

PHYSIOLOGICAL PARAMETERS FOR MODELLING DIFFERENCES IN CANOPY DEVELOPMENT BETWEEN SUGARCANE CULTIVARS

MM ZHOU¹, A SINGELS² and M J SAVAGE³

¹*Zimbabwe Sugar Association Experiment Station, P/Bag 7006, Chiredzi, Zimbabwe*

²*South African Sugar Association Experiment Station, P/Bag X02, Mount Edgecombe, 4300, South Africa*

³*University of Natal, Pietermaritzburg, P/Bag X01, Scottsville, 3209, South Africa*

Abstract

For crop models to be used as an aid to plant improvement programmes, they should adequately represent cultivar traits. Biomass production depends on photosynthetically active radiation (PAR) intercepted by the canopy. Canopy development depends on the production and senescence of tillers and leaves on tillers, processes that are controlled mainly by temperature and PAR. Cultivar traits could be simulated by physiological parameters where these are stable across environments, show significant differences between cultivars and have physiological meaning. Our aim was to quantify cultivar control of canopy development by defining key physiological parameters and determining the values for these in sugarcane cultivars ZN6, ZN7, N14 and NCo376 grown in Zimbabwe. The parameters studied were thermal time requirements for shoot emergence, leaf and tiller appearance, surface area and leaf number of the youngest biggest leaf, PAR transmission at the start of tiller senescence and PAR extinction coefficient. The potential use of a new phyllochron reference point as a cultivar parameter is discussed. Cultivar ZN7 had the highest and NCo376 the lowest rate of leaf emergence. Cultivar N14 had the largest and NCo376 the smallest leaves. Low stalk population cultivars ZN6 and ZN7 initiated tiller senescence at higher levels of transmitted PAR than higher population cultivars N14 and NCo376. Results indicated that cultivars with higher tiller production rates were more efficient in capturing PAR. The importance of traits such as leaf size and canopy architecture was secondary.

Keywords: sugarcane, canopy, modelling, tiller population, leaf area, thermal time

Introduction

The ability of simulation models to predict growth and development can make them attractive tools for crop improvement (White, 1998). Appropriate models could assist breeders in understanding genotype by environment interaction by mimicking the genetic characteristics of plants. Crop models have been used to hypothesize ideal genetic traits in soybeans, groundnuts and cotton (Boote *et al.*, 1996). However, more insight into morphological development will be needed for application of the models in breeding programmes (Boote *et al.*, 2001). A serious shortcoming in some models is their inability to adequately represent cultivar traits. For example, the CANEGRO sugarcane model is based on data from the NCo376 cultivar only (O'Leary and Kiker, 2000). It accounts for differences in leaf size and leaf appearance, but has limited capacity for simulating cultivar differences in tiller development. A need exists to test the suitability of and expand the number of parameters that describe cultivar traits.

Biomass production is dependent on the amount of photosynthetically active radiation (PAR) intercepted by the crop canopy (Singels and Donaldson, 2000; Cock, 2001). The ability of models to accurately predict yields of different cultivars may depend largely on accurate descriptions of the canopy.

Canopy development comprises the production and senescence of tillers and leaves on tillers, and these processes are controlled by environmental factors (mainly air temperature and PAR). Environmental control is cultivar specific. Cultivar traits that regulate the response of canopy development could be simulated by physiological parameters.

The basic requirements for variety parameters to be useful for simulating cultivar response to environment are that:

- the value should be stable across environmental conditions
- significant difference in the value should exist between cultivars
- parameters should have some physiological meaning.

The objective of this work is to quantify cultivar control of canopy development by defining key physiological parameters and determining the values for these in selected cultivars grown in Zimbabwe. Aspects of canopy development that will be addressed are leaf and tiller phenology and canopy architecture. The influence of these on crop canopy formation and interception of PAR will be investigated in cultivars ZN6, ZN7, N14 and NCo376.

