Limited-Transpiration Trait May Increase Maize Drought Tolerance in the US Corn Belt

Carlos D. Messina,* Thomas R. Sinclair, Graeme L. Hammer, Dian Curan, Jason Thompson, Zac Oler, Carla Gho, and Mark Cooper

ABSTRACT

Yield loss due to water deficit is ubiquitous in maize production environments in the United States, even though it may not always be visually obvious. Stress conditions are associated with soil water deficit (Boyer, 1982) and high water demand (Lobell et al., 2013, 2014) and are often manifested in correlations between temperatures and maize yields (Schlenker and Roberts, 2009). In some instances, such as the drought occurring in 2012, the effects of drought can be devastating (Boyer et al., 2013). Impacts on yield, however, depend on the temporal pattern of water use by the cropping system and the physiological response characteristics of the hybrid to the developing water deficit. For example, significant genetic variation was demonstrated for leaf elongation rate response to water potential (Welcker et al., 2007) and transpiration response to drying soil (Gholipoor et al., 2013b). Hybrids expressing reduced early growth (Ray et al., 1997) or leaf elongation rate (Welcker et al., 2007) can lead to soil water conservation and yield increase under drought stress. Reduced plant population and skip-row planting systems are common agronomic practices implemented in the western US Corn Belt (Grassini et al., 2009; Lyon et al., 2003), which are conducive to increasing the proportion of water use during the reproductive phase. Similar results were reported by Shanahan and Nielsen (1987) and Kasel et al. (1994) for irrigated corn in Colorado to which growth retardants were applied to limit early-season leaf area development and water use.

Based on recent evidence identifying diversity among maize hybrids in the transpiration response to a vapor pressure deficit (VPD) (Gholipoor et al., 2013a; Yang et al., 2012), it is postulated that a limited-transpiration trait that it is expressed at high VPD may contribute to early-season water conservation and, as a consequence, improve yield under drought. By limiting transpiration (T) during times of the day when VPD is highest, this trait can increase daily transpiration efficiency (grams of mass produced per kilogram of water transpired by a crop; Sinclair et al., 1984). However, the largest effect

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Abbreviations: DMg, dry matter growth; FGFS, flowering and
grain-fill stress; FT SW, fraction of transpirable soil water; GFS, grain-
fill stress; NWL, no water limitation; TDS, terminal drought stress;
VPD, vapor pressure deficit; YD, yield difference.
of the limited-transpiration trait on yield is likely to arise from increasing the partitioning of water use from vegetative to reproductive stages of crop development (Sinclair, 2012; Cooper et al., 2014a; Vadez et al., 2014). Limiting early-season water use can also improve plant water status at flowering time, a well-known critical period for yield determination in maize (Andrade et al., 1999; Edmeades et al., 1993; Hall et al., 1982). Improvements in maize reproductive physiology, as measured by the anthesis to silking interval, as well as overall stress tolerance were postulated as underpinnings of simultaneous genetic improvement for maize yields under well-watered conditions, drought stress, and high planting density (Bolaños and Edmeades, 1993; Cooper et al., 2014a; Duvick et al., 2004). Water conservation may be one such component conferring stress tolerance in maize (Gaffney et al., 2015). An apparent distinction between drought-susceptible maize and a drought-tolerant hybrid relies on the capacity of the latter to restrict water use during the pre-flowering stage, and the consequential improvement in the plant water status at the time of flowering and increased post-flowering water use (Cooper et al., 2014a).

Limiting the transpiration rate under high VPD can have a negative impact on yield under some environmental conditions. Decreased stomatal conductance associated with the response to high VPD will also result in a decreased C assimilation rate during the high-VPD periods (Sinclair et al., 1984). A crucial issue is whether water conservation is sufficiently rewarded later in the season by water availability for sustained dry matter growth (DMg) during the seed-fill period, and increased yield if late-season water deficits develop. Thus, the impact of the trait on yield may vary with plant population and physiological background. The yield level at which a limitation in DMg and transpiration becomes detrimental to yield, the geographies where the trait may limit productivity and their frequency, and how the trait may impact productivity with changes in plant population all remain uncertain.

