

Modelling the effect of plant water use traits on yield and stay-green expression in sorghum

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This paper originates from a presentation at the Interdrought IV Conference, Perth, Australia, 2–6 September 2013.

Abstract. Post-rainy sorghum (*Sorghum bicolor* (L.) Moench) production underpins the livelihood of millions in the semiarid tropics, where the crop is affected by drought. Drought scenarios have been classified and quantified using crop simulation. In this report, variation in traits that hypothetically contribute to drought adaptation (plant growth dynamics, canopy and root water conducting capacity, drought stress responses) were virtually introgressed into the most common post-rainy sorghum genotype, and the influence of these traits on plant growth, development, and grain and stover yield were simulated across different scenarios. Limited transpiration rates under high vapour pressure deficit had the highest positive effect on production, especially combined with enhanced water extraction capacity at the root level. Variability in leaf development (smaller canopy size, later plant vigour or increased leaf appearance rate) also increased grain yield under severe drought, although it caused a stover yield trade-off under milder stress. Although the leaf development response to soil drying varied, this trait had only a modest benefit on crop production across all stress scenarios. Closer dissection of the model outputs showed that under water limitation, grain yield was largely determined by the amount of water availability after anthesis, and this relationship became closer with stress severity. All traits investigated increased water availability after anthesis and caused a delay in leaf senescence and led to a ‘stay-green’ phenotype. In conclusion, we showed that breeding success remained highly probabilistic; maximum resilience and economic benefits depended on drought frequency. Maximum potential could be explored by specific combinations of traits.

Additional keywords: APSIM, drought stress, *Sorghum bicolor* (L.) Moench, trait modelling.

Received 13 December 2013, accepted 23 May 2014, published online 25 July 2014

Introduction

Post-rainy (*rabi*) sorghum (*Sorghum bicolor* (L.) Moench) production is the staple source of livelihood for millions of food-insecure households in semiarid tropical regions of the Indian subcontinent (Murty *et al.* 2007) but its production is often limited by water availability, resulting in a high risk of crop failure (Kholová *et al.* 2013). Sorghum is also important for the subsistence economy of many households across the semiarid tropics of Africa, where it also faces water stress. Therefore, finding innovative and faster ways for improving sorghum productivity and resilience under water-limited conditions is a must.

The ‘stay-green’ phenotype has been described as the best characterised trait contributing to drought adaptation in sorghum (e.g. Borrell and Hammer 2000; Borrell *et al.* 2001; Jordan *et al.*

2003; Harris *et al.* 2007; Kassahun *et al.* 2010). The potential of stay-green technology could be fully explored for crop improvement only if the physiological mechanisms underlying this phenomenon were properly understood. Aside from ‘cosmetic’ stay-green (retention of nonfunctional chlorophyll; see reviews (e.g. Thomas and Howarth 2000; Cha *et al.* 2002)), there are basically two parallel streams of hypotheses explaining the maintenance of green leaves under water stress, one of which deals with the enhanced use of available N (Rajcan and Tollenaar 1999; Borrell and Hammer 2000; Borrell *et al.* 2001; Bertheloot *et al.* 2008; van Oosterom *et al.* 2010b) and another one favouring an improved plant water use status (van Oosterom *et al.* 2010b; Vadez *et al.* 2011, 2014). Several quantitative trait loci (QTLs) contributing to stay-green phenotype expression under drought (Stages 1–4, Stages A and B) have been validated across different

research groups (Tuinstra *et al.* 1996, 1997, 1998; Crasta *et al.* 1999; Subudhi *et al.* 2000; Tao *et al.* 2000; Xu *et al.* 2000; Kebede *et al.* 2001; Sanchez *et al.* 2002; Haussmann *et al.* 2002; Hash *et al.* 2003; Harris *et al.* 2007). Introgressing stay-green QTLs into two senescent parental lines (R16, S35) from the stay-green donor B35 produced lines showing differences in several traits related to the plant water budget (e.g. transpiration efficiency (TE), water extraction, leaf area) (Vadez *et al.* 2011). Here, we test the effect of several possible mechanisms affecting the plant water budget on stay-green expression, and grain and stover yield.

Breeding for improved varieties for water-limited environments has been slow, especially in developing countries, mostly because of the highly unpredictable drought environments. To tackle the season-to-season environmental variation, we have already classified and quantified five different stress scenarios across the *rabi* sorghum tract using the sorghum crop model in the APSIM software platform (Hammer *et al.* 2010; Keating *et al.* 2003). Environment types ranged from very severe (an average grain yield of ~ 100 kg ha⁻¹) to no stress conditions (an average grain yield of ~ 1500 kg ha⁻¹) and divided the *rabi* sorghum tract into four zones with similar environmental conditions (Kholová *et al.* 2013). This follows similar efforts in sorghum in Australia ((Chapman *et al.* 2000a, 2000b, 2000c), wheat (*Triticum aestivum* L.) (Chenu *et al.* 2011, 2013), maize (*Zea mays* L.) (Chauhan *et al.* 2013) or chickpea (*Cicer arietinum* L.) (Chauhan *et al.* 2008)). For the *rabi* sorghum region, which is the object of the current study, we also found that for the recommended management practices, the crop suffered severe water limitations causing substantial yield losses (typically more than half of the yield is lost during severe droughts) in around one-third of the seasons in the core production zone. Given these large variations in stress conditions, it is very likely that potential beneficial traits may not have similar effects in all scenarios, as noted by van Oosterom *et al.* (2001), Bidinger *et al.* (2007), Chapman *et al.* (2000a, 2000b, 2000c) and Tardieu (2012). Therefore, we have tested the effect of several traits involved in the plant water budget on grain and stover yield across the different stress scenarios that were previously identified.

Hence, the main aims of this study were to: (i) assess the genetic variation in the mechanisms and traits putatively related to the plant water budget in a series of introgression lines (ILs) developed into two genetic backgrounds (S35, R16); and (ii) use these ranges of genetic variation to model their putative effect on grain and stover yield across five different stress scenarios, using the most common *rabi* sorghum genotype (M35-1) as an *in silico* recipient of these traits; and (iii) assess the value of several mechanisms and traits in eventually conferring a stay-green phenotype and for crop improvement programs.

Materials and methods

Plant material

Two senescent recurrent parental lines (R16, S35) were introgressed with six individual stay-green QTLs (from the donor parent B35; the development of ILs has been described in Kassahun *et al.* 2010 and Vadez *et al.* 2011). These ILs were used to explore the variation in several mechanisms involved in

the plant water budget, and were expected to eventually lead to yield improvement under water stress and stay-green phenotype expression, which was further tested with the crop model (see below). Both of the senescent recipient lines as well as the stay-green QTL donor parent are considered to be limited-tillering materials. The stay-green donor was B35 (BT × 642) in both cases; B35 is a triple dwarf genotype.

Crop simulation approach – traits related to plant water budget and trait simulation

The sorghum (*Sorghum bicolor* (L.) Moench) model in APSIM (ver. 7.3; <http://www.apsim.info/Products/Downloads.aspx>; Keating *et al.* 2003; Hammer *et al.* 2010) and the original parameters developed for the common *rabi*-grown genotype M35-1 (Maldandi type; Ravi Kumar *et al.* 2009) were used to conduct simulations for the key locations within the five clusters of stress scenarios previously identified across the main *rabi* sorghum production tract (the simulations set is based on 404 years of historical weather records across 19 locations; the details are given in Kholová *et al.* 2013). These five stress scenarios were: (i) pre-flowering, (ii) flowering, (iii) post-flowering stress; (iv) stress relieved after flowering, and (v) no stress. Crop water demand is largely determined by the canopy size, the canopy conductance response to environmental stimuli (high evaporative demand of the air, soil water deficit) and the ability to extract water from the soil. Keeping how APSIM is structured in mind, our efforts focussed on the assessment of genetic variation in the set of stay-green QTL ILs in the R16 and S35 backgrounds for the production component traits related to (i) canopy development, (ii) capacity of the canopy and root to conduct water, and (iii) the canopy development response to water stress. The range of IL variations was then used to individually alter the crop parameters of the *rabi*-adapted sorghum variety M35-1 (as a ‘virtual introgression’ of individual traits), in a similar magnitude to that identified within the population of stay-green IL (i.e. original coefficient \pm % variation_{max}). These were used to simulate their effects on stover and grain yield across the sorghum production tract with APSIM. Consequently, these virtual trait introgressions were compared with the original stover and grain yield simulations that were carried out with M35-1 parameters only (Kholová *et al.* 2013). The virtual crop growth was then analysed in more detail in seasons facing severe water limitations at a representative production site (Solapur) to visualise how the traits affected the stress patterns and the expression of the stay-green phenotype. Finally, several trait combinations and their effects on crop production, resilience and economic importance were investigated.

