

SHORT COMMUNICATION

EXPLORING PROCESS-LEVEL GENOTYPIC AND ENVIRONMENTAL EFFECTS ON SUGARCANE YIELD USING A GLOBAL GROWTH ANALYSIS EXPERIMENTAL DATASET

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Introduction

Crop models have potential to assist sugarcane breeding by identifying desirable traits for target environments. Suitable crop models are strongly process-based, where complex trait values emerge as a consequence of process-level interactions with genotypic (G) (represented by G-specific model parameters) and environmental (E) control (represented by climate, soil/nutrient and management inputs) (Hammer and Jordan, 2007). Several sugarcane crop models, which represent our understanding of sugarcane plant processes, are available, e.g. DSSAT-Canegro (Singels *et al.*, 2008; Jones and Singels, 2018), Mosicas (Martine *et al.*, 1999), APSIM-Sugar (Keating *et al.*, 1999) and Canesim (Singels and Donaldson, 2000). These – and their underlying process-level concepts – need to be evaluated for breeding applications.

The objective was to evaluate existing concepts (as embodied in crop models) of G and E control of plant processes for explaining crop development, growth and yield using a global growth analysis dataset. The approach was to analyse G and E variation in phenotypic development and growth parameters and relate these to yield differences.

Methods and Materials

Experiments

Cultivars N41, R570 and CP88-1762 were grown in five 12-month unstressed experiments, at four sites: a first ratoon (R1) crop at La Mare on Reunion Island (France) harvested January 2017; plant (P) crop at Pongola, South Africa, harvested March 2015; P and R1 crops at Belle Glade, Florida, USA, harvested January 2015 and January 2016; and an R1 crop at Chiredzi, Zimbabwe, harvested June 2016. Adequate fertiliser was applied to ensure no nutrient limitations on growth.

Measurements of total leaf number per shoot (tagged shoots, TLFN (leaves/shoot) and shoot population (2 m row length, were conducted frequently. Destructive samples (of 18 m²) were taken at 3-month intervals to determine above-ground dry biomass (ADM, t/ha) and stalk dry mass (SDM, t/ha). Canopy fractional interception (FiPAR, %) of photosynthetically-active

radiation (PAR, MJ/m²) was measured using ceptometers. Solar radiation (SRAD, MJ/m²), air temperature, rainfall and relative humidity were recorded at nearby stations to characterise Es. More detail is available on the International Consortium for Sugarcane Modelling (ICSM) website (<https://sasri.sasa.org.za/agronomy/icsm/>).

Data analysis protocols

Thermal time (TT) is a key concept that describes the strong effect that temperature exerts over many plant processes. It is temperature within the effective range, integrated over time. Cumulative thermal time (TT10 and TT16 with base temperatures of 10°C and 16°C respectively) was calculated as described by Jones and Singels (2018).

Along with observed phenotypic parameters (ADM and SDM), experimental data were used to assess physiological concepts embodied in the following phenotypic parameters, per G and E (fully described in Jones *et al.*, 2019):

- The duration of the germination phase is determined by thermal time (TT10) from crop start to primary shoot emergence (TT_EM50, °Cd), and was derived from shoot population observations.
- Tiller appearance rate (TAR, shoots/°Cd) is driven by thermal time, as determined by TT16 from primary shoot emergence, and was derived from shoot population observations.
- Leaf appearance rate is driven by thermal time, with the leaf phyllochron interval (PI, °Cd) defined as the TT10 between successive leaves, and was derived from leaf number observations.
- Canopy development rate is driven by thermal time, as quantified by TT16 from primary shoot emergence to 50% canopy cover; this parameter (TT_Fi50, °Cd) was derived from FiPAR observations.
- Well-watered biomass yields are determined by intercepted radiation (IntPAR, MJ/m²) and maximum radiation use efficiency (RUE_{max}, g/MJ), derived from ADM, FiPAR and SRAD observations.
- Well-watered stalk yield is determined by (1) the onset of stalk growth, as determined by TT10 from primary shoot emergence, (TT_OSG, °Cd), and (2) the fraction of biomass growth partitioned to stalks (STKPF, t/t), which were derived from ADM and SDM observations. La Mare data had to be excluded for the STKPF calculation.

