IDENTIFYING QUANTITATIVE TRAIT ALLELES FOR PHYSIOLOGICAL TRAITS IN SUGARCANE: AN EXPLORATORY STUDY

By

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Abstract

THIS STUDY attempted to shed light on the feasibility of high throughput phenotyping of physiological traits and the detection of quantitative trait alleles (QTA) for these traits. Stalk elongation rate per unit thermal time before and after the 14 leaf stage (SER_{14} and SER_{24}), leaf appearance rate per unit thermal time (LAR_{14} and LAR_{24}), fully expanded leaf area per leaf (LA) and photochemical light use efficiency (PI_{ABS}) were measured for 80 clones of a mapping population in three experiments conducted at Mount Edgecombe, South Africa. Within-experiment clonal repeatability was highly significant for all traits. Inter-experiment correlations show that SER_{24}, LA and PI_{ABS} were reasonably stable across experiments. Significant single marker-trait associations were found for all traits and multiple marker-trait associations explained from 39% (six QTAs to predict LAR_{24}) to 55% (five QTAs to predict SER_{24}) of clonal variance. However, the low number of markers detected in all three experiments cast doubt on the reliability of marker-based predictions for LAR_{14}, LAR_{24} and SER_{24}. Results indicate that LA and PI_{ABS} were reasonably stable across environments and can be predicted reliably from genomic information. PI_{ABS}, as estimated through rapid, non-destructive chlorophyll *a* fluorescence measurements, in particular shows great promise because it has the potential for high throughput phenotyping at an early stage in the plant life cycle. The promising results obtained here suggest that further research is warranted in refining experimental protocols and validating marker-trait associations in other germplasm and environments. This could pave the way to explore the exciting possibilities that gene-to-phenotype modelling offers for enhancing sugarcane breeding.

Introduction

Crop yield is a complex trait governed by numerous dynamic interactions between plant processes and environment and management factors. Accelerated improvement in plant performance is only likely when these interactions and the underlying physiological mechanisms and genetic basis are better understood. Crop simulation models take some of these interactions into account by simulating the impact of physiological processes such as plant growth rate, leaf appearance rate, leaf size and photosynthetic capacity. Models therefore have the potential to identify trait sets that are most likely to enhance yields in target environments (Hammer *et al.*, 2006).

In parallel, genetics have determined genetic markers or quantitative trait loci (QTL) for various traits. This information can be used to better understand processes and interactions that contribute towards yield, and to enhance breeding (Hammer and Jordan, 2007) For sugarcane, QTLs have been detected for sucrose content (Ming *et al.*, 2001; Aitken *et al.*, 2006; Aitken *et al.*,

2008), stalk mass and number (Ming *et al*., 2002; Hoarau, *et al.*, 2002; Aitken *et al*., 2008) and stalk length and stalk diameter (Hoarau *et al*., 2002; Aitken *et al*., 2008). These studies all focused on complex yield component traits rather than simple physiological traits related to yield formation processes of resource capture, resource conversion and biomass partitioning. It is believed that despite the genetic influence on yield and its components, there are strong environmental impacts that will make it difficult to detect stable QTLs.

An alternative approach is to define simple, genetically determined, physiological traits and detect stable QTLs for these. Crop models can then be used to simulate the integrated effect of many of these traits in a given environment and thereby identify desirable ones. Sadok *et al*. (2007) speak of 'analysing the behaviour of virtual genotypes in silico for large number of environmental scenarios'. Once the ideotype has been identified, the genomic information could be used for rapid screening of genotypes for crossing or selection. Chenu *et al.* (2008) gave an excellent example of incorporating a QTL based physiological trait module into the APSIM maize model to accurately predict growth of individual leaves and whole crop response to environmental stresses. The model is based on the work by Sadok *et al*. (2007) and Reymond *et al.* (2003). They found that maize leaf elongation rate per unit thermal time, when normalised with respect to vapour pressure deficit (VPD) and soil water potential, were genetically determined and that genotype values could be predicted reliably from QTL information.

In sugarcane, it has been shown that stalk elongation rate per unit thermal time is genetically determined to a large extent (Smit and Singels, 2007). There is also evidence that leaf size and leaf elongation rate show large and consistent genotypic variation (Bonnet, 1998; Robertson *et al.*, 1998). However, little genetic and phenotypic information on these traits are available for the wide range of genotypes in existence.