The complexity associated with genotype × environment × management interactions can be explored in a quantitative assessment using a simulation model (Cooper et al., 2009; Hammer et al., 2009). For example, the Agricultural Production Systems Simulator (Hammer et al., 2010; Keating et al., 2003) model was utilized to consider the roles of leaf angle in light capture and of root angle and soil profile occupancy on water capture as processes underpinning the observable genotype × density interactions in historical maize yield improvement in the United States (Hammer et al., 2009). Other studies in maize have sought to assess individual traits and trait combinations across environments (Sinclair, 1994; Sinclair and Muchow, 2001) and environment types (Boote and Tollenaar, 1994; Messina et al., 2011). Modeling and simulation proved useful to evaluate the impact of a limited transpiration rate at high VPD in sorghum [Sorghum bicolor (L.) Moench] (Sinclair et al., 2005) and soybean [Glycine max (L.) Merr.] (Sinclair et al., 2010, 2014). The objective of this study was to assess the value of the limited-transpiration trait in maize as a target for selection and genetic improvement. This knowledge can inform selection strategies and decisions within breeding programs and identify management practices that maximize the realization of the benefit of the trait.

**MATERIALS AND METHODS**

In this study, a mechanistic model was used to conduct simulation experiments (Muchow and Sinclair, 1991; Muchow et al., 1990). Given the structure of the model, we follow the terminology introduced by Solani and Sinclair (2012) and refer to it here as a simple simulation model (SSM). The SSM proved to reasonably simulate observations from field experiments (Muchow and Sinclair, 1991; Muchow et al., 1990; Sinclair, 1994), and it was used in simulation studies in the United States (Sinclair and Muchow, 2001; Sinclair and Rawlins, 1993).

The SSM was developed using the concepts of resource capture, resource use efficiency, and partitioning of mass to grain. Crop and canopy development are determined as a function of temperature. Thermal time (°C) is calculated as the average between daily maximum and minimum temperatures, with a base temperature for pre-flowering of 8°C and post-flowering of 0°C (Muchow et al., 1990). At any point in time (t), DMg is modeled as a function of solar radiation (SR), leaf area per plant (LAPP), plant population (PPOP), a coefficient of light extinction, which was set to 0.38, and radiation use efficiency, which was set to 1.85 g MJ⁻¹ (Hammer et al., 2009):

\[ DMg_t = SR_t \times 1.85 \times \left[1 - \exp\left(-0.38 \times LAPP_t \times PPOP_t\right)\right] \]  \hfill [1]

Grain yield is simulated based on the linear increase of harvest index during seed fill. Simulated yield is calculated on a dry matter basis and adjusted to 0.155 g g⁻¹ moisture content. Both canopy expansion and DMg are dependent on soil water content, with effects modeled as a function of the fraction of transpirable soil water (FTSW). Transpiration is calculated from DMg and atmospheric VPD, using a transpiration efficiency coefficient (k) for maize of 9 Pa (Tanner and Sinclair, 1983):

\[ T_r = \frac{DMg_t \times VPD_t}{k} \]  \hfill [2]

Crop growth was terminated when FTSW was <0.0 (Muchow and Sinclair, 1991).

**Implementing the Limited-Transpiration Trait in the Simple Simulation Model**

Because the limited-transpiration trait restricted the transpiration rate during periods of high VPD during the day, it was necessary to modify the SSM to calculate the transpiration rate at hourly time steps (h) rather than daily time steps. This change required that the daily weather input be interpolated for hourly time steps. A simple function was introduced such that when the VPD at any hourly time step exceeded a threshold VPD₀, water loss was held to the rate calculated for a VPD at the threshold:

\[ T_h = \frac{DMg_h \times VPD_h}{k} \]  \hfill if VPD ≥ VPD₀

\[ T_h = \frac{DMg_h \times VPD_h}{k} \]  \hfill otherwise  \hfill [3]

Figure 1a shows an example of the transpiration response to VPD using Eq. [1–3] when the leaf area index is 4 and SR is
3.4 MJ m\(^{-2}\) h\(^{-1}\). Transpiration for a genotype expressing the trait is less than for a genotype not expressing the trait when the VPD is greater than VPD\(_0\) (Fig. 1b). The consequence of this behavior in the model is soil water conservation, with the amount depending on the frequency and size of the difference between the VPD and VPD\(_0\). The resulting effects on soil water use are manifested in the value of FTSW, which determines the level of stress on leaf expansion and DMg under drought conditions (Muchow and Sinclair, 1991). When the hourly transpiration rate at high VPD (VPD > VPD\(_0\)) limits DMg, this variable is updated:

\[
\text{DMg}_{\text{h}} = \frac{T_{\text{h}} k}{\text{VPD}}
\]  

[4]

to simulate the reduction in crop growth (Fig. 1c).