Materials and Methods

Hypothesis

The canopy is made up of leaves carried on tillers, and its development occurs through different phenological phases (King *et al.*, 1965). Shoot emergence from the ground is driven by temperature (van Dillewijn, 1952). Thermal time and PAR environment within the stool drive tiller appearance (Barnes, 1964; van Dillewijn, 1952). Tillers cease to appear after PAR transmission has decreased below a given threshold (Inman-Bamber, 1994). A given fraction of tillers survive after a period of tiller senescence (Barnes, 1964; Inman-Bamber, 1994). Leaf appearance is also driven by temperature (Inman-Bamber, 1994). The final area of leaves depends largely on the order in which they appear on the stalk (Hay and Walker, 1989). Initial leaves are small; leaf size increases and reaches a maximum after a given number of leaves have appeared on the tiller, and then leaf size remains constant for a period before decreasing (Inman-Bamber, 1991, 1994).

Temperature drives many of the processes responsible for canopy development. The effect of temperature is often quantified using the thermal time concept, with air temperature being the most convenient measure of temperature (Ong and Monteith, 1985). Thermal time is defined as the sum of all positive values of the mean daily temperature minus the base temperature. Base temperature is defined as the temperature below which the rate of a given process is zero (Campbell and Norman, 1998).

Canopy architecture also affects the interception of PAR. The extinction coefficient describes the transmission of PAR through the crop canopy according to Beer's Law ($L_i/L_o = 1 - e^{-k.LAI}$), where LAI is the leaf area index, k is the extinction coefficient, L_i is PAR intercepted by the crop and L_o is PAR incident at the top of the canopy (Monteith and Unsworth, 1990).

Parameters

All relationships are cultivar-specific, and parameters are required to describe the cultivar effect. These are proposed in Table 1.

Table 1. Description of proposed cultivar parameters.

Parameter name	Parameter description	Units
TTE	The thermal time from planting or ratooning to the emergence of 50% of potential shoots. Base temperatures of either 10 or 16°C were used	°C.day
TTL	Thermal time requirement (base 10°C) for the appearance of a leaf, called a phyllochron	°C.day
LAMAX	Surface area of the biggest leaf of an unstressed crop	cm ²
LNO	Leaf number of the youngest biggest leaf	Number
LTT	PAR transmission threshold for start of tiller senescence	Fraction
TTPT	Thermal time required to produce one tiller (base 16°C)	Number
TSR	The number of mature tillers at a thermal time of 1600 °C.day expressed as a fraction of the peak tiller population	Fraction
TTTP	Thermal time required to reach peak tiller population accumulated from emergence (base 16°C)	°C.day
<i>k</i>	PAR extinction canopy coefficient	

Inman-Bamber (1994) described the ‘broken stick’ approach to the phyllochron concept. Two phyllochron values are used. The first (TTL1) applies to all leaves that appear before a given leaf number and the second (TTL2) applies to all leaves that appear thereafter. The leaf number where the ‘stick’ breaks is called the phyllochron ‘switch’. TTL1 and TTL2 were determined as the inverse of the slope of a linear regression on leaf number versus thermal time (base 10°C) data. Data were divided into two lots using various leaf numbers as the cut-off. The leaf number that resulted in the best fit for the two regressions was taken as the phyllochron switch.

The thermal time per tiller was calculated as the thermal time required from emergence to peak tiller population divided by peak tiller population.

The extinction coefficient was calculated by solving for *k* in the Beer’s Law expression.

Experiment details

Data were collected from experiments at the Zimbabwe Sugar Association Experiment Station, Chiredzi, Zimbabwe (ZSAES, 21°01’S, 28°38’E, 430 m altitude). The experiments were conducted on a sandy clay loam soil and were furrow irrigated. Water stress was avoided, except during the first three weeks of February (between 108 and 126 days after planting) due to a labour strike. All the experiments were in their plant crop cycle.