This study attempted to shed light on the feasibility of high throughput phenotyping of physiological traits and the detection of quantitative trait alleles (QTA) for the following physiological traits namely, leaf appearance rate per unit thermal time (LAR), stalk elongation rate per unit thermal time (SER), fully expanded leaf area per leaf (LA), and photochemical light use efficiency (PI_{ABS}). These traits were selected based on (1) their importance in determining resource capture and yield formation, (2) the presence of these or similar traits in crop models (3) ability to derive trait values from experimental measurements, and (3) the expected extent of genetic determination.

The specific objectives were to (1) determine the phenotyping repeatability of these traits, (2) identify genetic markers that can be associated with each trait, and (3) determine the reliability of predicting trait values from genetic marker information.

Methods

Mapping population

A population of 80 sugarcane clones, derived from the South African Sugarcane Research Institute (SASRI) breeding program, were mapped using linkage disequilibrium methods (Butterfield *et al.*, 2008). The map consists of 2054 AFLP and DArT markers arranged on 492 haplotype fragments.

Experiments

Three field experiments (T1, T2, T3) were conducted at Mount Edgecombe ($29^{o}42$'S, $31^{o}03$'E) on a sandy clay loam soil covered with a trash blanket to discourage tillering. Plants were adequately fertilised and irrigated. T1 and T2 have been described by Singels *et al.* (2009). In T1, five setts of each clone were planted in each of four replicates in May 2006. In T2, setts were germinated in vermiculite in a germination chamber at 30^{o}C and transplanted into the field between 29 May and 7 June 2007, when a seedling height of around 10 cm was reached. The number of plants per replicate and number of replicates were the same as in T1. In T3, the germination

chamber and a heated glasshouse were used to manipulate early development of clones to further improve synchronisation of development stage and planting date. Planting in the field took place from 14 to 30 October 2008 and eight setts of each clone were used as individual replicates. In all experiments, secondary tillers were removed as soon as they were visible and only healthy plants were measured.

On a weekly basis, the emergence date of the youngest fully expanded leaf (top visible dewlap (TVD) leaf) was estimated and numbered (starting from the base), and the leaf length and width recorded together with the TVD collar height from ground level. SER for each plant was taken as the slope of the regression of TVD height vs. thermal time. LAR for each plant was taken as the slope of the regression of number of fully expanded leaves vs. thermal time. A distinction was made between the phase between leaf number 8 and 14 (denoted by LAR_{14} or SER_{14}), and the phase between leaf number 15 and 24 (denoted by LAR_{24} or SER_{24}). Leaf area per leaf (LA) was taken as the average of the fully expanded area (estimated as leaf length x leaf width x 0.71, Sinclair *et al*., 2004) of leaf number 15 to 24. Due to limited manpower and changes in measurement protocol, the number of plants and replications that were measured for some traits varied.

Photochemical light use efficiency of TVD leaves was only determined in T2 and T3 by recording fast polyphasic chlorophyll *a* fluorescence transients (Strasser and Govindjee, 1992) at night with a fluorimeter (Plant Efficiency Analyser , Hansatech Instruments Ltd., UK). Four measurements were taken in the mid-section of each TVD leaf on three plants of each clone in each replication (total of 48 measurements per clone). The recorded chlorophyll *a* fluorescence data were used to calculate the Performance Index (PI_{ABS}), which is a sensitive indicator of photosynthetic electron transport efficiency and photosynthetic capacity (Strasser *et al*., 2000).

Photosynthetic gas exchange measurements were conducted on three clones that represented groups of clones that displayed consistently high, intermediate and low PI_{ABS} values (i.e. high, intermediate and low photochemical light use efficiency). Measurements were conducted with a portable photosynthesis system (Li-Cor 6400, Lincoln, NE, USA) on attached TVD leaves. Measurement of CO_2 assimilation rate (A) were taken at incident photon flux (Q) levels of 0, 50, 75, 100, 125, 200, 400, 800, 1500 and 2000 µmol/m^2/s provided by an LED light source (LI-6400-02) at an atmospheric CO_2 concentration (c_a) of 400 µmol/mol. Leaf temperatures in the leaf chamber were maintained at 25ºC and vapour pressure deficits at 1.3 kPa.