**Simulation Studies**

The US maize production region, defined as the region where the area sown with maize is >2023 ha within a 30- by 30-km grid cell, was divided into 2603 individual geographical units. The EnClass system, which uses a GIS, public and proprietary databases, and a crop model to support environmental characterization applications (Löffler et al., 2005), was used to determine model inputs for each grid cell. Sowing date, plant population, and hybrid maturity were defined using EnClass and proprietary databases of yield trials. Total soil water holding capacity was determined using soil depth from the STATSGO database (Soil Survey Staff, 2015) and a constant (0.13 cm\(^3\) cm\(^{-3}\)) volumetric fraction of available soil water (Muchow and Sinclair, 1991). A scenario of soil moisture initial conditions was constructed using public data from the US Climate Reference Network and NOAA (Bell et al., 2013; Supplementary Fig. 1). Time series of daily minimum and maximum temperatures and precipitation data for the period 1950 to 2012 were from NOAA. Hourly temperature, from which VPD was calculated after Muchow and Sinclair (1991), was modeled from minimum and maximum temperatures by assuming a harmonic change in the temperature cycle each day (Monteith and Unsworth, 1990). Hourly solar radiation was calculated assuming a sinusoidal change in incident radiation during daylight hours (Monteith and Unsworth, 1990), and the daily integral was estimated from temperature records (Bristow and Campbell, 1984) with parameters provided by Mud Springs Geographers, Inc. The model was run independently for each season and grid for a total of 163,989 environments (63 seasons \(\times\) 2603 grids).

The base plant population ranged from 8 to 6 plants m\(^{-2}\) in an east–west gradient based on DuPont Pioneer proprietary yield trial data. Because plant population affects the development of...
leaf area, dry matter growth (Eq. [1]), transpiration (Eq. [2]),
and water use, two additional populations were simulated for
each environment by multiplying the base plant population
for the grid by 0.75 and 1.25. In addition, three hypothetical
hybrids with differing VPD thresholds were explored. The
VPD breakpoints were set to 1.5, 2.0, and 2.5 kPa based on the
observed range of responses of transpiration to VPD (Gholipoor
et al., 2013a; Yang et al., 2012). An additional hybrid not
expressing the limited-transpiration trait was set as a reference.

Environmental Characterization
The methods described by Chapman et al. (2000) were
adapted to characterize environments for the type of stress
pattern. In this study, drought-stress patterns were determined
by the temporal trajectories of FTSW rather than relative
transpiration, and the temporal series of FTSW were
centered on the anthesis date. Cluster analysis was conducted
by applying the k-means algorithm (Hartigan and Wong,
1979) to the FTSW time series for the control hybrid. The
algorithm seeks to assign temporal patterns of FTSW to one
of k groups such that the sum of squares from the series to
the center of the group, which is a characteristic temporal
pattern of FTSW, is minimized. The complete set of 163,989
environments that resulted from the combination of year
and location (grid) was analyzed, and 163,161 environments
were summarized by grouping the individual environments in
groups of environment types characterized by the average stress
pattern: no water limitation (NWL), grain-fill stress (GFS),
flowering and grain-fill stress (FGFS), and terminal drought
stress (TDS) (Fig. 2). A small fraction of the simulations, 0.5%,
terminated during the vegetative phase of crop development,
and these simulations were excluded from the genotype ×
environment × management interaction analysis.

RESULTS
Simulated Yields Using the Standard Model
Average simulated yields for control runs, i.e., hybrids not
expressing the limited-transpiration trait, show large spatial
variation for yield (Fig. 3). The highest values were simulated
for the east-central US Corn Belt, with average yields in the
range of 1000 to 1600 g m⁻². The locations of highest yield

Fig. 2. Characteristic dynamics of water use estimated from
the fraction of transpirable soil water (FTSW) determined by cluster
analyses for four environment types: no water limitation (NWL),
grain-fill stress (GFS), flowering and grain-fill stress (FGFS), and
terminal drought stress (TDS). The horizontal line indicates
the value below which relative transpiration decreases relative to
1. Thermal time is calculated as the average between daily
maximum and minimum temperature, with a base temperature
for pre-flowering of 8°C and post-flowering of 0°C.