Leaf area growth dynamics and its simulation

Observed variation in canopy parameters

The growth of ILs was assessed under field conditions following standard methods for APSIM genotype parameterisation (Birch *et al.* 1990). This method builds on dynamic observations of plant phenological phases, leaf appearance during the season and leaf size distribution in plants grown under optimal conditions. The combination of these three parameters defined the canopy development as a

function of thermal time and allow the estimation of APSIM coefficients to reflect the genotypic variability. Data were collected in field conditions during three seasons: 2010–11 (16 November to 20 March), 2011–12 (13 October to 10 February) and 2012–13 (8 November to 12 March). Field management and organisation were very similar to that of Kassahun *et al.* 2010. The analysis of 3 years of these field trials provided us with a range of variation in the corresponding parameters characterising crop canopy development in APSIM 7.3 within the population of ILs. The maximum observed variation in IL parameters (see below, Table 1 and Figs 1–3) was applied to change M35–1 coefficients in a similar range: $\gamma \pm 5\%$ (2.82 ± 0.141); $\beta \pm 10\%$ (0.66 ± 0.066); $\alpha \pm 10\%$ (0.011 ± 0.0011); Leaf Appearance Rate 1 $\pm 10\%$ (45.5 ± 4.55); Leaf Appearance Rate 2 $\pm 10\%$ (20 ± 2) (see below and Figs 1–3).

Simulation of canopy development

Canopy development is simulated on a whole-plant basis through a relationship between total plant leaf area (TPLA) and thermal time. TPLA integrates the number of fully expanded leaves, their individual size and tiller number, and includes an adjustment for the area of expanding leaves, as calculated by Eqns 1 and 2 (Hammer *et al.* 1993):

$$TPLA = \frac{TPLA_{\max}}{1 + e^{-\alpha(TT-\beta)}}; \quad (1)$$

$$TPLA_{\max} = (1 + FTN)^{0.66} \times TLN^{\gamma}, \quad (2)$$

where $TPLA_{\max}$ is the maximum value of TPLA; TT was calculated from daily maximum and minimum temperatures as per Hammer and Muchow (1994); α , β and γ are fitted coefficients; FTN is fertile tiller number and TLN is total leaf (node) number. The value of β is usually set at 66% of the thermal time from emergence to flag leaf full expansion (Hammer *et al.* 1993). Variation in $TPLA_{\max}$ is associated with differences in TLN or γ (i.e. leaf size), resulting in the crop type attaining smaller or larger TPLA throughout the crop's life cycle (Fig. 1a).

Variation of the other coefficients in the TPLA function

Variation of the other coefficients in the TPLA function (α and β , the TPLA production coefficient and the TPLA inflection ratio coefficient in APSIM, respectively) can be used to separate and mimic the effect of faster canopy development at

earlier growth phases combined with slower canopy development in the later phases (plants with high 'early vigour') or *vice versa*, with initial slower and later increased canopy developmental rates (low 'early vigour'). Both of these plant types (early or late vigour) would ultimately develop similar total leaf area at booting (given the same $TPLA_{\max}$ attributes) under optimal conditions (Fig. 2a), although with a different dynamic through the vegetative phase of the crop cycle. There are four hypothetical combinations shown on Fig. 2a but only two combinations were used for modelling – bold curves).

Simulation of leaf appearance rate

The number of fully expanded leaves is the product of thermal time elapsed since emergence and the leaf appearance rate. The rate of leaf appearance is characterised by a constant thermal time per leaf or phyllochron (Leaf Appearance Rate 1), except for the top 3.5 leaves, which appear at a more rapid rate (Leaf Appearance Rate 2). Although any change in phyllochron does not affect total leaf number, it does affect crop phenology, as the type with an extended (or reduced) phyllochron interval reaches full flag leaf expansion and thus flowering, later (or sooner) (Fig. 3a). Affecting the phyllochron parameters thus leads to changes in flowering time (short or long crop duration) while keeping the same canopy size attributes via $TPLA_{\max}$ and TPLA attributes.

Limited maximum transpiration rate under high vapour pressure deficit, soil water extraction rate and their simulation

Observed variation in maximum transpiration rate

The transpiration rate (TR, g H₂O transpired cm⁻² h⁻¹) of well watered plants subjected to a range of vapour pressure deficit (VPD) regimes was measured in controlled environment growth chambers according to previous work (Kholová *et al.* 2010). The VPD regimes used in the assay represent the range of VPD conditions that plants usually face during *rabi* season cultivation. Ten ILs in both the R16 and S35 genetic backgrounds were assessed. There was limited variation in the S35 background but significant variation in the R16 background, which was further modelled (Fig. 3b).

Simulation of limits on maximum transpiration rate

The variation in this trait was simulated through APSIM by imposing a restriction on transpiration at the time of the day

Table 1. The range of variability in crop characteristics assessed in stay-green isogenic lines (ILs) of sorghum, the corresponding APSIM coefficients and the variability virtually introgressed in M35–1 (a Maldandi *rabi* cultivar)

Simulation	APSIM coefficient(s) altered	Variability modelled	Original M35–1 coefficients \pm range of variability
Phyllochron	<i>leaf_app_rate1</i>	$\pm 10\%$	45.4 ± 4.54
	<i>leaf_app_rate2</i>	$\pm 10\%$	20 ± 2
Plant vigour	<i>c_tpla_inflection_ratio</i>	$\pm 10\%$	0.66 ± 0.066
	<i>-p_tpla_prod_coef</i>	$\pm 10\%$	0.011 ± 0.0011
Canopy size	<i>mainStemCoef</i>	$\pm 5\%$	2.82 ± 0.141
Maximum transpiration rate	<i>max TR</i>	$\pm 10\%$	0.8 ± 0.1
Root water extraction capacity	<i>kl</i>	$\pm 10\%$	0.7 ± 0.1
Responsiveness of leaf expansion to soil drying	<i>sw_def_leaf</i>	$\pm 20\%$	$<0.1; 1 \pm 0.2.>$