Daily maximum and minimum temperature were recorded throughout all three experiments by a nearby automatic weather station and was used to calculate thermal time using a base temperature of 16^{o}C.

Data analysis

Clonal repeatability (CR – the ratio of genetic variance to phenotypic variance) was determined from an analysis of variance for each experiment separately. The stability of phenotypic measurements was further assessed by determining the correlation between values of a given trait measured in different experiments.

The average value for each trait for each clone in each experiment was calculated from values for individual plants. Data were pooled over experiments by calculating the average of all values over all plants of a given clone. Correlations between traits were determined by comparing the pooled average trait values.

Association between trait values and marker presence or absence was determined for each experiment separately, using the Pearson's correlation coefficient. A significance level of P=0.05 was chosen. Stepwise linear regression was then used to select markers ascribing maximum phenotypic variation for each trait. This was done using the pooled average trait value for each clone. Selection for markers was limited to those that had significant marker-trait associations in at least two of the three trials. The prediction error (PE) was taken as the standard error of the regression, expressed as a percentage of the observed range in values of each trait.

Responses of A to Q were fitted with the aid of non-linear regressions. The maximum apparent quantum yield of photosynthesis (ϕ) was determined from the linear response of A to Q that persisted between 50 – 400 µmol/m^2/s (Long & Hällgren, 1993). The CO_2 assimilation rate at a Q of 2000 µmol/m^2/s was regarded as the light saturated rate of CO_2 assimilation (A_{sat}). The calculated values of ϕ and A_{sat} were used to establish in the three selected clones to what extent differences in photochemical light use efficiency (deduced from PI_{ABS} values) translated into differences in overall CO_2 assimilation capacity.

Results

Clonal repeatability

CR was significant (P = 0.001) for all traits in all experiments and exceeded 0.9 in all cases, except for LAR_{14} in T1 and T2, LAR_{24} in T2 (Table 1). The range of values is similar to that obtained by Aitken *et al*. (2008) and Hoarau *et al*. (2002) for yield component traits. Correlations between trait values from different experiments (Table 2) show that most traits were reasonably stable across experiments, with the exception of LAR_{14}, LAR_{24} and possibly SER_{14}. These correlations were also generally in the same range than those reported by Aitken *et al*. (2008). The results suggest that all traits except LAR and possibly SER_{14} are likely to be genetically determined and can be phenotyped with reasonable accuracy.

Table 1—Clonal repeatability for different traits in the three experiments.

Trait	T1	T2	T3
LAR_{14}	0.80	0.65	0.73
LAR_{24}	0.90	0.88	0.54
SER_{14}	0.95	0.96	0.89
SER_{24}	0.93	0.89	0.87
LA	0.95	0.99	0.95
PI_{ABS}		0.96	0.92

Table 2—Correlations between values determined in different experiments for each trait.

Trait	T1 x T2	T1 x T3	T2 x T3
LAR_{14}	0.323	0.559	0.471
LAR_{24}	0.607	.565	0.324
SER_{14}	0.676	0.327	0.774
SER_{24}	0.556	0.638	0.579
LA	0.657	0.864	0.882
PI_{ABS}			0.729

Screening of a large number of genotypes for physiological traits will be more useful for breeding programs when the method of phenotyping is quick and can be conducted at an early development stage of the plant. It would be useful, therefore, to determine the correlation between measurements made before leaf stage 14 and thereafter. When trait values were pooled over experiments, significant correlations were found between traits LAR_{14} and LAR_{24} (0.645), SER_{14} and SER_{24} (0.467), LA_{14} and LA_{24} (0.908). It seems that screening for leaf area before leaf stage 14 could be feasible.

Link between CO_2 assimilation capacity and photochemical light use efficiency (PI_{ABS})

The extent by which differences in photochemical light use efficiency translated into differences in overall CO_2 assimilation capacity was determined in clones 2, 60 and 79. These clones had PI_{ABS} values that were respectively 49% and 0.5% higher and 43% lower than the average PI_{ABS} value for all 80 clones, thus representing high, intermediate and low PI_{ABS}. This analysis revealed that values

for A_{sat} and ϕ corresponded with the relative positions of the three clones according to PI_{ABS}. For example, clone 2 (highest PI_{ABS}) had A_{sat} and ϕ values respectively 39% and 52% higher than in clone 79 (lowest PI_{ABS}), while clone 60 (intermediate PI_{ABS}) had values respectively 20% and 14% higher than in clone 79.

