensitivity analysis revealed that the initial water conditions do not affect the positive
341 impact on LT (Figure 6A).

342 Current climate variability (33 years) highlights the crop vulnerability (Figure 4A) in
343 western regions characterized by the high frequency of water deficit scenarios (Figure 5B) and
344 where the impact of LT sorghum is more significant (Figure 4G and Figure 5). Climate change
345 scenarios, disregarded in our simulations, project a VPD increase by the end of the century
346 (Yuan et al., 2019). Under high VPD, LT hypothetically leads to stomatal closure (Sinclair et al.,
347 2005); similarly, rising levels of CO_2 cause stomatal closure in C3 and C4 crops (Allen et al.,
348 2011). However, it is unknown whether the impact of CO_2 and LT would have a synergistic

349 effect or if the stomatal response to CO₂ would prevail over LT. Simulations under future
350 scenarios would be needed to elucidate these effects. Although, a simulation study hypothesized
351 that CO₂ and LT can compensate for detrimental impacts of climate change in the wheat belt of
352 Australia (Collins et al., 2021).

353 *Navigating G × E × M for deployment of LT*

354 The LT trait is expected to restrict water transpiration under good soil moisture and high VPD
355 (Sinclair et al., 2005). Therefore, this trait is undesirable for WW conditions because depriving
356 transpiration would penalize carbon fixation and final grain yield (Vadez et al., 2014).
357 Unexpectedly, in our study, simulation studies indicated that an LT sorghum can contribute to an
358 increase in grain yield of 4% for WW environments (Table S3, Figure 5C). Under WW
359 environments, predictions for wheat with the APSIM model indicated a yield increase of 0.2%
360 (Collins et al., 2021), while predictions for maize with a simple model indicated a yield decline
361 of -3% in the USA (mesna). Yield gains for WW environments in our study can be due to
362 differences in the model structure. In LD environments, sorghum grain yield increased by around
363 9 % (Figure 5C, Table S3), which is slightly higher than predictions for wheat (2 to 7 %, Collins
364 et al., 2021) and within the range of 0 to 24% reported for maize (Messina et al., 2015). Our
365 results for MD (10%) and ED (9%) align with the reported yield increase for wheat which ranged
366 between 3 to 13% (Collins et al., 2021). From a breeding perspective, LT sorghum would have a
367 more significant impact on water stress scenarios of the sorghum belt. It is essential to identify
368 the best combination of G_T × G_M × M in sorghum since it is planted late and across precipitation
369 gradients (Ciampitti et al., 2019; Roozeboom and Fjell, 1998; Shroyer et al., 1998). Overall, LT
370 sorghum increased grain yield across planting dates and maturity groups by 8%. Although
371 specific combinations of G_M × M (Table S3) can maximize crop yield either for a non-LT
372 (Figure 4C) or LT sorghum (Figure 4D).

373 Variety trials or multi-environment experiments have shown that, unlike full-season
374 varieties, medium- and short-season varieties can complete their growing cycle in regions with
375 low precipitation (Larson et al., 2021; Schnell et al., 2021) and limited growing degree days
376 (GDD) at higher latitudes (Kukul and Irmak, 2018). This strategy has led to the selection of
377 maturity groups that match precipitation and GDD gradients in the sorghum belt (Figures 4C and
378 4D). Since the impact of LT sorghum is more relevant in western regions (Figure 4E), this study
379 suggests introgressing this trait in medium- and short-season hybrids rather than in full-season
380 hybrids (Figure 4D, Figure 5B). Management practices need to be considered to enhance the
381 performance of LT sorghum. Shifting planting dates can change the frequency of water deficit
382 environments (Chenu et al., 2011) (Figure 3S) by increasing grain yield in early planting dates,
383 especially in Kansas (Figure 4B). Higher yields in early spring resulted from the synchronization
384 of planting dates with the onset of precipitation, which increased the frequency of WW
385 environments (Figure S3). Likewise, simulation and field studies demonstrated yield gains of up
386 to 11% in seasons with higher water availability (Carcedo et al., 2021; Francis et al., 1986;
387 Zander et al., 2021)

388 Genetic pyramiding for drought adapted phenotypes can be explored via crop modeling
389 (Cooper et al., 2002). A simulation study in sorghum revealed that LT is more effective than
390 stay-green in water scarcity scenarios (Kholová et al., 2014). Higher yields in early spring
391 suggests (Figure 4B and Figure S4D-F) a plausible interaction between early chilling tolerance
392 and LT trait. LT increases canopy temperature (Belko et al., 2013), and temperatures beyond 38
393 °C can penalize carbon assimilation and plant growth (Singh et al., 2015). Then, integrating field
394 experimentation and crop modeling for ideotyping LT with additional adaptation traits can
395 support breeding programs when developing a trait technology for water-limited scenarios.

396 *Next steps for water-optimized sorghum*

397 This simulation study has shown that LT trait can increase water productivity and benefit
398 farmers' economies in the sorghum belt. Nevertheless, LT is a hypothetical trait, implemented in
399 crop models (Bates et al., 2015; Messina et al., 2015; Sinclair et al., 2017; Truong et al., 2017),
400 and whose genetic variation is reported and limited to controlled environments (Collins et al.,
401 2021; Devi and Reddy, 2018; Gholipour et al., 2010; Medina et al., 2019; Vadez et al., 2015).
402 Although variation for LT was reported in controlled environments, the repeatability of this trait
403 has yet to be shown in sorghum-producing regions. Hence, including the LT trait in a sorghum
404 breeding program requires validating this trait under field conditions and testing the effectiveness
405 of phenomic approaches to discriminate this trait in large populations. Potential donors would
406 make feasible developing bi-parental populations to determine quantitative trait loci (QTLs)
407 controlling the phenotypic expression of this trait. Further isolating these QTL can assist in
408 dissecting the underlying physiological and molecular mechanisms of limited transpiration,
409 which remain enigmatic.

410 **ACKNOWLEDGEMENTS**

411 This study was supported by funding from the Foundation for Food and Agriculture Research -
412 Seeding Solution "CA18-SS-0000000094 – Bridging the Genome-to-Phenome Breeding Gap for
413 Water-Efficient Crop Yields (G2P Bridge)" to G.P.M. and S.S.B; the Kansas Department of
414 Agriculture "Collaborative Sorghum Investment Program Water Optimized Sorghum for
415 Kansas" to G.P.M; and the Kansas Grain Sorghum Commission.

416 **AUTHOR CONTRIBUTIONS**

417 G.P.M. and R.R. contributed to the conception and design of the work. R.R. collected
418 experimental data, conducted simulations, data analysis, interpretation, and drafting of the
419 article. S.S. contributed to data collection and critical revision of the article. G.M. provided
420 technical support with the APSIM-sorghum model and critical revision of the article. All authors
421 contributed to the final manuscript.