Fig. 3. Spatial distribution of mean simulated yields (g m⁻²) for
63 yr (1950–2012) in the maize-producing regions of the United
States for the reference hybrid not expressing the limited-
transpiration trait.

where the simulated yield (Yijk) of the rth hybrid in the rth
management within the kth environment (year–location
combination) within the jth environment type was modeled as
a function of an overall mean u; factors for the rth hybrid, jth
environment type, and kth management; two-way interactions
between hybrid, environment type, and management; the
three-way interaction among them; and the residual ejrk. An
F test was used to assess significance for fixed effects. Analyses
were conducted with ASReml (Gilmour et al., 2009).

Analyses and Assessment
Because the limited-transpiration trait restricts DMg, it
imposes a limitation to potential yield. Regressing the yield
difference (YD) between the hybrid expressing the limited-
transpiration trait and the reference hybrid without the
limited transpiration trait against the simulated yield for the
control hybrid for each grid and year combination provides a
quantitative assessment of the sensitivity of the trait (Sinclair
and Muchow, 2001) and enables an estimate of the yield level at
which the trait benefit equals zero (Y0).

Spatial distributions of the limited-transpiration trait impact
on yield were determined by calculating the first, second, and
third quartile for YD. These quartiles represent wet (first),
normal (second), and dry (third) seasons, herein noted as
YD25, YD50, and YD75, respectively. Positive values indicate
yield gain and negative values indicate yield loss due to the trait
modification.

To quantify sources of variation associated with hybrid
(H), environment type (E), and management (M) and their
interactions, the simulated yield data were analyzed using a
fixed effect model:

\[ Y_{ijkl} = u + H_i + E_j + M_k + (HE)_{ij} + (HM)_{jk} + (EM)_{jk} + (HEM)_{ijk} + \epsilon_{ijkl} \]  

[5]
Fig. 4. Boxplot of simulated yield difference associated with a change in transpiration response to limited (vapor pressure deficit breakpoint of 2 kPa) from the non-limited reference hybrid vs. the simulated yield level of the reference. The boxplot shows first and third quartiles and median. Boxplot whiskers extend 1.5 times the interquartile range out from the box.

Conform well to the areas where maize is a dominant crop. A steep reduction in yield from 1200 to 300 g m⁻² was simulated west of longitude 95° W for rainfed maize production systems, which is consistent with an east–west precipitation gradient and soil moisture at sowing (Supplementary Fig. 1). Simulated yields for most of the state of Missouri and the US Southeast were also lower relative to those simulated for the central Corn Belt. Because the version of the model used in these simulations does not simulate the effects of N and other nutrients, extreme heat and cold stress, and biotic effects on growth and development, simulated values were often higher than those reported at the county level (National Agricultural Statistics Service, 2015). However, when simulated yields were compared with the results from managed experiments, they proved to accurately reproduce observed yields (Muchow and Sinclair, 1991; Muchow et al., 1990; Sinclair, 1994). Yield reductions from those attained in the central Corn Belt are widespread and open the possibility to identify regions where the limited-transpiration trait can have a positive influence on yield.

Yield Response to Limited-Transpiration Trait

The yield difference between a hybrid with a breakpoint VPD₀ of 2 kPa and the reference hybrid not expressing a breakpoint is presented for each location and year in Fig. 4. Simulated yield differences for the hybrid expressing the limited-transpiration trait were consistently positive for yield levels <750 g m⁻². There is an increasing frequency of yield penalties associated with the limited-transpiration trait as yield levels increase above about 1150 g m⁻². Using regression analysis (y = 242 ± 0.6 – 0.17 ± 0.0005x; r² = 0.42), the yield level at which the average yield difference is zero for VPD₀ = 2 kPa was estimated at 1382 g m⁻². This point of no difference increased to 1416 g m⁻² when VPD₀ was set at 2.5 kPa (y = 127 ± 0.47 – 0.09 ± 0.0004x; r² = 0.23) and decreased to 1235 g m⁻² when VPD₀ was 1.5 kPa (y = 375 ± 0.67 – 0.30 ± 0.0006x; r² = 0.63). The level of expression of the trait determines the degree of limitation of transpiration and DMg (see example in Fig. 1), and consequently the tradeoff between yield improvement in lower yielding environments and the yield penalty under favorable conditions.