Analysis of variation

For each phenotypic parameter *p*, the coefficient of variation of *p* with E (Ecv) was quantified as the standard deviation of E means (averaged over Gs), divided by the overall mean (averaged over Es), expressed as a percentage. Where Ecv for some *p* exceeded 25%, that was taken as an indication of strong E impact, indicating model concept shortcomings relating to simulating E effects, e.g. that *p* is in fact dependent on E, or that more E variables and G parameters may need to be taken into account when driving a plant process.

Similarly, the coefficient of variation of *p* with G (Gcv) was quantified as the standard deviation of G means (averaged over Es), divided by the overall (averaged over Gs) mean value, expressed as a percentage. The G ranking of *p* per E was calculated by ordering *p* from highest to lowest and assigning an ordinal value (1-3). The variation in G rankings (GRcv, %) was quantified as the standard deviation of average G rankings across Es, divided by the mean G ranking, expressed as a percentage. G impacts were considered strong when Gcv exceeded 8% and GRcv exceeded 25%. High Gcv and consistent G rankings (high GRcv) indicate G control over the related plant process(es) (and a need for G-specific parameters in

models); while high Gcv or Ecv, with inconsistent G rankings (low GRcv), indicates unresolved GxE interaction effects.

Results and Discussion

Final yields (Table 1) showed significant E variation, highest in La Mare and lowest in Pongola. Cultivar rankings in yield varied significantly in Es.

Table 1. Final (at harvest) above-ground dry mass (ADM, t/ha) and stalk dry mass (SDM, t/ha), per experiment and cultivar.

Experiment	N41	R570	CP88-1762	Average
	ADM			
La Mare, R1	68.3	71.2	56.4	65.3
Pongola, P	43.4	35.9	38.4	39.2
Belle Glade, P	41.9	52.3	62.4	52.2
Belle Glade, R1	34.7	46.6	48.1	43.1
Chiredzi, R1	45.8	45.7	50.0	47.2
Average	46.8	50.3	51.1	49.4
	SDM			
La Mare, R1	43.6	42.7	34.5	40.3
Pongola, P	32.9	26.3	28.8	29.3
Belle Glade, P	34.3	39.9	52.2	42.1
Belle Glade, R1	29.7	35.1	42.0	35.6
Chiredzi, R1	29.8	28.8	33.7	30.8
Average	34.1	34.6	38.2	35.6

Differences in average ADM between Es were significant, and could be linked to climatic parameters. For example, La Mare R1 (highest ADM) had 38% greater TT10 and 20% greater SRAD than Pongola P (lowest ADM). Canopy development therefore occurred more rapidly and more incoming radiation was intercepted for La Mare R1 than Pongola P. La Mare R1 also had a higher average RUEmax than Pongola P, probably due to a more favourable temperature regime (24.8 compared to 21.7°C).

GxE interaction in ADM was significant, and G rankings changed with E. For example, N41 yielded higher than CP88-1762 in La Mare R1, but yielded lower in Belle Glade R1. This could be explained by differences in FiPAR and RUEmax. A notable difference between these Es is the average range in daily temperature, with Belle Glade R1 at 10.3 compared to 7.4°C for La Mare R1. CP88-1762 may be better adapted to the larger temperature range than N41.

G variance in SDM was significant. CP88-1762 yielded highest and N41 lowest. This coincided with a higher RUEmax, a quicker canopy (TT_Fi50) and earlier OSG (TT_OSG).

These investigations demonstrate that yield differences between G and E can be linked to genotypic differences in process responses to environmental factors.

Table 2. Coefficient of variance (%) of phenotypic parameter values. Gcv indicates variation in mean values across three cultivars (N41, R570 and CP88-1762); Ecv indicates variation in mean values across experiments. Mean G rankings and coefficient of variation (%) in rankings are also shown.