422 **REFERENCES**

- 423 Blum, A., 2011. Drought Resistance and Its Improvement, Plant Breeding for Water-Limited
424 Environments. Springer-Verlag Berlin, Berlin. [https://doi.org/10.1007/978-1-4419-7491-](https://doi.org/10.1007/978-1-4419-7491-4_3)
425 [4_3](https://doi.org/10.1007/978-1-4419-7491-4_3)
- 426 Challinor, A.J., Müller, C., Asseng, S., Deva, C., Nicklin, K.J., Wallach, D., Vanuytrecht, E.,
427 Whitfield, S., Ramirez-Villegas, J., Koehler, A.-K., 2018. Improving the use of crop
428 models for risk assessment and climate change adaptation. *Agricultural Systems* 159,
429 296–306. <https://doi.org/10.1016/j.agsy.2017.07.010>
- 430 Abdel-Ghany, S.E., Ullah, F., Ben-Hur, A., Reddy, A.S.N., 2020. Transcriptome Analysis of
431 Drought-Resistant and Drought-Sensitive Sorghum (*Sorghum bicolor*) Genotypes in
432 Response to PEG-Induced Drought Stress. *Int J Mol Sci* 21, 772.
433 <https://doi.org/10.3390/ijms21030772>
- 434 Abreha, K.B., Enyew, M., Carlsson, A.S., Vetukuri, R.R., Feyissa, T., Motlhaodi, T., Ng'uni, D.,
435 Geleta, M., 2021. Sorghum in dryland: morphological, physiological, and molecular
436 responses of sorghum under drought stress. *Planta* 255, 20.
437 <https://doi.org/10.1007/s00425-021-03799-7>
- 438 Allen, L.H., Kakani, V.G., Vu, J.C.V., Boote, K.J., 2011. Elevated CO₂ increases water use
439 efficiency by sustaining photosynthesis of water-limited maize and sorghum. *Journal of*
440 *Plant Physiology* 168, 1909–1918. <https://doi.org/10.1016/j.jplph.2011.05.005>
- 441 Araus, J.L., Serret, M.D., Edmeades, G.O., 2012. Phenotyping maize for adaptation to drought.
442 *Front Physiol* 3, 305. <https://doi.org/10.3389/fphys.2012.00305>
- 443 Barbier, N., 2015. Vulnerability to water shortages in the 21st Century's arid and semi-arid
444 American West. *L'Ordinaire des Amériques*. <https://doi.org/10.4000/ordea.1956>
- 445 Bates, D., Maechler, M., Bolker, B.M., Walker, S.C., 2015. Fitting Linear Mixed-Effects Models
446 Using lme4. *J. Stat. Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- 447 Belko, N., Zaman-Allah, M., Diop, N.N., Cisse, N., Zombre, G., Ehlers, J.D., Vadez, V., 2013.
448 Restriction of transpiration rate under high vapour pressure deficit and non-limiting water
449 conditions is important for terminal drought tolerance in cowpea. *Plant Biol (Stuttg)* 15,
450 304–316. <https://doi.org/10.1111/j.1438-8677.2012.00642.x>
- 451 Bernardo, R., 2020. Reinventing quantitative genetics for plant breeding: something old,
452 something new, something borrowed, something BLUE. *Heredity* 125, 375–385.
453 <https://doi.org/10.1038/s41437-020-0312-1>
- 454 Carcedo, A.J.P., Cejas, E., Gambin, B.L., 2021. Adapting sorghum sowing date and genotype
455 maturity to seasonal rainfall variation in a temperate region. *in silico Plants* 3, diab007.
456 <https://doi.org/10.1093/insilicoplants/diab007>
- 457 Carcedo, A.J.P., Mayor, L., Demarco, P., Morris, G.P., Lingenfelter, J., Messina, C.D.,
458 Ciampitti, I.A., 2022. Environment Characterization in Sorghum (*Sorghum bicolor* L.) by
459 Modeling Water-Deficit and Heat Patterns in the Great Plains Region, United States.
460 *Front Plant Sci* 13, 768610. <https://doi.org/10.3389/fpls.2022.768610>
- 461 Challinor, A.J., Müller, C., Asseng, S., Deva, C., Nicklin, K.J., Wallach, D., Vanuytrecht, E.,
462 Whitfield, S., Ramirez-Villegas, J., Koehler, A.-K., 2018. Improving the use of crop
463 models for risk assessment and climate change adaptation. *Agricultural Systems* 159,
464 296–306. <https://doi.org/10.1016/j.agsy.2017.07.010>
- 465 Chenu, K., Cooper, M., Hammer, G.L., Mathews, K.L., Dreccer, M.F., Chapman, S.C., 2011.
466 Environment characterization as an aid to wheat improvement: interpreting genotype-
467 environment interactions by modelling water-deficit patterns in North-Eastern Australia.