Regional Patterns of Yield Response to Limited-Transpiration Trait

Spatial and temporal patterns of yield response to the expression of a breakpoint in the transpiration response to a VPD were studied for a hybrid with VPD₀ of 2 kPa compared with the reference hybrid not expressing any limitation. Three regions corresponding approximately to the western Corn Belt (west of 95° W), the east-central Corn Belt (north of 37° N), and the Mississippi Delta and US Coastal Plains could be identified by comparing the YD₂₅, YD₅₀, and YD₇₅ maps (Fig. 5). Yield gains in the western Corn Belt were greater than zero in at least 75% of the years, with YD₅₀ ranging from 10 to >50 g m⁻². In contrast, yield penalties were clearly observable in the other two regions. The value of YD₅₀ varied from positive (9 g m⁻²) to negative (~15 g m⁻²) in the Mississippi Delta and US Coastal Plains, while it varied around zero (~15 to 25 g m⁻²) in the east-central Corn Belt. A noteworthy characteristic of both the east-central Corn Belt and the Mississippi Delta and US Coastal Plains is the large oscillation from negative to positive benefits from expression of the limited-transpiration trait. In years with high rainfall, the yield penalty as estimated by YD₂₅ was around ~50 g m⁻² and consistently distributed throughout the regions, while in environments with low rainfall, yield gains as estimated by YD₇₅ were on the order of 25 g m⁻².

Yield Response is Associated with Dynamics of Water Use

Figure 6 shows the average temporal dynamics of the FTSW for three hybrids expressing a VPD₀ breakpoint at 1.5 and 2.0 kPa and a reference hybrid not expressing the trait. Means were calculated across years, and grids that were classified either as environment-type FGFS or TDS. The reduction in transpiration rate during periods of high VPD resulted in an observable increase, although not large, in FTSW starting around 400°C before anthesis. The magnitude of the shift relative to the non-limited reference was greater for the hybrid expressing a VPD₀ breakpoint at 1.5 kPa than that at 2.0 kPa. The water conservation was not directly proportional to the expression of VPD₀. Considering an average 1.8-m-deep soil with 0.13 volumetric fraction of available soil water, the average difference in FTSW between the hybrids and the reference hybrid translates into 25 mm (VPD₀ = 1.5 kPa) and 17 mm (VPD₀ = 2.0 kPa) of water at anthesis.

Yield Response Depends on Environment and Management

Analyses of variance of the simulated yields indicated that hybrid, environment, management, and their interactions significantly affected yields and the value of the limited-transpiration trait (P < 0.001). Simulated yields for both hybrids expressing a breakpoint VPD₀ of 2 kPa and the non-limited reference hybrid were largest for environment type NWL and lowest for environment type TDS, which on average across all management and genotype combinations were 1487 and 624 g m⁻², respectively (Table 1). Across genotype and environment-type class, the effects of changes in plant population relative to the normal planting density for the geographic region were significant yet small relative to the effects of environment-type class. Mean simulated yields
for low, normal, and high planting densities were 1078, 1166, and 1217 g m\(^{-2}\), respectively. There was a positive difference of 39 g m\(^{-2}\) between the hybrid expressing a transpiration limitation (VPD\(_0\) = 2 kPa) and the non-limited reference hybrid across environment-type classes and management regimes.

The effects of increasing plant population on simulated yields were positive within environment-type classes NWL, GFS, and FGFS (Table 1). Although the greatest effect of increasing plant population relative to normal density was simulated for a hybrid expressing the breakpoint in environment type NWL (122 vs. 117 g m\(^{-2}\)), the highest mean yield was simulated for the reference hybrid (1642 vs. 1613 g m\(^{-2}\)). In contrast, under severe water limitation, a genotype \(\times\) management interaction was evident. Within environment type TDS, mean simulated yields decreased from 569 to 549 g m\(^{-2}\) when the plant population increased from low to high for the non-limited reference hybrid, while the mean simulated yield increased from 684 to 692 g m\(^{-2}\) for the hybrid expressing the trait (Table 1).

The value of the limited-transpiration trait increased with increasing levels of water-deficit stress and plant density (Table 1). The largest difference between the hybrid expressing transpiration limitation (VPD\(_0\) = 2.0 kPa) and the non-limited reference hybrid was observed under high plant density within environment type TDS (143 g m\(^{-2}\)), while the largest yield penalty was observed under a low plant population within environment type NWL (–34 g m\(^{-2}\)). In GFS environments, the trait had a negative (positive) impact on yield under a low (high) plant population. This significant hybrid \(\times\) environment \(\times\) management interaction was consistent with the negative slopes calculated when regressing yield differences vs. yield for the reference hybrid not expressing the trait (Fig. 4).