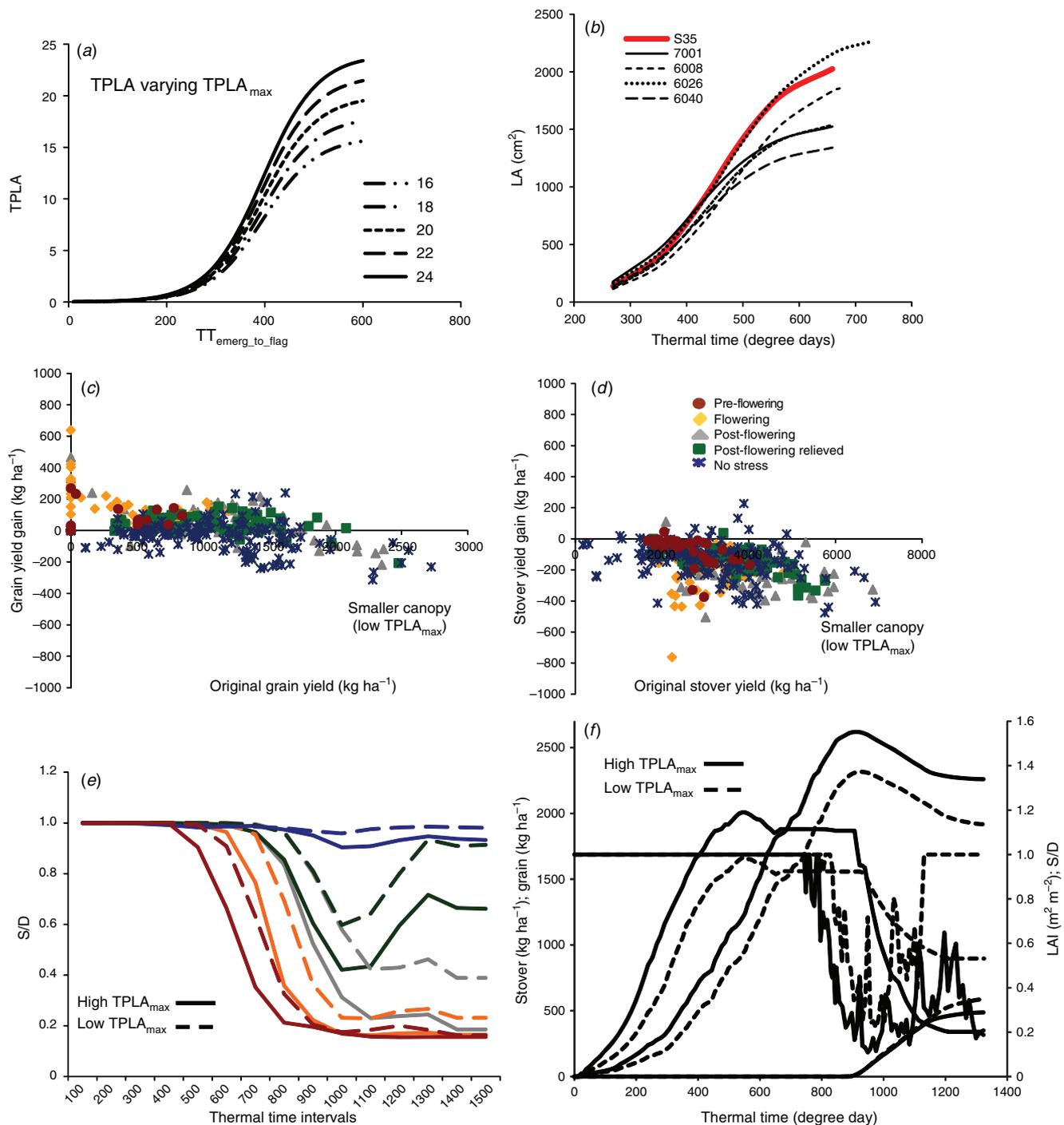


Fig. 1. Effects of canopy size in sorghum. (a) Maximum total plant leaf area ($TPLA_{max}$) function in APSIM which is illustrated by the example of variable growth dynamics of plants with different leaf numbers (different line styles) and reflects (b) the observed variability in total plant leaf area (TPLA) in introgressed lines (black line styles) originating from S35 (red line). Simulation of the effect of a smaller canopy on (c) grain and (d) stover yield compared with the original yields of M35-1 (x-axes). (e) Effects of a smaller or larger canopy size in APSIM on water stress trajectories (water use patterns under the five water stress scenarios expressed by different line colours) for M35-1 and (f) dissection of the effects of canopy size on crop growth parameters. $TT_{emerg_to_flag}$, thermal time from emergence to the development of flag leaf; LA, leaf area; S : D, water supply : demand ratio; LAI, leaf area index.

when potential crop water use is the highest. To do so, APSIM was adapted to calculate crop growth on an hourly basis, instead of a daily basis as in the standard model. This

incorporated procedures to generate hourly weather variables from daily values (Hammer and Wright 1994; Glassy and Running 1994). A restriction on crop TR was then imposed in

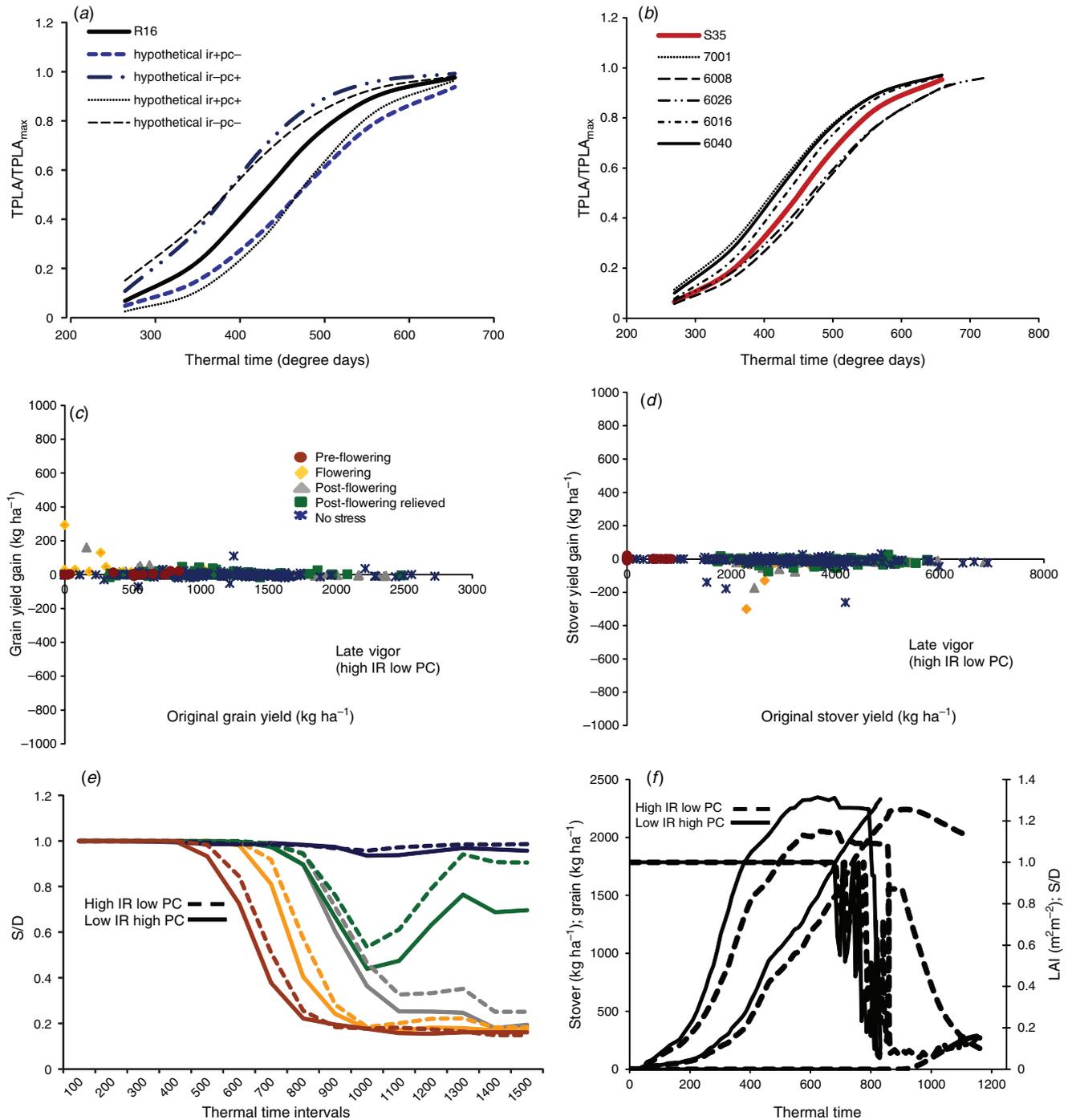


Fig. 2. Effects of plant vigour in sorghum. (a) Total plant leaf area (TPLA) inflection ratio and TPLA production coefficient in APSIM corresponding to (b) variability in crop vigour in introgressed lines originating from S35 in introgressed lines (black line styles) originating from S35 (red line). Simulation of the effect of decreased early vigour on (c) grain and (d) stover yield compared with the original yields of M35-1 (x-axes). (e) Effects of low or high early vigour in APSIM on water stress trajectories (water use patterns under the five water stress scenarios expressed by different line colours) for M35-1 and (f) dissection of the effects of plant vigour on crop growth parameters. TPLA_{max}, maximum total plant leaf area; IL, introgression lines; PC, TPLA production coefficient; IR, TPLA inflection ratio; S : D, water supply : demand ratio; LAI, leaf area index.

a manner similar to that of Sinclair *et al.* (2005) (Fig. 4a). The limit on the maximum TR was imposed at 0.8 (mm H₂O m⁻² of leaf area (LA) h⁻¹) ± 0.1 (±10%), which reflected the variation

in stay-green ILs (Table 1). Additionally, simulations of the limited maximum TR in combination with other traits investigated in this study were evaluated and are summarised