- 468 J. Exp. Bot. 62, 1743–1755. <https://doi.org/10.1093/jxb/erq459>
- 469 Chenu, K., Porter, J.R., Martre, P., Basso, B., Chapman, S.C., Ewert, F., Bindi, M., Asseng, S.,
470 2017. Contribution of Crop Models to Adaptation in Wheat. *Trends in Plant Science* 22,
471 472–490. <https://doi.org/10.1016/j.tplants.2017.02.003>
- 472 Ciampitti, I.A., Prasad, P.V.V., Schlegel, A.J., Haag, L., Schnell, R.W., Arnall, B., Lofton, J.,
473 2019. Genotype × Environment × Management Interactions: US Sorghum Cropping
474 Systems, in: *Sorghum*. John Wiley & Sons, Ltd, pp. 277–296.
475 <https://doi.org/10.2134/agronmonogr58.c13>
- 476 Collins, B., Chapman, S., Hammer, G., Chenu, K., 2021. Limiting transpiration rate in high
477 evaporative demand conditions to improve Australian wheat productivity. *in silico Plants*
478 3, diab006. <https://doi.org/10.1093/insilicoplants/diab006>
- 479 Cooper, M., Chapman, S.C., Podlich, D.W., Hammer, G.L., 2002. The GP Problem: Quantifying
480 Gene-to-Phenotype Relationships. *In Silico Biology* 2, 151–164.
- 481 Cooper, M., Messina, C.D., 2022. Breeding crops for drought-affected environments and
482 improved climate resilience. *The Plant Cell* koac321.
483 <https://doi.org/10.1093/plcell/koac321>
- 484 Devi, M.J., Reddy, V.R., 2018. Transpiration Response of Cotton to Vapor Pressure Deficit and
485 Its Relationship With Stomatal Traits. *Frontiers in Plant Science* 9.
- 486 Doggett, H.J., Majisu, B.N., 1968. Disruptive selection in crop development. *Heredity* 23, 1–23.
487 <https://doi.org/10.1038/hdy.1968.1>
- 488 Francis, C.A., Moomaw, R.S., Rajewski, J.F., Saeed, M., 1986. Grain Sorghum Hybrid
489 Interactions with Tillage System and Planting Dates1. *Crop Science* 26,
490 crops1986.0011183X002600010046x.
491 <https://doi.org/10.2135/cropsci1986.0011183X002600010046x>
- 492 Gholipoor, M., Prasad, P.V.V., Mutava, R.N., Sinclair, T.R., 2010. Genetic variability of
493 transpiration response to vapor pressure deficit among sorghum genotypes. *Field Crops*
494 *Research* 119, 85–90. <https://doi.org/10.1016/j.fcr.2010.06.018>
- 495 Guiguitant, J., Marrou, H., Vadez, V., Gupta, P., Kumar, S., Soltani, A., Sinclair, T.R., Ghanem,
496 M.E., 2017. Relevance of limited-transpiration trait for lentil (*Lens culinaris* Medik.) in
497 South Asia. *Field Crops Research* 209, 96–107. <https://doi.org/10.1016/j.fcr.2017.04.013>
- 498 Hammer, G., McLean, G., Doherty, A., van Oosterom, E., Chapman, S., 2019. Sorghum Crop
499 Modeling and Its Utility in Agronomy and Breeding, in: *Sorghum*. John Wiley & Sons,
500 Ltd, pp. 215–239. <https://doi.org/10.2134/agronmonogr58.c10>
- 501 Hammer, G.L., van Oosterom, E., McLean, G., Chapman, S.C., Broad, I., Harland, P., Muchow,
502 R.C., 2010. Adapting APSIM to model the physiology and genetics of complex adaptive
503 traits in field crops. *J Exp Bot* 61, 2185–2202. <https://doi.org/10.1093/jxb/erq095>
- 504 Holzworth, D.P., Huth, N.I., deVoil, P.G., Zurcher, E.J., Herrmann, N.I., McLean, G., Chenu,
505 K., van Oosterom, E.J., Snow, V., Murphy, C., Moore, A.D., Brown, H., Whish, J.P.M.,
506 Verrall, S., Fainges, J., Bell, L.W., Peake, A.S., Poulton, P.L., Hochman, Z., Thorburn,
507 P.J., Gaydon, D.S., Dalgliesh, N.P., Rodriguez, D., Cox, H., Chapman, S., Doherty, A.,
508 Teixeira, E., Sharp, J., Cichota, R., Vogeler, I., Li, F.Y., Wang, E., Hammer, G.L.,
509 Robertson, M.J., Dimes, J.P., Whitbread, A.M., Hunt, J., van Rees, H., McClelland, T.,
510 Carberry, P.S., Hargreaves, J.N.G., MacLeod, N., McDonald, C., Harsdorf, J.,
511 Wedgwood, S., Keating, B.A., 2014. APSIM – Evolution towards a new generation of
512 agricultural systems simulation. *Environmental Modelling & Software* 62, 327–350.
513 <https://doi.org/10.1016/j.envsoft.2014.07.009>

- 514 Hoogenboom, G., Porter, C.H., Boote, K.J., Shelia, V., Wilkens, P.W., Singh, U., White, J.W.,
515 Asseng, S., Lizaso, J.I., Moreno, L.P., Pavan, W., Ogoshi, R., Hunt, L.A., Tsuji, G.Y.,
516 Jones, J.W., 2019. The DSSAT crop modeling ecosystem, in: *Advances in Crop*
517 *Modeling for Sustainable Agriculture*. Burleigh Dodds Science Publishing, Cambridge,
518 United Kingdom, pp. 173–216.
- 519 Jones, J.W., Hoogenboom, G., Porter, C.H., Boote, K.J., Batchelor, W.D., Hunt, L.A., Wilkens,
520 P.W., Singh, U., Gijsman, A.J., Ritchie, J.T., 2003. The DSSAT cropping system model.
521 *European Journal of Agronomy, Modelling Cropping Systems: Science, Software and*
522 *Applications* 18, 235–265. [https://doi.org/10.1016/S1161-0301\(02\)00107-7](https://doi.org/10.1016/S1161-0301(02)00107-7)
- 523 Kassambara, A., 2017. *Practical Guide to Cluster Analysis in R: Unsupervised Machine*
524 *Learning*. STHDA.
- 525 Kaufman, L., Rousseeuw, P., 1990. Clustering Large Applications (Program CLARA), in:
526 *Finding Groups in Data*. John Wiley & Sons, Ltd, pp. 126–163.
527 <https://doi.org/10.1002/9780470316801.ch3>
- 528 Keating, B.A., Carberry, P.S., Hammer, G.L., Probert, M.E., Robertson, M.J., Holzworth, D.,
529 Huth, N.I., Hargreaves, J.N.G., Meinke, H., Hochman, Z., McLean, G., Verburg, K.,
530 Snow, V., Dimes, J.P., Silburn, M., Wang, E., Brown, S., Bristow, K.L., Asseng, S.,
531 Chapman, S., McCown, R.L., Freebairn, D.M., Smith, C.J., 2003. An overview of
532 APSIM, a model designed for farming systems simulation. *European Journal of*
533 *Agronomy, Modelling Cropping Systems: Science, Software and Applications* 18, 267–
534 288. [https://doi.org/10.1016/S1161-0301\(02\)00108-9](https://doi.org/10.1016/S1161-0301(02)00108-9)
- 535 Kholová, J., Murugesan, T., Kaliamoorthy, S., Malayee, S., Baddam, R., Hammer, G.L.,
536 McLean, G., Deshpande, S., Hash, C.T., Craufurd, P.Q., Vadez, V., 2014. Modelling the
537 effect of plant water use traits on yield and stay-green expression in sorghum. *Functional*
538 *Plant Biol.* 41, 1019–1034. <https://doi.org/10.1071/FP13355>
- 539 Kukal, M.S., Irmak, S., 2018. U.S. Agro-Climature in 20th Century: Growing Degree Days, First
540 and Last Frost, Growing Season Length, and Impacts on Crop Yields. *Sci Rep* 8, 6977.
541 <https://doi.org/10.1038/s41598-018-25212-2>
- 542 Laingen, C., 2015. A Spatiotemporal Analysis of Sorghum in the United States. *Papers in*
543 *Applied Geography* 1, 307–311. <https://doi.org/10.1080/23754931.2015.1084359>
- 544 Larson, K.J., Jones-Diamond, S.M., Johnson, J.J., Bartolo, M.E., Tanabe, K.J., Pettinger, B.T.,
545 2021. 2021 Sorghum Hybrid Performance in Eastern Colorado (No. TR22-1). Colorado
546 State University.
- 547 Maechler, M., Rousseeuw, P., Anja, S., Hubert, M., Hornik, K., 2022. *Cluster Analysis Basics*
548 *and Extensions*.
- 549 Medina, S., Vicente, R., Nieto-Taladriz, M.T., Aparicio, N., Chairi, F., Vergara-Diaz, O., Araus,
550 J.L., 2019. The Plant-Transpiration Response to Vapor Pressure Deficit (VPD) in Durum
551 Wheat Is Associated With Differential Yield Performance and Specific Expression of
552 Genes Involved in Primary Metabolism and Water Transport. *Frontiers in Plant Science*
553 9.
- 554 Messina, C.D., Podlich, D., Dong, Z., Samples, M., Cooper, M., 2011. Yield–trait performance
555 landscapes: from theory to application in breeding maize for drought tolerance. *J Exp Bot*
556 62, 855–868. <https://doi.org/10.1093/jxb/erq329>
- 557 Messina, C.D., Sinclair, T.R., Hammer, G.L., Curan, D., Thompson, J., Oler, Z., Gho, C.,
558 Cooper, M., 2015. Limited-Transpiration Trait May Increase Maize Drought Tolerance in
559 the US Corn Belt. *Agronomy Journal* 107, 1978–1986.