**Discussion and Conclusions**

The limited-transpiration trait is now well described across crop genotypes and species, including maize (Choudhary and Sinclair, 2014; Choudhary et al., 2013, 2014; Gholipoor et al., 2010, 2013a; Devi et al., 2010; Seversike et al., 2013; Shekoofa et al., 2014; Yang et al., 2012). However, knowledge about the physiological determinants and impacts on crop performance is limited (Buckley and Schymanski, 2014; Choudhary et al., 2014; Seversike et al., 2013; Sinclair et al., 2010). Considering a limited physiological understanding of the limited-transpiration trait, simulation experiments designed to
The limited-transpiration trait has consistent value in the US Corn Belt and other production regions were conducted using a simple maize model, a parsimonious implementation of the trait (Sinclair et al., 2010), and environmental inputs to the model. Results demonstrated that the limited-transpiration trait can underpin improved maize performance in drought-prone environments and that the impact of the trait on maize productivity varies with geography (Fig. 5), environment type (Table 1), expression of the trait (Fig. 4), and plant density (Table 1). Because limiting canopy transpiration may result in a small increase canopy temperature (Monteith and Unsworth, 1990), the magnitude of the estimated value of the limited-transpiration trait could be improved by incorporating temperature effects on the degree of limitation of transpiration and on VPD gradients, as well as on the effects of heat stress on radiation use efficiency. We suggest, however, that outcomes from this simulation study highlight the need to advance the understanding and modeling of the conductance response to VPD, provide a hypothesis to further investigate the ubiquitous nature of variation for the trait in modern maize germplasm, and provide insights into the plausible role of the trait in past and future maize genetic improvement.

### Opportunities for Intensification of Cropping Systems

The simulated yield increased with increasing plant density under severe drought stress (environment type TDS), except for the case of the reference hybrid not expressing the limited-transpiration trait. The increase in simulated yield across environment classes that include drought-prone environments for hybrids expressing the limited-transpiration trait in response to increased plant density can provide a plausible explanation for the widespread trends toward increasing cropping systems intensification across the US maize production regions. In addition, the results from the simulation conform well to the observed yield response to plant-density field studies conducted for drought-tolerant and -susceptible hybrids (Cooper et al., 2014a; Gaffney et al., 2015). Empirical evidence for increased performance under drought stress and higher than normal plant density was presented for DuPont-Pioneer AQUAmax hybrids relative to non-DuPont Pioneer AQUAmax checks (Cooper et al., 2014a; Gaffney et al., 2015). The yield difference between these two groups of hybrids evaluated in severe-stress environments (26 yr–location combinations) increased from 0 g m\(^{-2}\) at 2 plants m\(^{-2}\) to 50 g m\(^{-2}\) at 7 plants m\(^{-2}\). In contrast with other interpretations of the role of system intensification in maize production (Lobel et al., 2014), the results presented in this study indicate the feasibility for further intensification of maize cropping systems operating in drought-prone regions or under high-VPD environments by means of selection for the limited-transpiration trait in maize breeding programs.

### Harnessing the Benefits within Breeding Programs

In well-watered environments (environment type NWL) and production systems producing yields >1300 g m\(^{-2}\), detrimental effects of the limited-transpiration trait were evident and consistent. This prediction conforms well to (i) theory (Buckley and Schymanski, 2014), (ii) postulates about the reduction in stomatal conductance sensitivity to VPD in response to selection for high productivity in wheat (Triticum aestivum L.) (Franks and Farquhar, 1999) and bean (Phaseolus vulgaris L.) (Mencuccini and Comstock, 1999), and (iii) the existence of maize hybrids with a linear response of transpiration to VPD (Gholipoor et al., 2013a). Because limiting conductance in NWL environments is associated with reductions in growth and yield, it was postulated that the observed reduced sensitivity of stomatal conductance to increased VPD in wheat and bean resulted from selection for yield in these NWL environments (Franks and Farquhar, 1999; Mencuccini and Comstock, 1999). However, contrary to the expectation set on the premise that maize selection in high-yielding environments of the central Corn Belt would have decreased stomatal sensitivity to VPD, significant genotypic

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### Table 1. Predicted mean yields and yield difference (d) between a hybrid expressing the limited-transpiration trait (LT) and a reference hybrid not expressing any limitation (NLT) as affected by plant population density and environment type: no water limitation (NWL), grain-fill stress (GFS), flowering and grain-fill stress (FGFS), and terminal drought stress (TDS).