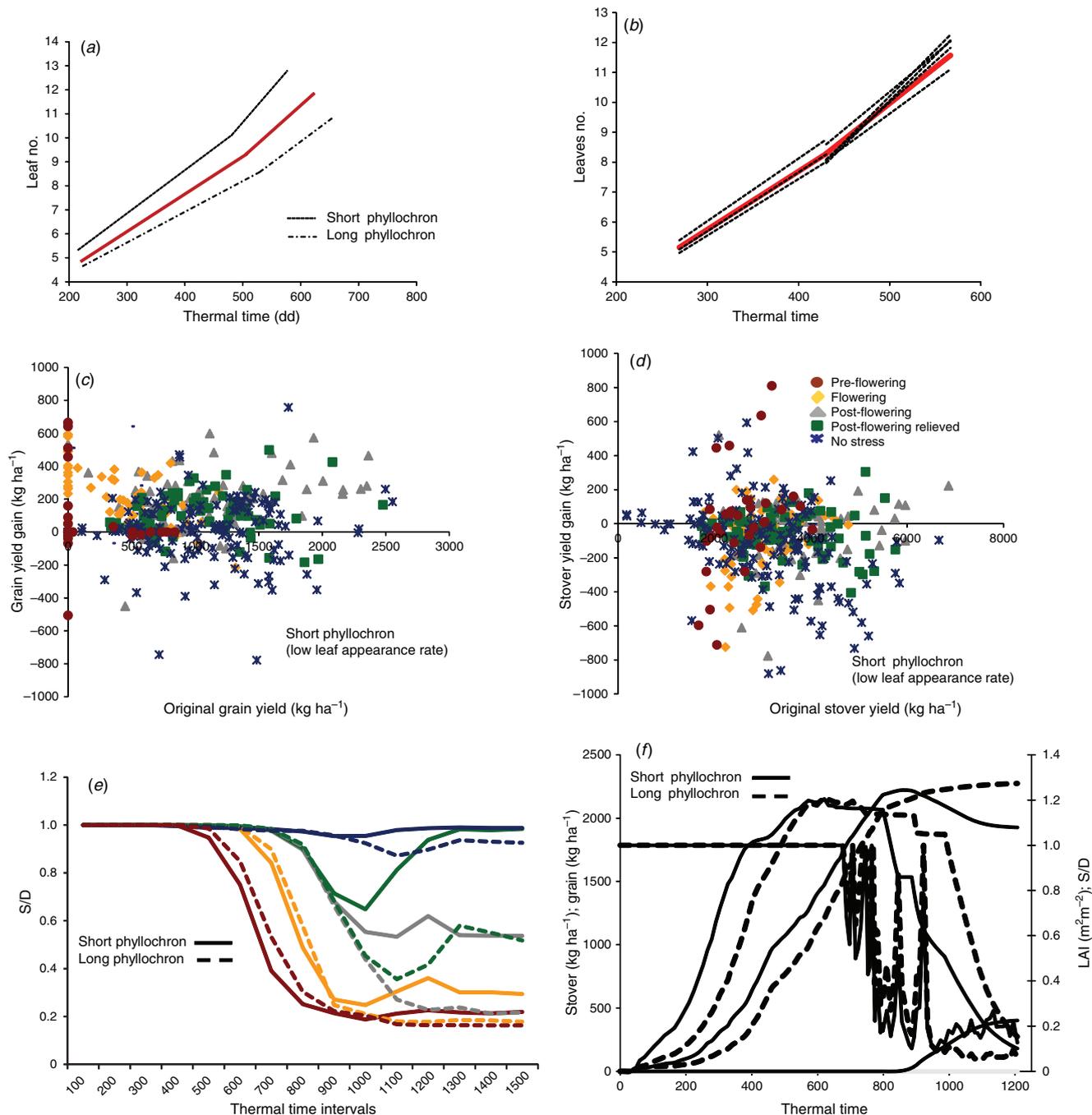


Fig. 3. Effects of phyllochron interval in sorghum. (a) Leaf growth rate 1 and 2 functions in APSIM and (b) the corresponding variability in phyllochron interval in introgressed lines originating from S35 in introgressed lines (black line styles) originating from S35 (red line). Simulation of the effect of a shorter phyllochron on (c) grain and (d) stover yield compared with the original yields of M35-1 (x-axes). (e) Effects of shorter or longer phyllochron intervals in APSIM on water stress trajectories (water use patterns under the five water stress scenarios) for M35-1 and (f) dissection of the effects of phyllochron length intervals on crop growth parameters. S : D, water supply : demand ratio; LAI, leaf area index.

in Table S1, available as Supplementary Material to this paper, but are not discussed in details.

Observed variability in soil water extraction rates

Recent research indicates that the restriction of transpiration under high VPD conditions could be of a hydraulic nature and

linked to the extraction capacity of roots, for instance in barley (*Hordeum vulgare* L.), wheat (*Triticum aestivum* L.) or pearl millet (*Pennisetum glaucum* (L.) R. Br.) (Manschadi et al. 2006; Bramley et al. 2009; J. Kholová, M. Tharanya, S. Sakhti, unpubl. data). This possibility was then approached through an alteration of the *kl* coefficient in APSIM, which determines the soil water

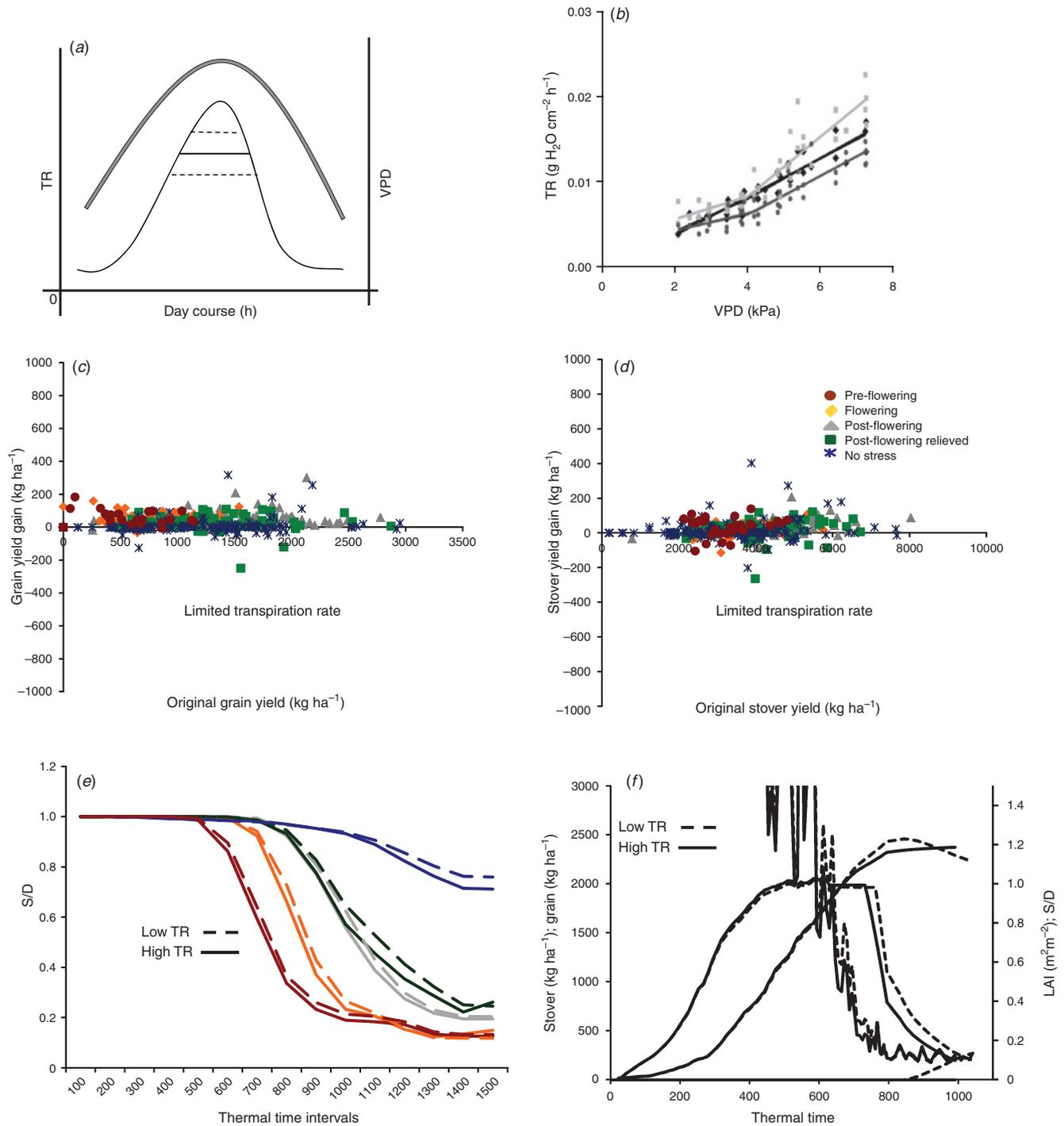


Fig. 4. Effects of transpiration rate (TR) in sorghum. (a) Effect of different maximum TR coefficients in APSIM on transpiration rates during the day course corresponding to (b) the maximum variability in TR found in introgressed lines (grey lines) originating from R16 (black line). Simulation of the effect of decreased TR on (c) grain and (d) stover yield compared with the original yields of M35-1 (x-axes). (e) Effect of low or high TR in APSIM on water stress trajectories (water use patterns under the five water stress scenarios expressed by different line colours) for M35-1 and (f) dissection of the effects of low and high TR on crop growth parameters. S : D, water supply : demand ratio; LAI, leaf area index.