- 560 <https://doi.org/10.2134/agronj15.0016>
- 561 Monneveux, P., Jing, R., Misra, S., 2012. Phenotyping for drought adaptation in wheat using
562 physiological traits. *Frontiers in Physiology* 3.
- 563 Monteith, J.L., Unsworth, M.H., 2013. Chapter 2 - Properties of Gases and Liquids, in: Monteith,
564 J.L., Unsworth, M.H. (Eds.), *Principles of Environmental Physics (Fourth Edition)*.
565 Academic Press, Boston, pp. 5–23. <https://doi.org/10.1016/B978-0-12-386910-4.00002-0>
- 566 Murray, F.W., 1967. On the Computation of Saturation Vapor Pressure. *Journal of Applied*
567 *Meteorology and Climatology* 6, 203–204. [https://doi.org/10.1175/1520-0450\(1967\)006<0203:OTCOSV>2.0.CO;2](https://doi.org/10.1175/1520-0450(1967)006<0203:OTCOSV>2.0.CO;2)
- 568 NOAA, 2020. The High Cost of Drought | January 23, 2020 [WWW Document]. Drought.gov.
569 URL <https://www.drought.gov/news/high-cost-drought> (accessed 12.7.22).
- 570 Ojeda, J.J., Huth, N., Holzworth, D., Raymundo, R., Zyskowski, R.F., Sinton, S.M., Michel,
571 A.J., Brown, H.E., 2021. Assessing errors during simulation configuration in crop models
572 – A global case study using APSIM-Potato. *Ecological Modelling* 458, 109703.
573 <https://doi.org/10.1016/j.ecolmodel.2021.109703>
- 574 Pachta, C.J., 2007. Improving irrigated cropping systems on the high plains using crop
575 simulation models (Thesis). Kansas State University.
- 576 Parton, W.J., Logan, J.A., 1981. A model for diurnal variation in soil and air temperature.
577 *Agricultural Meteorology* 23, 205–216. [https://doi.org/10.1016/0002-1571\(81\)90105-9](https://doi.org/10.1016/0002-1571(81)90105-9)
- 578 Pournasiri-Poshtiri, M., Towler, E., Pal, I., 2018. Characterizing and understanding the
579 variability of streamflow drought indicators within the USA. *Hydrological Sciences*
580 *Journal* 63, 1791–1803. <https://doi.org/10.1080/02626667.2018.1534240>
- 581 Rippey, B.R., 2015. The U.S. drought of 2012. *Weather and Climate Extremes, USDA Research*
582 *and Programs on Extreme Events* 10, 57–64. <https://doi.org/10.1016/j.wace.2015.10.004>
- 583 Roozeboom, K., Fjell, D., 1998. Selection of grain sorghum hybrids, in: *Grain Sorghum*
584 *Production Handbook*. Kansas State University.
- 585 Schnell, R.W., Horn, K., Biar, E., Rooney, W.L., 2021. 2021 Texas Grain Sorghum Performance
586 Variety Trials (No. SCS-2021-13). The Texas A&M University Systems, College Station,
587 Texas.
- 588 Shroyer, James., Kok, H., Fjell, D., 1998. Seedbed preparation and planting practices, in: *Grain*
589 *Sorghum Production Handbook*. Kansas State University, pp. 5–9.
- 590 Sinclair, T.R., Devi, J., Shekoofa, A., Choudhary, S., Sadok, W., Vadez, V., Riar, M., Rufty, T.,
591 2017. Limited-transpiration response to high vapor pressure deficit in crop species. *Plant*
592 *Science* 260, 109–118. <https://doi.org/10.1016/j.plantsci.2017.04.007>
- 593 Sinclair, T.R., Hammer, G.L., Oosterom, E.J. van, 2005. Potential yield and water-use efficiency
594 benefits in sorghum from limited maximum transpiration rate. *Functional Plant Biol.* 32,
595 945–952. <https://doi.org/10.1071/FP05047>
- 596 Singh, V., Nguyen, C.T., van Oosterom, E.J., Chapman, S.C., Jordan, D.R., Hammer, G.L.,
597 2015. Sorghum genotypes differ in high temperature responses for seed set. *Field Crops*
598 *Research* 171, 32–40. <https://doi.org/10.1016/j.fcr.2014.11.003>
- 599 Smith, C.W., Frederiksen, R.A., 2000. *Sorghum: Origin, History, Technology, and Production*.
600 John Wiley & Sons.
- 601 Tang, C., Piechota, T.C., 2009. Spatial and temporal soil moisture and drought variability in the
602 Upper Colorado River Basin. *Journal of Hydrology* 379, 122–135.
603 <https://doi.org/10.1016/j.jhydrol.2009.09.052>
- 604 Thornton, P., Dinesh, D., Cramer, L., Loboguerrero, A.M., Campbell, B., 2018. Agriculture in a
605