Marker-trait associations

The phenotypic variation accounted for by genetic markers and the reliability of marker-based predictions are given in Table 3. The number of markers detected in all three experiments was considerably lower than the number detected in any two experiments, especially for traits LAR_{14}, LAR_{24}, SER_{24}, suggesting that some of these detections may be false. These results highlight the necessity of multi-experiments for true marker detection and for the need for more precise phenotyping.

The multiple marker-trait associations determined for all traits were promising, with R^2 values 0.4 or more, and PE values of 15% or less. The strongest single marker-trait associations explained between 14.3 and 25.3% of the phenotypic variance, which compares well with values reported by Aitken *et al.* (2008) and Aitken *et al.* (2006).

Table 3—Number of markers with significant correlations with trait values in all three experiments, in two out of three experiments and the highest number of markers detected in any one experiment; the number of markers selected in the stepwise multiple regression to predict the trait value, the coefficient of determination for the regression, the highest and lowest R^2 contribution from individual markers to the regression, and the prediction error (PE)between predicted and observed trait values.

	Single marker-trait associations			Multiple marker-trait associations				
Trait	Markers detected in 3 exp	Markers detected in 2 exp	Markers detected in 1 exp	Markers in regression	R^2	Highest individual R^2	Lowest individual R^2	PE (%)
LAR_{14}	4	42	148	5	0.460	.156	.057	12.3
LAR_{24}	1	48	97	6	0.392	.143	.019	12.9
SER_{14}	29	123	165	5	0.553	.174	.045	14.3
SER_{24}	7	56	118	3	0.425	.253	.041	13.7
LA	63	144	185	4	0.521	.193	.086	15.3
PI_{ABS}		57	165	5	0.42	.171	.081	13.6

Discussion

Results suggest that LA and PI_{ABS} are reasonably stable across environments and can be predicted reliably from genomic information. PI_{ABS}, as estimated through rapid, non-destructive chlorophyll *a* fluorescence measurements, in particular shows great promise because it has the potential for high throughput phenotyping at an early stage in the plant life cycle. At least in the three clones on which detailed measurements of CO_2 assimilation capacity were conducted, a strong agreement between photochemical light use efficiency and overall CO_2 assimilation capacity (which is most probably an important contributor to high biomass and sucrose yields) was clearly demonstrated.

Observations of stalk elongation and leaf appearance traits were not that repeatable and marker-based predictions were not sufficiently reliable. Possible reasons could be inappropriate sampling techniques or problems with experimental procedures. For example, it was very difficult to synchronise all clones to reach the same developmental stage at the same time. In T2 and T3, germinating setts were initially exposed to artificial environments for different time periods to achieve this. Pests (monkeys, thrips) and disease (pokka boeng) also affected some plants.

Unreliable marker-based predictions could also be due to insufficient separation of genetic and environmental aspects in the trait definition. For example, Robertson *et al.* (1998) found that

temperature affected LA and Smit and Singels (2007) found that genetic control of SER was confounded by site and season effects. Reymond *et al*. (2003) showed that SER in maize was controlled by soil water potential and atmospheric VPD. In our study, we tried to eliminate soil water status as a source of variation. The impact of VPD on observed SER still needs to be investigated.

The promising results obtained here suggest that further research is warranted in refining experimental protocols and validating marker-trait associations in other germplasm and environments. This could pave the way to explore the exiting possibilities that gene-to-phenotype modelling offers for enhancing sugarcane breeding.

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IDENTIFICATION DES ALLÈLES À EFFET QUANTITATIF POUR DES CARACTÈRES PHYSIOLOGIQUES DE LA CANNE À SUCRE: UNE ÉTUDE EXPLORATOIRE

Par

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MOTS CLÉS: Trait Quantitatif, Élongation de la Tige,
Apparition de la Feuille, Capacité de Photosynthèse,
Modèle de Croissance, Variance Phénotypique.