Parameter	Mean value	Units	Rankings					
			E cv	G cv	N41	R570	CP88-1762	G Rank cv
TT_EM50 (P crops)	419	°Cd	34.2	10.5	1.5	2.0	2.5	25.0
TT_EM50 (R1 crops)	345	°Cd	39.4	37.8	1.7	2.7	1.7	28.9
PI	138	°Cd/leaf	15.5	8.7	1.6	3.0	1.4	43.6
TAR	0.027	shoots/°Cd	51.6	16.4	2.4	2.0	1.6	20.0
TT_Fi50	352	°Cd	19.8	10.3	2.5	2.3	1.3	33.1
RUEmax	3.11	g/MJ	18.8	6.9	1.5	2.0	2.5	25.0
TT_OSG	911	°Cd	39.2	6.9	2.6	2.0	1.4	30.0
STKPF	0.83	t/t	2.8	1.6	2.3	2.0	1.8	12.5
ADM	49.4	t/ha	20.4	4.6		1.8	2.4	17.3
SDM	35.6	t/ha	15.8	6.4	2.0	1.6	2.4	20.0

For P crops, strong E variation in TT_EM50 (Table 2) was evident, suggesting that the TT concept (based on air temperatures) is not sufficient for capturing differences between Es. TT_EM50 was lower for P crops started in autumn (when soils can be warmer than air), and vice versa for spring starts. R570 required greater TT_EM50 than other cultivars at cooler sites, indicating a higher base temperature requirement for TT accumulation (consistent with Poser *et al.*, 2019). TT for TT_EM50 should be based on soil rather than air temperatures, and related base temperatures should be G-specific.

High Gcv and Ecv values for TAR confirm that there is significant G control over tillering/shoot population traits, but suggest that TT is not an adequate basis for predicting shoot population (challenging conventional understanding of TT as the sole driver of unstressed tillering, e.g. Bezuidenhout *et al.*, 2003; Keating *et al.*, 1999; Singels, 2013). TAR was strongly correlated ($p < 0.01$) with photo-thermal quotient (Nix (1976)); a simple proxy for source-sink balance, calculated as the ratio of solar radiation to TT accumulation) for unstressed crops, hence tillering models should additionally include an SRAD response.

Low Ecv, moderate Gcv and high GRcv for PI confirm that PI is strongly G-controlled (Bonnet, 1998 and Inman-Bamber, 1994) with minimal E and GxE interaction influences.

G variation in TT_Fi50 for the common Gs is considered strong, and the rankings are sufficiently consistent (relatively high GRcv) to indicate G control over this trait. Models that predict canopy size from TT directly should support G-specific parameters.

RUEmax rankings were identical at Belle Glade R1 and La Mare R1, for five Gs. This, combined with moderate G variation for common Gs at unstressed Es, and the strong GRcv, makes a compelling case for RUEmax being G-specific.

TT_OSG is not G-specific, but it is clear that TT alone is insufficient for predicting OSG. A strong negative relationship between SRAD and TT_OSG was noted, and it is recommended that this is investigated for inclusion in crop models for improving SDM predictions. This may also make it possible to isolate G differences that are confounded by GxE interactions with the TT_OSG concept.

This study provides compelling evidence (low Gcv and Ecv) that under well-watered conditions, STKPF is stable across Gs and Es.

Conclusion

E and GxE variation in ADM and SDM yields at final harvest could be explained in terms of E effects (such as temperature and SRAD differences) and phenotypic process parameters (such as RUEmax, TT_Fi50 and TT_OSG).

Significant E variation (Ecv) was observed for phenotypic parameters TT_EM50, TAR and TT_OSG, indicating model concept weaknesses. Soil temperature is proposed as a more accurate driver of germination than air temperature, while SRAD seemed to influence tillering rate per unit TT, as well as TT_OSG.

Significant G variation was found for TT_EM50, PI, TT_Fi50, and RUEmax, indicating strong G control of these processes.

This study has identified opportunities for improved model concepts that have the potential to explain more E variation, and hence support the definition and evaluation of more stable and accurate G-specific model parameters. This may lead to less GxE confounding of modelled processes, and hence crop models that are better-equipped for supporting sugarcane breeding.

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