- 606 changing climate: Keeping our cool in the face of the hothouse. *Outlook Agric* 47, 283–
607 290. <https://doi.org/10.1177/0030727018815332>
- 608 Truong, S.K., McCormick, R.F., Mullet, J.E., 2017. Bioenergy sorghum crop model predicts
609 VPD-limited transpiration traits enhance biomass yield in water-limited environments.
610 *Front. Plant Sci.* 8. <https://doi.org/10.3389/fpls.2017.00335>
- 611 Vadez, V., Kholová, J., Hummel, G., Zhokhavets, U., Gupta, S.K., Hash, C.T., 2015. LeasyScan:
612 a novel concept combining 3D imaging and lysimetry for high-throughput phenotyping
613 of traits controlling plant water budget. *J Exp Bot* 66, 5581–5593.
614 <https://doi.org/10.1093/jxb/erv251>
- 615 Vadez, V., Kholova, J., Medina, S., Kakker, A., Anderberg, H., 2014. Transpiration efficiency:
616 new insights into an old story. *Journal of Experimental Botany* 65, 6141–6153.
617 <https://doi.org/10.1093/jxb/eru040>
- 618 van Ittersum, M.K., Leffelaar, P.A., van Keulen, H., Kropff, M.J., Bastiaans, L., Goudriaan, J.,
619 2003. On approaches and applications of the Wageningen crop models. *European Journal*
620 *of Agronomy, Modelling Cropping Systems: Science, Software and Applications* 18,
621 201–234. [https://doi.org/10.1016/S1161-0301\(02\)00106-5](https://doi.org/10.1016/S1161-0301(02)00106-5)
- 622 Wallach, D., Makowski, D., Jones, J.W., Brun, F., 2014. Chapter 9 - Model Evaluation, in:
623 Wallach, D., Makowski, D., Jones, J.W., Brun, F. (Eds.), *Working with Dynamic Crop*
624 *Models (Second Edition)*. Academic Press, San Diego, pp. 345–406.
625 <https://doi.org/10.1016/B978-0-12-397008-4.00009-5>
- 626 Wang, E., Robertson, M.J., Hammer, G.L., Carberry, P.S., Holzworth, D., Meinke, H., Chapman,
627 S.C., Hargreaves, J.N.G., Huth, N.I., McLean, G., 2002. Development of a generic crop
628 model template in the cropping system model APSIM. *European Journal of Agronomy,*
629 *Process Simulation and Application of Cropping System Models* 18, 121–140.
630 [https://doi.org/10.1016/S1161-0301\(02\)00100-4](https://doi.org/10.1016/S1161-0301(02)00100-4)
- 631 Yuan, W., Zheng, Y., Piao, S., Ciais, P., Lombardozzi, D., Wang, Y., Ryu, Y., Chen, G., Dong,
632 W., Hu, Z., Jain, A.K., Jiang, C., Kato, E., Li, S., Lienert, S., Liu, S., Nabel, J.E.M.S.,
633 Qin, Z., Quine, T., Sitch, S., Smith, W.K., Wang, F., Wu, C., Xiao, Z., Yang, S., 2019.
634 Increased atmospheric vapor pressure deficit reduces global vegetation growth. *Sci Adv*
635 5, eaax1396. <https://doi.org/10.1126/sciadv.aax1396>
- 636 Zander, A., Lofton, J., Harris, C., Kezar, S., 2021. Grain sorghum production: Influence of
637 planting date, hybrid selection, and insecticide application. *Agrosystems, Geosciences &*
638 *Environment* 4, e20162. <https://doi.org/10.1002/agg2.20162>

639 **FIGURES AND TABLES**

640

641 **Table 1. Characteristics for the study locations across the US sorghum belt.**

State	County	VPD (KPa)	Prec. (mm)	Planted area (ha)	Soil texture	Soil depth (cm)	Plant density (Plants m ⁻²)
CO	Bent	3.2	356	318	Sandy loam	150	6
	Lincoln	2.7	377	1129	Loam	200	6
	Logan	2.7	426	2488	Sandy Loam	150	6
	Phillips	2.6	460	1708	Complex	150	6
	Prowers	3.1	407	1768	Silty loam	200	6
KS	Clay	2.5	784	8249	Silty clay loam	200	14
	Gray	2.9	527	3509	Loam	200	8
	Morris	2.3	898	2316	Complex	116	14
	Morton	3.2	442	1455	Silty loam	200	6
	Russell	2.7	666	16205	Silty clay loam	200	8
	Colby*	2.6	520	1708	Silty clay loam	200	6
	Garden City*	3.2	480	1455	Silty clay	200	6
	Hays*	2.7	680	16205	Silty clay loam	200	8
	Manhattan*	2.5	900	8249	Clay	200	14
	TX	Andrews	3.7	380	401	Sandy loam	150
Coleman		3.3	694	847	Clay	200	8
Hansford		3.3	505	5140	Clay loam	200	6
Jim Wells		3.1	663	12559	Clay	180	6
Refugio		2.4	927	10517	Clay	200	14
Terry		3.5	482	2730	Loamy sand	150	6
Milam		2.8	913	2498	Complex	200	14

642 *Model evaluation sites.

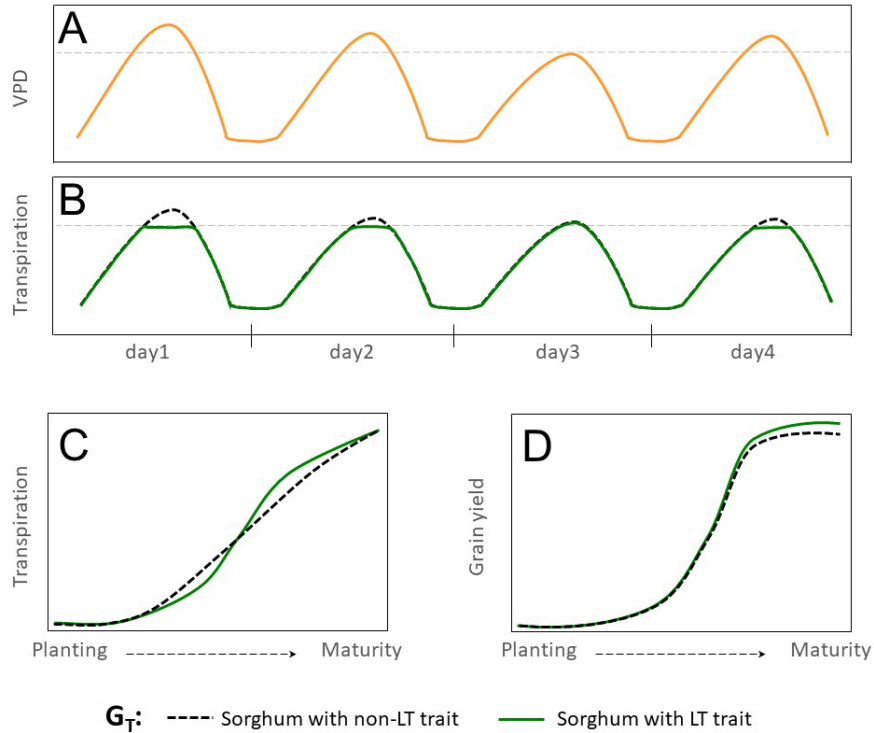


Figure 1. Hypothetical effect of LT trait in grain sorghum under rainfed conditions. (A) Hourly trajectory of VPD during four days with contrasting, (B) Hourly trajectory of transpiration for sorghum with non-LT and LT traits (G_T). The dashed gray line indicates the threshold of VPD at which genotypes express differences in transpiration VPD response. (C) Cumulative transpiration during the growing season, and (D) trajectory of grain yield during the growing season.