extraction rate (Robertson *et al.* 1993; Meinke *et al.* 1993). The differences in soil water extraction dynamics for various soil water levels were re-analysed from earlier data (Vadez *et al.* 2011)

and different types of water use dynamic patterns were found among R16 ILs and S35 ILs. In R16 ILs, the total amount of water extracted from lysimeters differed little; however, there

was variation in the dynamic of water extraction following irrigation withdrawal, suggesting variability in root hydraulics in ILs in the R16 background (Fig. 5*b*; the actual lysimeter

weight is normalised by the field capacity lysimeter weight during the intervals after stress exposure). In S35 ILs, the total amount of water extracted from lysimeters differed among lines

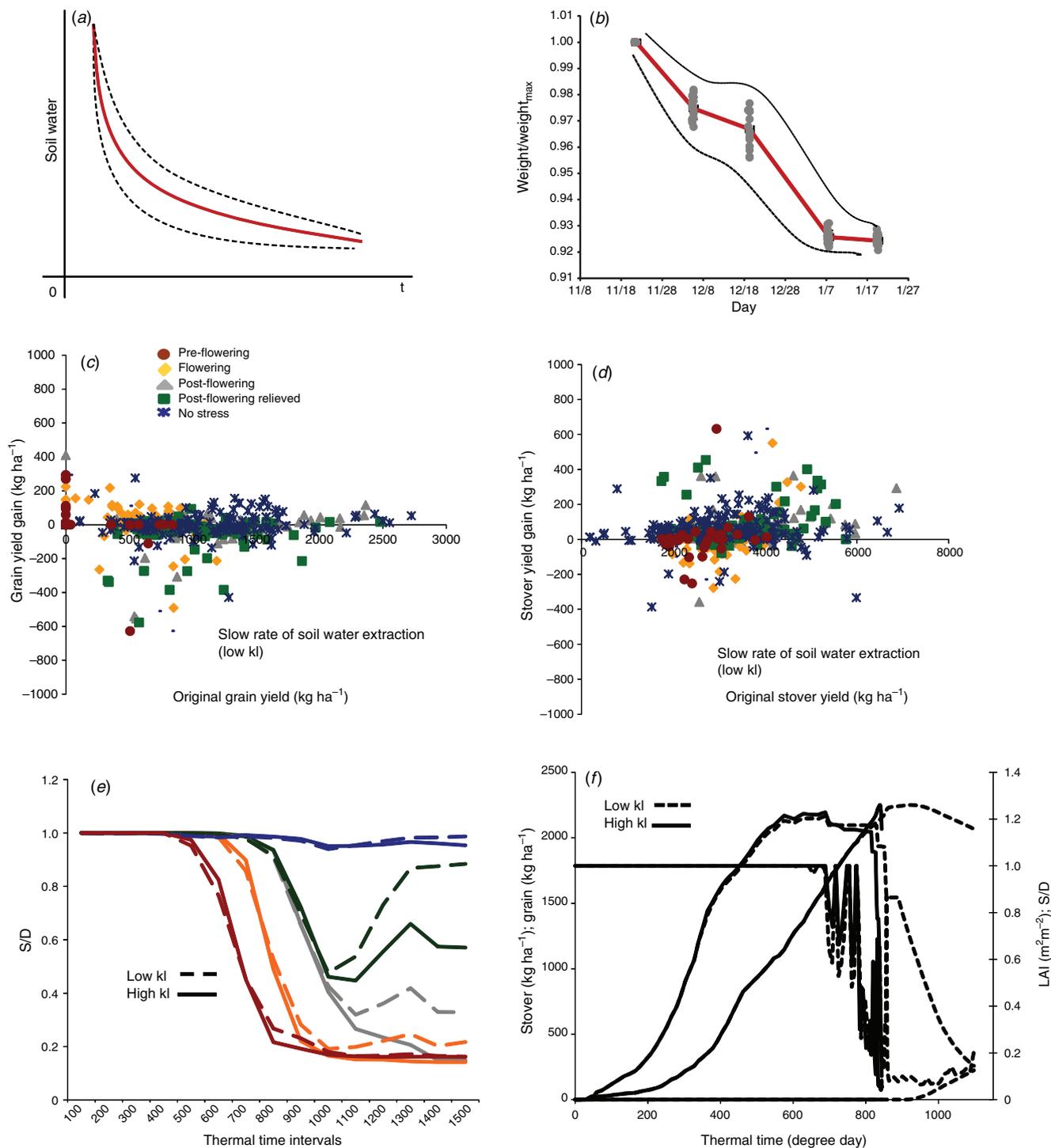


Fig. 5. Effect of soil water extraction in sorghum. (a) The original (red line) and altered (dashed lines) APSIM *kl* constant corresponding to (b) maximum variability in crop water extraction capacity in introgression lines (dashed lines) originating in R16 (red line). Simulation of the effects of decreased *kl* on (c) grain and (d) stover yield compared with the original yields of M35-1 (x-axes). (e) Effect of low or high *kl* in APSIM on water stress trajectories (water use patterns under the five water stress scenarios expressed by different line colours) for M35-1 and (f) dissection of the effects of low or high *kl* effect on crop growth parameters. S : D, water supply : demand ratio; LAI, leaf area index.

(Vadez *et al.* 2011), suggesting the involvement of different mechanisms in these S35 ILs and these were not investigated further here.

Simulation of soil water extraction rates

The APSIM *kl* constant determines the rate of soil water extraction as a function of soil moisture (Fig. 5a). It is an empirically derived coefficient representing a combination of soil–root hydraulic properties (*k*) and root length density (*l*) (Passioura 1983). Hence, it captures hydraulic limitation to water absorption by the crop. Apart from *kl* representing consequence of crop variability in root hydraulic conductance (Bramley *et al.* 2009; Sadok 2013; J. Kholová, M. Tharanya, S. Sakhti, unpubl. data), it can also reflect variations in root architecture (Manschadi *et al.* 2006). *Kl* and soil water content determine the potential supply of water to the crop for transpiration. This determines the crop water status via the transpiration supply : demand ratio, which drives the plant response factors that affect crop phenology, biomass production and LA development (Chapman *et al.* 1993; Hammer *et al.* 2010). Therefore, altering the *kl* coefficient simulates changes in the timing of water stress limitations on the crop. It was used here to mimic a possible change in root hydraulic conductance. The data on water extraction as a function of soil moisture from the ILs were fitted to changes in the *kl* coefficient ($kl = 0.07 \pm 0.01$ (~10%); Fig. 5; Table 1).

Canopy sensitivity to declining soil water and its simulation

Observed variability in responsiveness of leaf expansion to stress

A decline in leaf expansion at high soil moisture levels would save water and would potentially be an important plant feature for drought adaptation, although it would also restrict the plant leaf area and eventually light interception and biomass accumulation (Chenu *et al.* 2008, 2009). Here, the different ILs were grown in lysimeters during two seasons (2010–11 and 2011–12) and exposed to terminal drought as described earlier (Vadez *et al.* 2011). Several times during the advancing water stress, the canopy leaf area was nondestructively assessed (LA was equal to leaf length \times width \times 0.69). The genotypic variability in the response of leaf area development to soil drying was expressed by measuring the LA difference from a fully irrigated control after cessation of watering (Fig. 6b).

Simulation of responsiveness of leaf expansion to stress

The differences in the sensitivity of leaf expansion to drought were approached through alterations in the stress response coefficients (*sw_def_leaf*) of APSIM. The *sw_def_leaf* coefficients quantify the range of crop water status via the transpiration supply : demand ratio over which reduction in leaf growth is imposed. Therefore, a higher upper limit of this supply–demand window ($<0.1; 1.2>$), instead of the standard window ($<0.1, 1.0>$), would slow down leaf growth sooner (e.g. at higher soil moisture). This range in the *sw_def_leaf* coefficients was assessed from the ILs measured behaviour and its variation estimated ($<0.1; 1 \pm 0.2>$ ($\pm 20\%$); Fig. 6).