<table>
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<tr>
<th>Genotype</th>
<th>NWL</th>
<th>GFS</th>
<th>FGFS</th>
<th>TDS</th>
<th>Density</th>
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<td>1480</td>
<td>1188</td>
<td>692</td>
<td>High</td>
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<tr>
<td>NLT</td>
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<tr>
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<td>Normal</td>
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<td>35*</td>
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*Significant at P < 0.005; ns, not significant.

assess its impact on maize productivity in the US Corn Belt and other production regions were conducted using a simple maize model, a parsimonious implementation of the trait (Sinclair et al., 2010), and environmental inputs to the model. Results demonstrated that the limited-transpiration trait can underpin improved maize performance in drought-prone environments and that the impact of the trait on maize productivity varies with geography (Fig. 5), environment type (Table 1), expression of the trait (Fig. 4), and plant density (Table 1). Because limiting canopy transpiration may result in a small increase canopy temperature (Monteith and Unsworth, 1990), the magnitude of the estimated value of the limited-transpiration trait could be improved by incorporating temperature effects on the degree of limitation of transpiration and on VPD gradients, as well as on the effects of heat stress on radiation use efficiency. We suggest, however, that outcomes from this simulation study highlight the need to advance the understanding and modeling of the conductance response to VPD, provide a hypothesis to further investigate the ubiquitous nature of variation for the trait in modern maize germplasm, and provide insights into the plausible role of the trait in past and future maize genetic improvement.

### Improving Maize Adaptation to Drought-Prone Environments

The limited-transpiration trait has consistent value in the western Corn Belt and parts of the east-central Corn Belt. Simulated changes in the soil water balance due to the limited-transpiration trait can explain the simulated yield gains and compare well with simulation studies conducted for sorghum (Sinclair et al., 2005). The calculated average values between 17 and 25 mm of conserved soil moisture as a result of the trait compares well with soil water measurement differences between a drought-tolerant maize DuPont-Pioneer AQUAmax hybrid and a drought-susceptible hybrid (Cooper et al., 2014a). Improved drought tolerance underpinned by increased stomatal sensitivity to VPD and water conservation was also demonstrated in pearl miller (Pennisetum glaucum (L.) R. Br.) (Kholová et al., 2010) and chickpea (Cicer arietinum L.) (Zaman-Allah et al., 2011). Due to the sensitivity of silk elongation and emergence to water deficit in maize (Andrade et al., 2002; Hall et al., 1982; Westgate and Boyer, 1985), it is possible that improvements in soil moisture content at anthesis could be conducive to improved kernel set and harvest yield maintenance under severe drought stress. Both effects of the trait (shift of water use from the vegetative to the reproductive period and improved kernel set) can contribute to yield improvement.
variation in the transpiration response to a VPD was recently documented for maize elite germplasm (Choudhary et al., 2014; Gholipoor et al., 2013a; Yang et al., 2012).

Results documenting spatial variation (Fig. 4) and genotype × environment × management interactions (Table 1) help reconcile the notion of selection under high-productivity environments and the ubiquitous nature of genetic variation for the limited-transpiration trait in modern elite maize germplasm. Results also provide evidence for a functional contribution of the limited-transpiration trait to the observed long-term trend of gain in yield of maize under drought conditions that has been associated with selection for yield in US Corn Belt environments (Cooper et al., 2014b; Duvick et al., 2004). Because major breeding programs were implemented in regions where, in some years and within a year in some locations, the limited-transpiration trait can have a positive or a negative effect, it can be hypothesized that the combination of genotype × environment × management interactions and environmental heterogeneity have resulted in positive selection for the limited-transpiration trait in some years and negative selection against the trait in other years. The slight advantage on average and the presence of genotype × environment × management interaction may have contributed to the maintenance of significant genetic variation for the trait in the elite germplasm of the breeding programs (Cooper and Podlich, 1999; Podlich et al., 1999). Mapping the genetic architecture and haplotype diversity of the limited-transpiration trait in the elite germplasm of breeding programs will enable further testing of this hypothesis. Results from the studies will enable the design and implementation of selection strategies for dealing positively with characterized genotype × environment × management interactions (Cooper and Podlich, 1999) and further leveraging of the trait in breeding maize for long-term improved drought tolerance (Cooper et al., 2014b).

REFERENCES