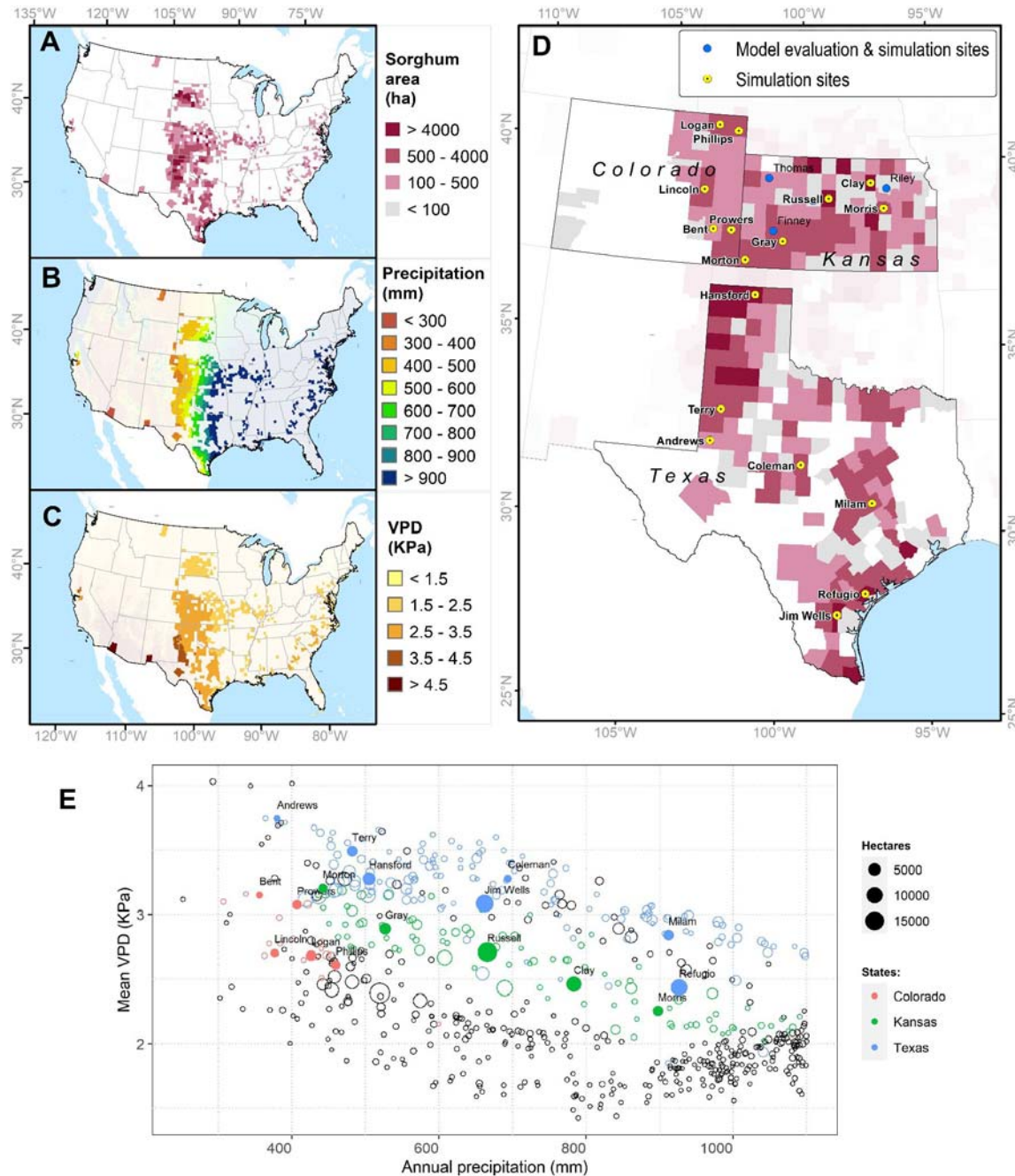


Figure 2. Study system to evaluate the impact of the limited transpiration (LT) trait. (A) Geographic distribution of grain sorghum production area (ha^{-1}) in the United States in 2019. (B) Annual precipitation (mm) in sorghum producing areas. (C) Mean of the monthly maximum vapor pressure deficit (VPD, kPa) from May to August in sorghum producing areas. (D) Distribution of grain sorghum in Colorado, Kansas, and Texas and sites for model evaluation and simulation sites. (E) Mean VPD and annual precipitation in sorghum producing regions. Sorghum production areas were obtained from the National Agricultural Statistical Service (NASS, <https://www.nass.usda.gov/>). Precipitation and vapor pressure deficit information for sorghum-producing areas were acquired from the PRISM Climate Group (<https://prism.oregonstate.edu/>).