Statistical analysis

Transpiration rate response to VPD was analysed via a broken linear model using GENSTAT (VSN International, Hemel Hempstead, UK) and visualised using GraphPrismPad ver. 6.1 (GraphPad Software, San Diego, CA, USA). Canopy development parameters (i.e. leaf size and leaf appearance) were analysed using a two-way randomised block ANOVA (with leaf numbers and weekly leaf counts as blocks; Table 2) across seasons and genotypes to illustrate the influence of season, genotype and genotype \times season interactions. We further used a one-way block ANOVA to analyse the genotypic differences of leaf appearance within the season and the effect of season within genotype (Tables 3, 4).

Simulation outputs were analysed within the stress scenarios defined by Kholová *et al.* (2013). This work is intended to assist sorghum breeding programs in which the final economic value of the trait is of central importance. Therefore, a preliminary attempt was made to estimate the economic value of each mechanism for each stress pattern, in order to explore economic trade-offs, knowing that the usual stover price is around one-third (worst quality) to half (best quality) of the grain price. In this study, we used an average fixed price of ₹15 per kg for grain and ₹5 per kg for stover (Directorate of Marketing & Inspection 2014). These results are summarised in Table S1 but are not discussed in detail.

Results

Leaf area growth dynamics and its simulation

Observed variation in canopy parameters

The two-way ANOVA of three seasons of field data showed a significant effect of season and genotype on leaf size and a significant genotype \times season interaction effect (Tables 2, 3). Significant differences in the rates of leaf appearance between genotypes were also found (Table 4, Fig. 3b) and were accompanied by variation in flowering time ($\pm \sim 5$ days, data not shown). This variability was reflected in the derivation of APSIM coefficients.

Simulation of $TPLA_{max}$

A simulated smaller canopy size is predicted to improve yield in all water stress environments of the *rabi* tract except for the limited stress or unstressed scenarios (Table S1, Fig. 1c). At the same time, less canopy development decreased the expected stover yield across all stress scenarios (Table S1, Fig. 1d). Simulation of larger canopy size had the opposite effect on predictions of grain and stover production (Table S1). A smaller canopy size delayed the onset of stress in terminal stress scenarios (Fig. 1e). It also led to a grain yield advantage, which was caused by a delay in water exhaustion during the season. This shift in water usage also delayed leaf senescence and led to an expression of a virtual stay-green phenotype (Fig. 1f).

Simulation of plant vigour ($TPLA$ coefficients α and β)

Simulation of plants with high early vigour showed a grain yield penalty in all environments except in the unstressed scenario, but it led to higher stover production across all scenarios (Table S1). On the contrary, plants with low early vigour led to a mild grain yield production increase in all stress

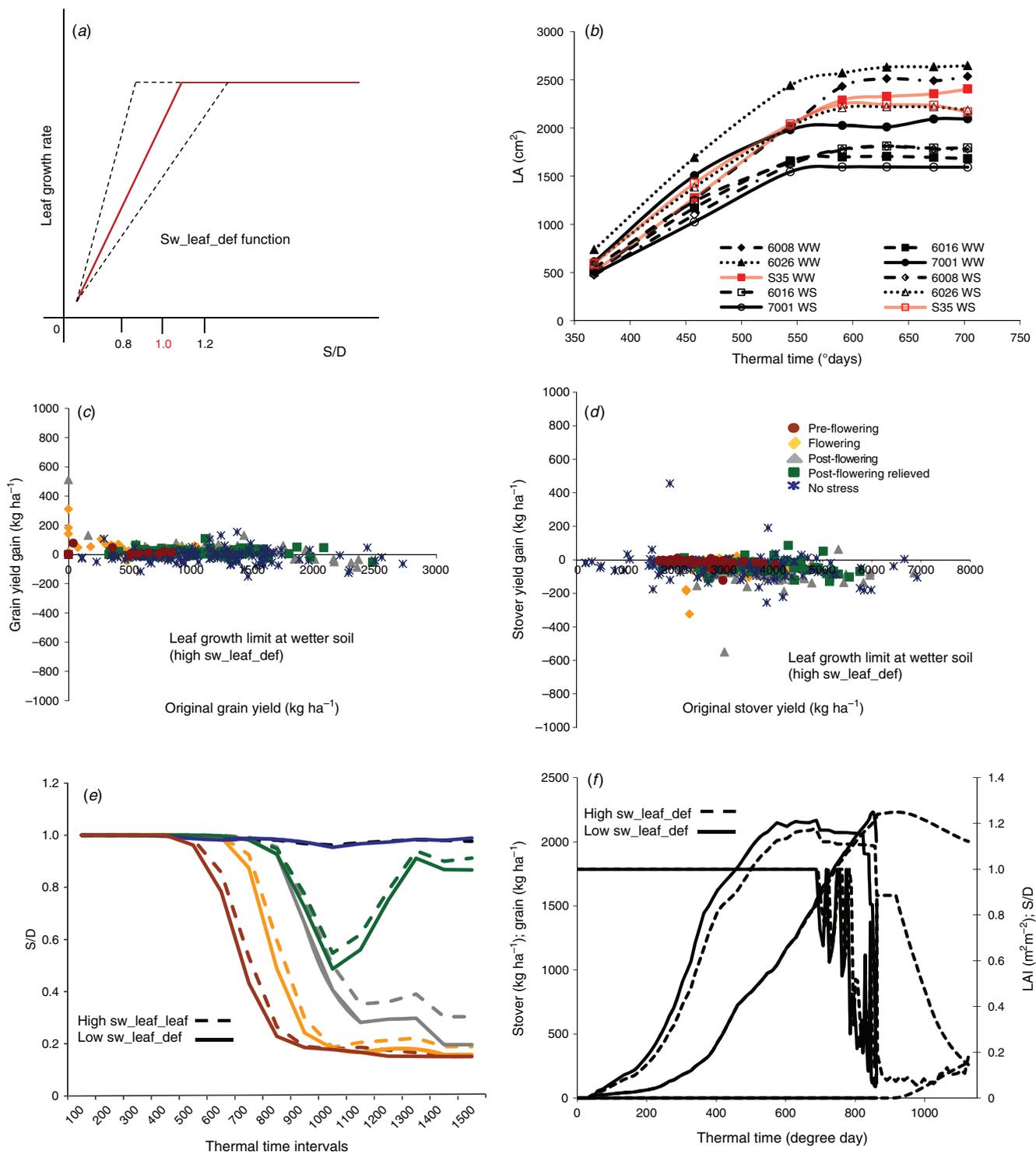


Fig. 6. Effect of leaf expansion stress response in sorghum. (a) The original (red line) and altered (dashed lines) APSIM *sw_leaf_def* interval and the maximum variability in leaf expansion upon exposure to drought in introgression lines (dashed lines) originating in S35 (red lines) and (b) the corresponding variability in leaf expansion upon exposure to drought. Simulation of the effect of the increased *sw_leaf_def* interval (i.e. crops limiting leaf growth in wetter soil) on (c) grain and (d) stover yield compared with the original yields of M35-1 (x-axes). (e) Effect of expanded or shortened *sw_leaf_def* interval in APSIM on stress trajectories (water use patterns under the five water stress scenarios) for M35-1 and (f) dissection of the effects of expanded or shortened *sw_leaf_def* interval on crop growth parameters. S : D, water supply : demand ratio; LA, leaf area; WW, well-watered; WS, water stressed; LAI, leaf area index.

Table 2. Overall evaluation of genotypic, seasonal and genotype × season effects on average leaf size of two senescent sorghum genotypes (R16 and S35) and stay-green QTL introgressed lines descended from R16 (i.e. K359w) and S35 (i.e. 7001)

The table shows the significance of the differences among the seasons across genotypes, significance of differences between genotypes across the seasons and significance of season × genotype interactions. *** means the significant at $P < 0.001$

Genotype	Effect of season	Effect of genotype	Effect of season × genotype
R16 and K359w (2010–13)	***	***	***
S35 and 7001 (2010–13)	***	***	***

scenarios, except the unstress scenario, accompanied by a mild loss in stover production in all environments (Table S1; Fig. 2c, d). This also led to water conservation, as in the case discussed above (Fig. 2e, f). Overall, altering the TPLA inflection coefficient and the production ratio had only mild effects on the evolution of the stress patterns (Fig. 2e, f), and very small effect on grain and stover yield (Fig. 2c, d), although it appeared to increase yield stability (Table S1).