Résumé

CETTE ÉTUDE explore les possibilités du déterminisme phénotypique haut débit des caractères physiologiques et la détection des allèles à effet quantitatif (QTA) pour ces traits. Le taux d'élongation des tiges par unité thermale de temps avant et après le stade 14-feuille (SER_{14} et SER_{24}), la vitesse d'apparition de la feuille par unité thermale de temps (LAR_{14} et LAR_{24}), l'expansion totale de la surface foliaire (LA) et l'efficience de l'utilisation photochimique (PI_{ABS}) ont été mesurés sur 80 clones caractérisés moléculairement à partir de trois essais à Mount Edgecombe, Afrique du Sud. La répétitivité clonale intra-essai était hautement significative pour tous les traits. Les corrélations inter-expérimentation ont montré que SER_{24}, LA et PI_{ABS} étaient raisonnablement stables à travers les expérimentations. Des associations significatives de marqueurs-traits simples étaient observées pour tous les caractères alors que les associations des marqueurs-multiples expliquent entre 39% (six QTAs pour prédire LAR_{24}) à 55% (cinq QTAs pour prédire SER_{24}) de la variance clonale. Cependant, le nombre restreint de marqueurs détectés dans les trois expérimentations émet des doutes quant à la fiabilité des prédictions basées sur les marqueurs associés à LAR_{14}, LAR_{24} et SER_{24}. Les résultats indiquent que LA et PI_{ABS} sont raisonnablement stables à travers les environnements et peuvent être prédites avec fiabilité à partir de l'information génomique. La PI_{ABS}, estimée à partir des mesures rapides et non-destructives de fluorescence de chlorophylle *a*, est prometteuse en particulier car elle démontre un potentiel pour le phénotypage à haut débit à un stade précoce du cycle de la plante. Les résultats prometteurs obtenus suggèrent que davantage de recherche est nécessaire pour raffiner les protocoles expérimentaux et valider les associations marqueurs-traits chez d'autres sources de germoplasme et dans d'autres environnements. Ceci pourrait préparer le terrain pour une exploration des possibilités excitantes qu'offre la modélisation gène-phénotype dans l'amélioration de la canne à sucre.

IDENTIFICANDO ALELOS CUANTITATIVOS PARA CARACTERES FISIOLÓGIOS EN CAÑA DE AZÚCAR: UN ESTUDIO EXPLORATORIO

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PALABRAS CLAVE: Caracteres Cuantitativos, Alargamiento del Tallo, Apariencia de Hoja, Capacidad Fotosintética, Variación Fototípica.

Resumen

ESTE ESTUDIO ha intentado clarificar sobre la posibilidad de un sistema eficiente de determinación de caracteres fenotípicos fisiológicos y su detección de alelos de caracteres cuantitativos (QTA). La tasa de alargamiento del tallo por unidad de tiempo termal antes y después de la hoja 14 (SER14 y SER 24), apariencia de la hoja por unidad de tiempo termal (LAR 14 y LAR 24), área de la hoja expandida totalmente por hoja (LA) y eficiencia fotoquímica en el uso de la luz (PI_{ABS}) se midieron en 80 clones de las poblaciones en mapeo en tres experimentos realizados en Mount Edgecombe, Sur África. La repetitividad clonal dentro de los experimentos fue altamente significativa para todos los caracteres. Las correlaciones entre experimentos mostraron que SER_{24}, LA y PI_{ABS} fueron razonablemente estables a lo largo de los experimentos. La asociación simple entre carácter-marcador fue significativa para todos los caracteres y la asociación múltiple entre marcador-carácter se explica desde 39% (seis QTAs para predecir LAR_{24}) a 55% de la variación clonal (cinco QTAs para predecir SER_{24}). Sin embargo, el bajo número de marcadores detectados en los tres experimentos dejan dudas en la relatividad de las predicciones basadas en marcadores para LAR_{14}, LAR_{24} and SER_{24}. Los resultados indican que LA y PI_{ABS} fueron razonablemente estables en los experimentos y se puede predecir con confianza desde la información genética. El PI_{ABS}, como un estimado rápido, de medida de la clorofila *a* mediante fluorescencia, en particular, se muestra promisorio para clasificar fenotípicamente en estados tempranos del ciclo de vida de la planta. Estos resultados promisorios obtenidos aquí sugieren que se justifican otros estudios para que garanticen los protocolos experimentales y la validación de la asociación marcador-carácter en otros germoplasmas y ambientes. Esto podría preparar el terreno para explorar la posibilidad de que modelos existentes gen-a-genotipo ayuden a fortalecer los programas de mejora genética.