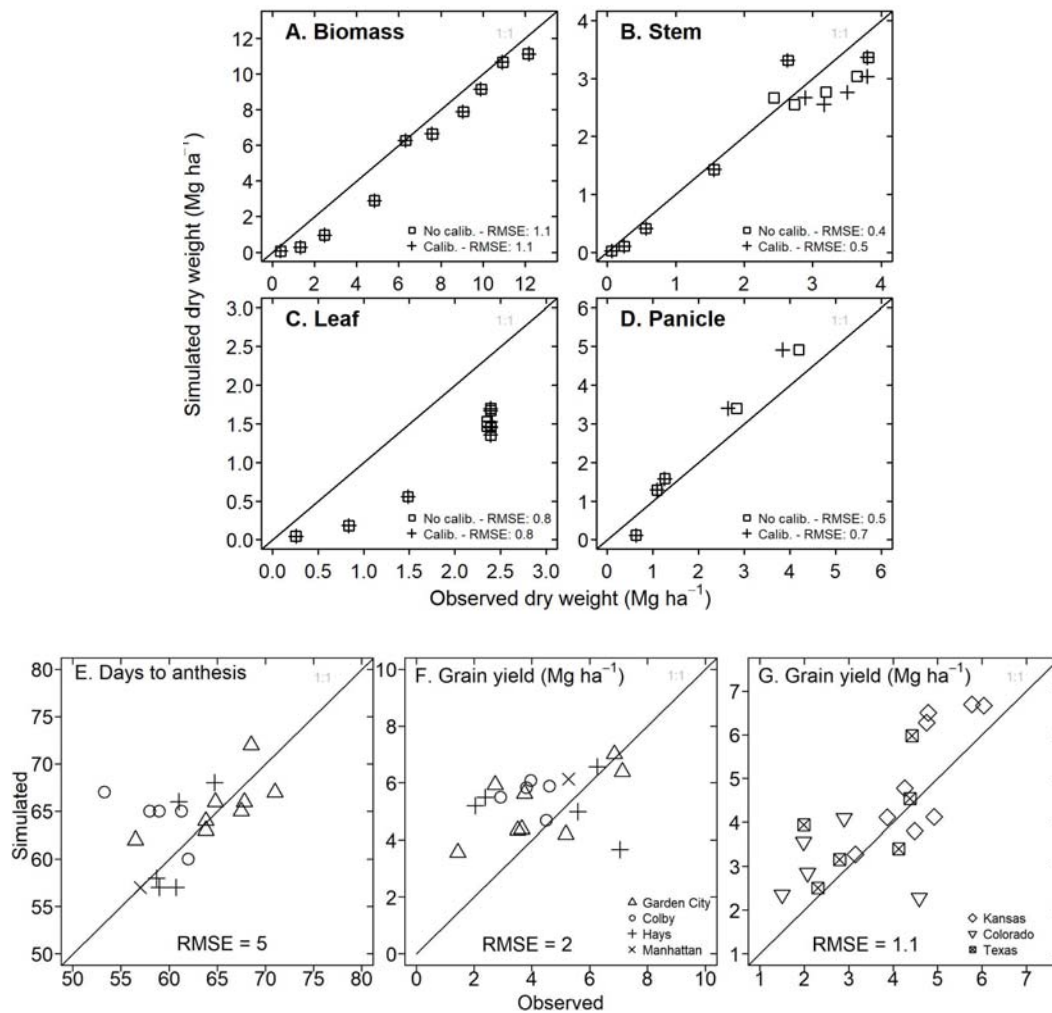


Figure 3. Model testing for APSIM-Sorghum in the study system. (A) Observed versus simulated in-season dry biomass for hybrid 87G67 in Manhattan, Kansas (2007). (B) Observed versus simulated in-season stem dry weight for hybrid 87G67 in Manhattan, Kansas (2007). (C) Observed versus simulated in-season leaf dry weight for hybrid 87G67 in Manhattan, Kansas (2007). (D) Observed versus simulated in-season panicle dry weight for hybrid 87G67 in Manhattan, Kansas (2007). (E) Observed versus simulated days to anthesis for hybrid 87G67 under rainfed conditions for experiments in Garden City, Colby, Hays, and Manhattan (Kansas). (F) Observed versus simulated dry grain yield for hybrid 87G67 under rainfed conditions across the Kansas precipitation gradient (Garden City, Colby, Hays, and Manhattan). Each point (Figures E and F) represents results for single seasons between 1997 to 2007. Information of (G) Observed versus simulated grain yield for Kansas, Colorado, and Texas study sites (indicated in Figure 4D). The y axis represents the mean of simulated yields over 33 years (1986-2018), three planting dates, and three maturity groups. The x axis represents the mean of observed data over 21 years (2010 to 2021). Observed sorghum grain yield (Figure G) was obtained from the National Agricultural Statistical Service (NASS, <https://www.nass.usda.gov/>).

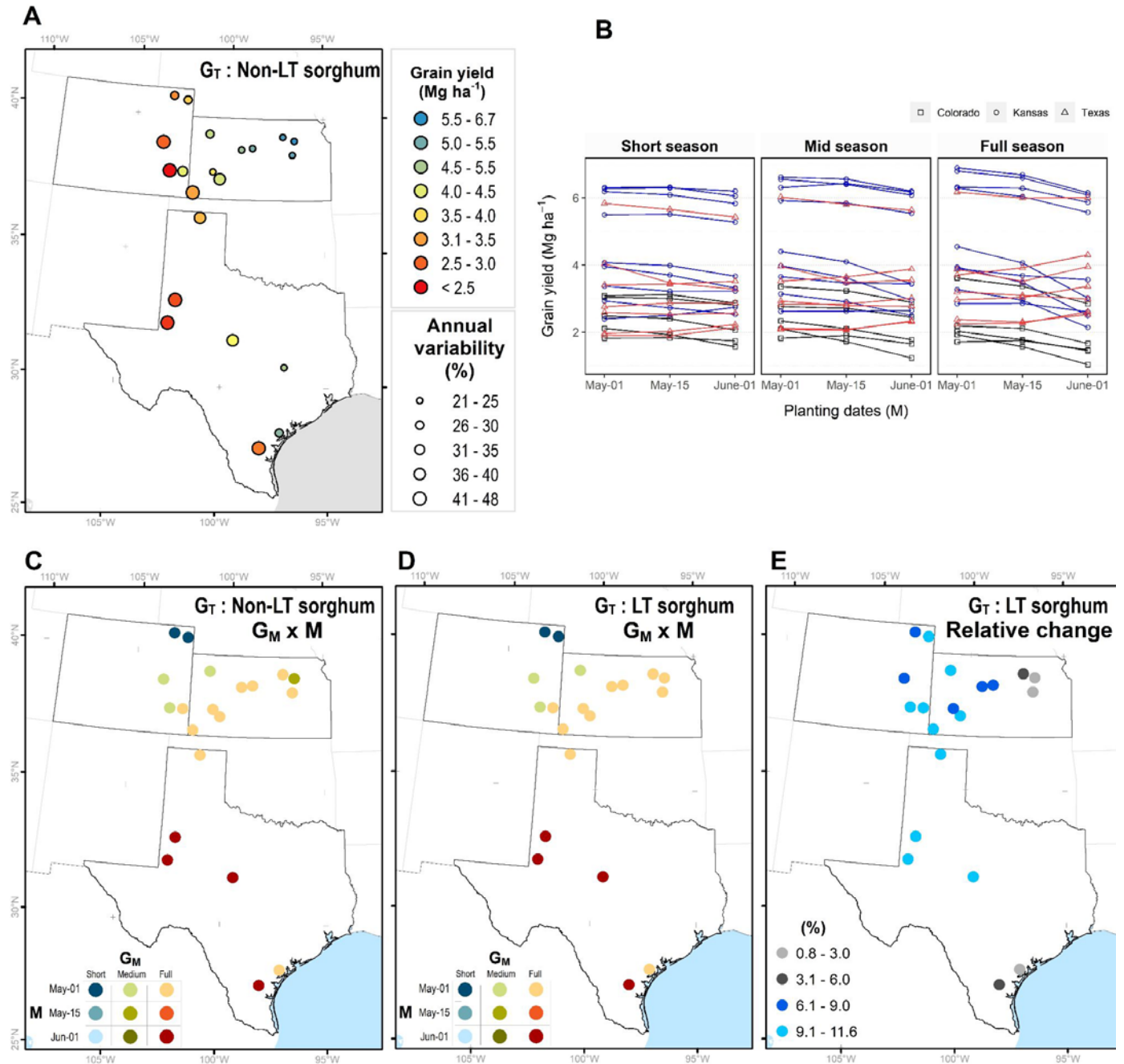


Figure 4. Maturity (G_M) \times planting date (M) combinations to achieve maximum yield for non-LT versus LT sorghum. (A) Average grain yield and interannual variability. (B) Average grain under different planting dates and maturity groups. Each point represents the mean of 33 years (1986-2018), the annual variability (coefficient of variability) is the quotient of the standard deviation and mean. Best $G_M \times M$ combination for a sorghum with (A) non-LT and (B) LT trait. Relative increase in grain yield for a sorghum with LT trait.