Simulation of phyllochron (Leaf Appearance Rate 1 and 2)

Simulations of longer crop duration via longer phyllochron intervals decreased grain yield in all stress scenarios, although it

Table 3. Evaluation of genotypic and seasonal effects on average leaf size of two senescent sorghum genotypes (R16 and S35) and stay-green QTL introgressed lines descended from R16 and S35

Lines 7001, 6008, 6026 and 6040 originated from S35; lines K359w, K260, K648 and K606 originated from R16. The table shows the average leaf size for each of three seasons (2010–2012), total LA in brackets and the significance of the differences among the seasons and genotypes. Different letters mean significant differences according to the Tukey–Kramer test; the respective LSD values are also displayed. LA, leaf area; NE, not estimated; ***, significant at $P < 0.001$

Genotype	Effect of season	Average leaf size (total LA, cm ²)			Difference among seasons			LSD for season	Difference among genotypes		
		2010–11	2011–12	2012–13	2010–11	2011–12	2012–13		2010–11	2011–12	2012–13
S35	***	118 (1291)	200 (2453)	180 (1955)	c	a	b	8.0	a	b	b
7001	***	110 (1190)	207 (2349)	152 (1551)	c	a	b	8.0	b	b	cd
6008	***	–	202 (2136)	162 (1622)	–	a	b	7.0	–	b	c
6026	***	–	237 (2728)	197 (2134)	–	a	b	8.0	–	a	a
6016	NE	–	–	142 (1579)	–	–	–	–	–	–	d
6040	NE	–	–	125 (1367)	–	–	–	–	–	–	e
LSD for genotype	–	–	–	–	–	–	–	–	5.0	6.3	8.7
R16	***	175 (1770)	218 (2530)	148 (1537)	b	a	c	8.0	a	a	b
K359w	***	166 (1807)	219 (2559)	173 (1818)	b	a	b	8.3	b	a	a
K260	NE	–	205 (2528)	–	–	–	–	–	–	b	–
K648	NE	–	–	140 (1446)	–	–	–	–	–	–	C
K606	NE	–	188 (2165)	–	–	–	–	–	–	c	–
LSD for genotype	–	–	–	–	–	–	–	–	5.9	6.6	7.4

Table 4. Evaluation of genotypic effects on average leaf number of two senescent sorghum genotypes (R16 and S35) and stay-green QTL introgressed lines descended from R16 and S35

Lines 7001, 6008, 6026 and 6040 originated from S35; lines K359w, K260, K648 and K606 originated from R16. The table shows the average leaf number for each of three seasons (2010–2012), total leaf number in brackets and the significance of the differences among the genotypes. Different letters mean significant differences according to the Tukey–Kramer test; the respective LSD values are also displayed. LA, leaf area; NE, not estimated

Genotype	Average number of expanded leaves (maximum leaf no.)			Difference between genotypes		
	2010–11	2011–12	2012–13	2010–11	2011–12	2012–13
S35	8.1 (14)	9.3 (16)	9.9 (14)	b	b	b
7001	8.4 (14)	9.4 (16)	9 (14)	a	b	d
6008	–	9.4 (15)	10.2 (14)	–	b	a
6026	–	9.7 (16)	9.6 (14)	–	a	bc
6016	–	–	9.5 (14)	–	–	c
6040	–	–	9.4 (14)	–	–	c
LSD for genotype	–	–	–	0.18	0.19	0.21
R16	8.8 (14)	10.3 (14)	9.3 (14)	b	a	b
K359w	9.1 (14)	9.8 (16)	9.8 (14)	a	b	a
K260	–	9.7 (16)	–	–	b	–
K648	–	–	9.2 (14)	–	–	b
K606	–	10 (16)	–	–	b	–
LSD for genotype	–	–	–	0.14	0.21	0.18

increased stover yield to a similar magnitude except for in the preflowering stress scenario (Table S1). Shortening the phyllochron interval and therefore crop duration substantially increased the predicted grain yield, although it decreased stover production (Fig. 4c, d; Table S1). Here, the estimated decrease in stover yield (in kg ha⁻¹) was of a smaller magnitude than the gain in grain yield. In the most severe stress scenarios, the shorter duration crop exhausted water resources faster. However, it improved water use after anthesis in less severe stress scenarios (Fig. 3e). Under severe stress, the crops with shorter phyllochron intervals had a larger part of their preflowering phase taking place under no stress conditions, compared with the crop with a longer phyllochron (Fig. 3f). The crops with a short phyllochron has grown the LA earlier and also exhausted the available water and senesced before the crops with a longer phyllochron. Thus, in this specific case, the differences relate to avoiding water limitation at critical stages rather than water conservation.

Limited maximum TR and soil water extraction rate, and their simulation

Observed variation in limits on maximum TR

The rates of transpiration upon exposure to a range of VPD conditions varied between the senescent parental lines and the ILs especially within the ILs in the R16 background, with either higher or lower TR than R16 (Fig. 4b). There was little variation among ILs in the S35 background (data not shown) and therefore the variation within R16 ILs was used to guide the modelling of these effects.

Simulation of limits on maximum TR

Setting the limits on the TR by ~10% in M35-1-generated crops with a high probability of increasing both the grain and stover yields across all stress scenarios (Fig. 4c, d). This implies that, in contrast to all the other traits tested in this paper, the limited transpiration trait did not involve production trade-offs between grain and stover but increased overall water productivity (TE). The lowest yield gains were predicted within the unstressed scenario. Limiting the maximum TR in the severe stress scenarios restored yield due to improved water use after anthesis, in several cases where there was otherwise a crop failure. However, the delay in the onset of stress due to the limited TR was small compared with other traits (Fig. 4e) but was sufficient for expression of the stay-green phenotype (Fig. 4f).

Observed variability in the soil water extraction rate

Reanalysis of data from Vadez *et al.* (2011) showed substantial genetic variability in the rates of water extraction especially in R16-derived ILs (Fig. 5b). This variability was estimated to be in the range of \pm ~10% from the reference senescent parental line (R16) and justified further simulation analysis.

Simulation of soil water extraction rate

The virtual M35-1 crop with lower water extracting capacity at declining soil moisture (lower *kl*) realised a modest increase in stover yield in most of the stress scenarios but maintained

similar grain yield levels (Table S1; Fig. 5c, d). However, there was large variability in the *kl* effect under particular stress scenarios (Fig. 5c, d). The plants with a lower *kl* entered the water stress slightly earlier but were able to extend the duration of water availability (due to a simultaneous slow-down in biomass accumulation). This was especially notable in the scenarios of stress imposed after flowering and relieved stress after flowering (Figs 4, 5). Also, in the severe stress situation, the low-*kl* crop had slightly improved TE by limiting supply to the crop. So, although limitations in root extraction generated slightly early stress onset, they resulted in an extended period for which growth was maintained, which would contribute to the improved crop resilience and potential for stay-green expression (Fig. 5f).

Canopy sensitivity to declining soil water and its simulation

Observed variability in responsiveness of leaf expansion to stress

Upon stopping irrigation at 5 weeks after sowing, most of the ILs restricted their leaf expansion upon exposure to soil drying, whereas their respective senescent parents developed similar LA as they did in the fully-irrigated treatment (Fig. 6b shows variability in S35 ILs, although there was a similar range of variability in R16 ILs).

Simulation of responsiveness of leaf expansion to stress

The simulated slow-down of leaf expansion in drier soil (broadening the *sw-leaf-def* interval) had little effect on yield across all environments, whereas it increased stover productivity across all environments (Table S1; Fig. 6c, d). Generally, a crop with a decline in leaf expansion in wetter soil slightly postponed the onset of stress and improved water extraction during the grain filling stage, especially in the case of the intermittent stress scenario (Fig. 6e). Furthermore, the crops restricting leaf expansion in wetter soil, under severe water stress, had a higher grain yield than crops with a decline in leaf expansion decline in drier soil (Fig. 6c-f). The failure of the crop with decreased leaf expansion in drier soil could be explained by its enhanced biomass accumulation during the early stages of growth and larger leaf area development followed by a restricted period of water use after anthesis which can therefore also lead to earlier senescence (Fig. 6f). In any case, different sensitivities of leaf expansion to stress had only small effects on grain and stover yield.

Economic value of traits

The proportion of various stress scenarios differs within the *rabi* sorghum production zones (defined in Kholová *et al.* 2013); therefore, the importance of the traits for use in breeding programs should be weighted accordingly. Initial insights into the putative breeding value of the investigated traits (and some of their combinations) within production zones are shown in Table S1 but the data are not discussed.