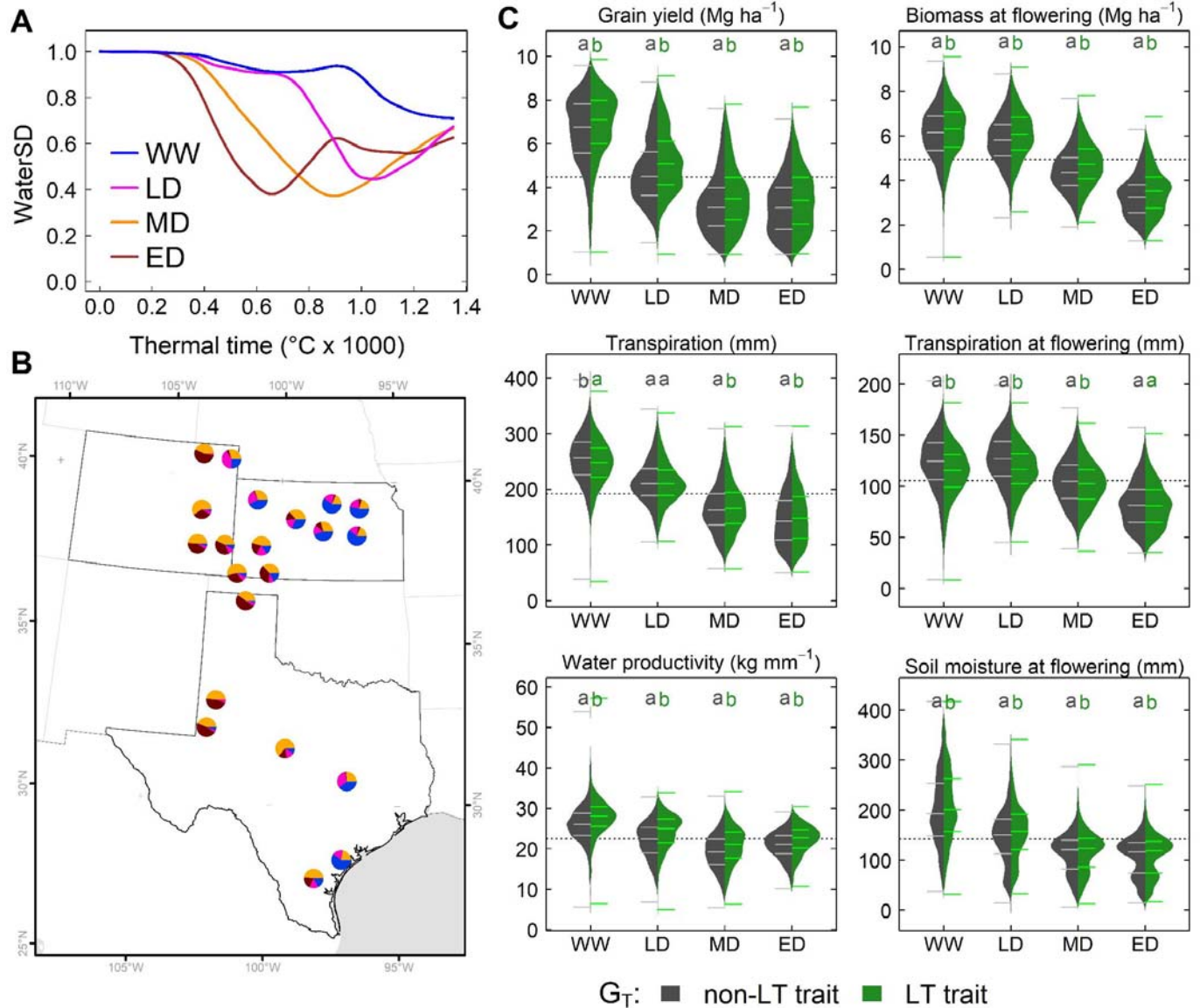


Figure 5. Simulated effects of LT (G_T) across the US sorghum belt. (A) Water stress environment identified via water supply and demand (WaterSD) at each site. (B) Frequency of water stress environments in Kansas, Texas and Colorado. (C) Distribution of simulated grain yield, transpiration, water productivity, biomass and soil extractable water for a phenotype with a non-LT (darkgray) and LT trait (green) in water stress environments. Each distribution represents simulations for all maturity groups (G_M), and planting dates (M) in all sites over 33 years. Letters indicate significant differences ($\alpha < 0.05$) of all pairwise comparisons using the Tukey HSD test.

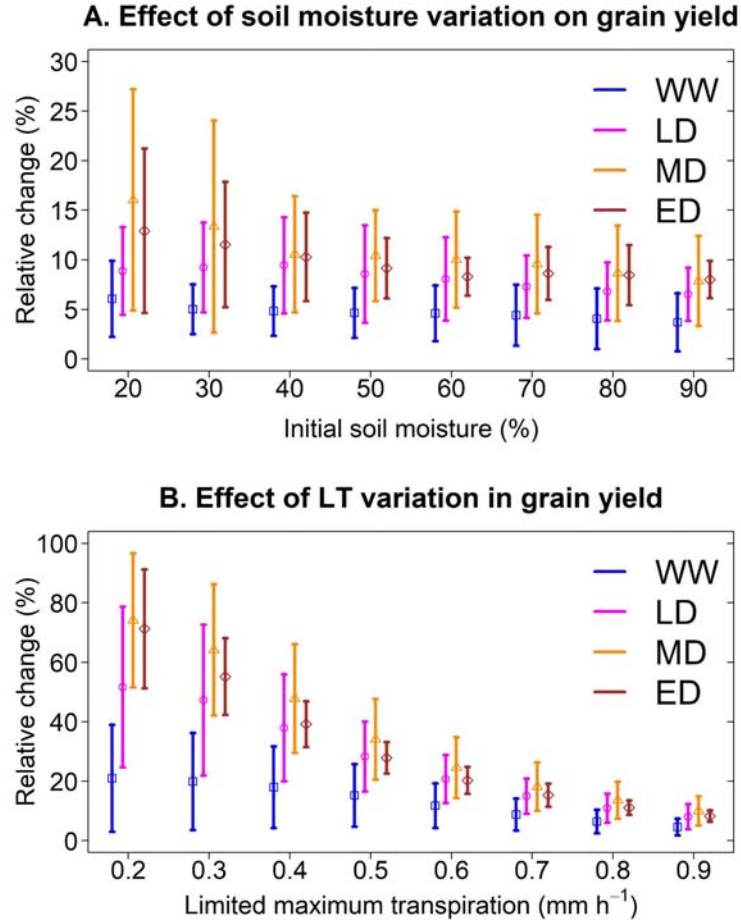


Figure 6. Sensitivity of a sorghum with LT trait to variation of initial conditions and genetic variability. (A) Relative change in grain yield under thresholds of initial soil moisture. The limited maximum transpiration was 0.9 mm h⁻¹. (B) Relative change in grain yield under thresholds of limited maximum transpiration. Initial soil moisture was 60%. The analysis was conducted for a representative location (Hays, Kansas; 1986-2018) at the center of the sorghum belt which presented all four water stress environments. Vertical lines represent the standard deviation of each environment.