Discussion

In this work, we have built up on previous modelling that characterises of stress environments across major *rabi*

sorghum production zones (details in Kholová *et al.* 2013) to assess the effect of traits related to the plant water budget on grain and stover yield. Several traits postponed the onset of stress and increased water use after anthesis, which is phenotypically expressed as delayed leaf senescence and led to a virtual stay-green phenotype, although other traits also affected TE. Maintenance of green leaf area generally led to improved grain productivity, although, in most scenarios, an increase in grain productivity was counterbalanced by a decrease in stover productivity and *vice versa*. The improvement of both grain and stover productivity was possible only through improvement of plant water productivity (TE) and was a result of simulating a restricted crop TR under high VPD. From a breeding point of view, a decreased TR under high VPD would be the most worthwhile strategy for crop drought adaptation improvement. Apart from a reduced TR, any other way of improving stover productivity would increase the risk of grain yield failure and *vice versa*; an increase in grain productivity was feasible only in crops with suppressed stover production. In short, we identified a set of physiological processes leading to the expression of the stay-green phenotype across the *rabi* sorghum belt that could improve grain and stover yield and their stability under current management practices. This knowledge allows us to construct crop ideotypes for particular locations, according to the proportion of stress scenarios and according to farmers' specific demands (for either stover or grain).

Observed variability in traits affecting plant water use

Introgression of stay-green QTLs led to either lower or higher canopy size in ILs. However, significant genotype \times season interactions, especially between earlier (October 2011–12) and later plantings (November 2010–11 and 2012–13), indicated that variability in photoperiod or temperature sensitivity could have affected canopy development (e.g. Bos and Neuteboom 1998; Kim *et al.* 2010a, 2010b; van Oosterom *et al.* 2011). Leaf expansion is also known to be sensitive to VPD (e.g. Reymond *et al.* 2003; Welcker *et al.* 2007) and VPD differences across season could have also affected the canopy development. Therefore, more work is needed to more thoroughly assess how VPD could have altered the leaf development coefficient, and also to develop the necessary loops in APSIM to reflect genetic differences in these effects. In addition, various ILs from both backgrounds (R16 and S35) limited leaf expansion upon soil drying, pointing to a genetic mean of modulating leaf area if drought prevails during the vegetative stages. Additional work is therefore needed to properly characterise how VPD and soil moisture affect the leaf canopy development across the different stay-green QTL introgressions.

There is much research describing the genotypic variability in canopy conductance under high VPD, related, in some cases, to the hydraulic properties of plant tissues (e.g. Fletcher *et al.* 2008; Bramley *et al.* 2009; Devi *et al.* 2010; Kholová *et al.* 2010a, 2010b; Gholipour *et al.* 2010) and resulting in differences in crop water use (e.g. Vadez *et al.* 2014). There are also modelling exercises predicting benefits of limited crop hydraulics in water-limited environments (Sinclair and Hammer *et al.* 2005; Manschadi *et al.* 2006; Sinclair *et al.* 2010). Here, we have documented that QTL introgressions indeed influence

plant canopy water conductivity and reduced or enhanced TR, especially under high VPD, although this was specific to the R16 background. This observation confirms that a given physiological mechanism may not be simply transferable to all genetic backgrounds and may depend on the genetic context of the recurrent parent (similarly in Vadez *et al.* 2011). In addition to these, differences in soil water absorption capacity were found among the ILs. Whether these were related to the differences in TR is unknown. In other studies, differences in TR were, in fact, linked to the difference in soil water absorption capacity (e.g. Bramley *et al.* 2009; Sadok 2013). In any case, our observations showed that stay-green QTLs could alter the rate of water loss by the canopy, or the rate of water absorption by the roots.

Traits affecting plant water use can lead to water saving and the stay-green phenotype

Altering of the canopy development parameters in APSIM altered stress patterns and led to the expression of a stay-green phenotype. Grain yield improvement in the water stress scenarios came from constitutive water conservation during vegetative growth via reduced canopy size during the entire growth period or particular phases of growth. An exception was the alteration of the phyllochron, resulting in different crop durations. In this case, in the severe stress scenario, the short-duration crop senesced and exhausted the water earlier but also escaped drought with a larger portion of its preanthesis period taking place under unstressed conditions. Thus, in this particular case the stay-green expression was linked to a long-duration genotype with less grain yield produced at the end of the season. This shows clearly that the stay-green phenotype under drought and plant canopy development are closely linked and the current APSIM model is adequate to mimic these relationships. Surprisingly, these relations between canopy development and stay-green were not seriously explored until quite recently (Hammer 2006; van Oosterom *et al.* 2011; Borrell 2013; Vadez *et al.* 2014). In fact, only a few reports on sorghum experimentally documented similar effects of canopy development (phyllochron, tillering) on crop production (van Oosterom *et al.* 2010a, 2010b; Borrell 2013).

Lower canopy TR under high VPD conditions and low rates of soil water extraction also led to stay-green expression in the severe water limited environments. In these two cases, stay-green expression in the crops also appeared to be linked to saving the water in the soil profile but to a lesser extent compared with crops with altered canopy growth (see above). In the case of low TR, the amount of water saved depended on the VPD throughout the day and the benefit mostly came from an increased TE rather than from a shift in water use before and after anthesis.

Canopy growth traits resulted in grain–stover production trade-offs

Alteration in the plant canopy traits saved water and increased yield, especially in the severe scenarios, but it resulted in trade-offs between grain and stover productivity, depending on the stress scenario. Also, increased soil water extraction rates (high *kl*) of the crop improved stover accumulation but resulted in a trade-off with grain production, similar to the case of manipulating the canopy parameters. To use these traits in

breeding, the crop grain and stover production benefits from canopy-related mechanisms would need to be weighted by the frequencies of a particular stress scenario in the target location so as to maximise the economic gains (as shown in Table S1). Our results indicate that particularly large economic gains (large gains in grain yield compared with minute stover yield losses) can come from shortening the crop duration (short phyllochron intervals) or from developing a smaller canopy size. The easiest and most effective breeding target should be the optimisation of crop duration within the production zones, upon which other traits can be further built. We also showed that generally, crops with higher stover productivity increase their chances of grain yield failure in severe stress environments. Therefore, our findings can be used not only to weight the production benefits but also leave the choice to the farmers themselves. If the current demand requires farmers to produce more biomass (e.g. as cattle fodder) with marginal interest in grain or *vice versa*, we could tailor or recommend the crop type that fits these particular needs. Additionally, the differences in canopy growth and development may also impact the grain and stover yield quality, which would affect the grain and stover prices (Blümmel and Rao 2006) but this variability has not yet been characterised sufficiently.

Restriction of TR under high VPD and lower soil water extraction rate improve TE, and grain and stover production

In contrast to canopy growth traits, which always led to trade-offs between grain and stover productivity, lower TR improved stover and grain production at the same time across most of the stress scenarios and so is expected to have high economic potential. This was possible only because the low TR crop had enhanced TE. The benefit for grain yield did not come only from a mere shifting in plant water use from before to after anthesis.

Decreased soil water extraction capacity (through *kl*) generated crops with a high variability in production benefits or losses within the particular stress scenario and had no major effect on the average crop production. Nevertheless, crops with lower soil water extraction capacity have the potential to enhance TE, which seems to improve the crops' resilience under severe stress scenarios. This is because reducing the roots' *kl* coefficient mimics a plant that enters more quickly into water stress but can maintain growth for longer (with increased TE at low soil moisture levels). Here again, the alteration of the *kl* coefficient was chosen as a means of altering root hydraulic conductance. However, the APSIM structure is such that altering the *kl* coefficient has other 'pleiotropic' effects on other plant development aspects and we would suggest that further work is needed in APSIM to improve the water capture loops in order to sensibly reproduce the crop variability presented here.

Conclusions

In this work, we demonstrated *in silico* that the variability in the traits and processes related to plant water use (canopy development, capacity of the canopy and root to conduct water and the canopy development response to water stress) improved grain yield and led to stay-green expression as a consequence of increased water availability after anthesis. Improvements in

grain yield showed negative stover production trade-offs but improved crop production stability across years. Simultaneous improvement of grain and stover yield along with crop resilience was possible only through enhancing water productivity (TE) and was the result of imposing limits on canopy transpiration under high VPD (TR). Therefore, this study provides a range of tools for constructing of zone- and demand-specific crop ideotypes that may be considered in breeding schemes. More work is underway to assess how alteration in management practices could affect stay-green expression, water use patterns and crop production. The present work provides a solid base to investigate these genotype \times management interactions further.

Acknowledgements

The authors acknowledge support from the CGIAR Research Program on Dryland Cereals, the Research Program on Climate Change, Agriculture and Food Security, and the Australian Center for International Agriculture Research (CIM-2007–120), which have supported some of the research activities presented in this article.

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