Experiments 1 and 3 were replicated; experiment 2 was not. The designs for experiments 1 (five replicates) and 3 (three replicates) were randomised blocks. Experiment 1 was planted on 19 October 2001 (late season planting), experiment 2 on 20 March 2002 (early season planting) and experiment 3 on 6 July 2002 (mid-season planting). The crops were planted using two cane setts laid side by side in the bottom of the planting furrows and spaced 1.5 m apart. Single superphosphate fertiliser was applied in the furrow at a rate of 100 kg P₂O₅ per hectare before planting. Potassium was applied as muriate of potash at 60 kg K₂O/ha four weeks after emergence. Nitrogen was applied as ammonium nitrate at 140 kg N/ha, in split applications of 60 and 80 kg N/ha at four and eight weeks respectively, after emergence.

Measurements

Weather data were collected throughout the growing season from an automatic weather station and a manual station situated adjacent to each other at ZSAES.

Data on the emergence of planted eyes were collected from experiments 2 and 3. At planting, the total number of eyes in each plot was counted. The emerged shoots were counted daily until all cultivars had attained more than 50% emergence of planted eyes. Tillering was measured in experiment 1 only, using destructive sampling done every two weeks. The total number of tillers in one metre of row was counted from emergence until harvest.

Leaf development was recorded in experiment 1 only. Leaf emergence was recorded daily on five tagged stalks per plot. The areas of individual leaves on stalks were measured using a Delta-T leaf area meter (Delta-T, Cambridge, UK). The area of all leaves from 1,5 m² (1 running metre and 1,5 m spacing) was measured using the Delta-T leaf area meter and used to calculate LAI.

In Experiment 1, photosynthetic irradiance was measured above and at the bottom of the crop canopy between 11h00 and 14h00 using a SunScan ceptometer (Decagon services, Pullman, USA). This instrument measured photosynthetically active irradiance (400 to 700 nm).

Results

Shoot appearance

Cultivar N14 had the fastest rate of emergence in both experiments, and cultivar ZN6 the slowest (Table 2). The difference in TTE between the two experiments was least when using a base temperature of 16°C, suggesting that this was a more likely base temperature for shoot emergence.

Table 2. Thermal time to 50% shoot emergence of cultivars ZN6, ZN7, N14 and NCo376, using base temperatures of 10°C (TTE10) and 16°C (TTE16) for experiments 3 and 4.

Cultivar	TTE10 (°C.day)		TTE16 (°C.day)	
	E4	E3	E4	E3
ZN6	654.1	378.7	262.4	228.7
ZN7	566.8	351.0	219.1	213.0
N14	531.3	317.2	199.6	191.2
NCo376	586.2	378.7	228.4	228.7

Tiller appearance

High population cultivars N14 and NCo376 required much less thermal time to produce a tiller than low population cultivars ZN6 and ZN7 (Table 3). Cultivar ZN6, which reached peak tiller population later than the other cultivars, required the most thermal time per tiller.

The results show that there were significant differences in peak tiller populations between cultivars. The final tiller population (millable stalks) and peak tiller population were well correlated. Cultivar ZN6 had the lowest tiller survival rate and cultivar NCo376 the highest. Generally, the tiller survival rate appeared to be similar in all four cultivars.

The PAR transmission threshold for initiating tiller senescence was lower in the high population cultivars N14 and NCo376 than in the low population cultivars ZN6 and ZN7. Variety ZN7, with the least stalk population, had the highest threshold (Table 3).

Table 3. Peak and final tiller populations, thermal time to peak tiller population, thermal time per tiller, tiller survival rate and light transmission threshold at start of tiller senescence for cultivars ZN6, ZN7, N14 and NCo376.

Cultivar	Peak tillers (m ⁻²)	Final tillers (m ⁻²)	Thermal time to peak tiller population (°C.day)	Thermal time per tiller (°C.day)	Tiller survival rate	PAR transmission threshold
ZN6	18.27	11.33	873.1	47.79	0.62	0.313
ZN7	15.07	9.73	576.3	38.24	0.65	0.447
N14	24.80	16.40	743.6	29.98	0.66	0.253
NCo376	26.53	18.13	774.4	29.19	0.68	0.251

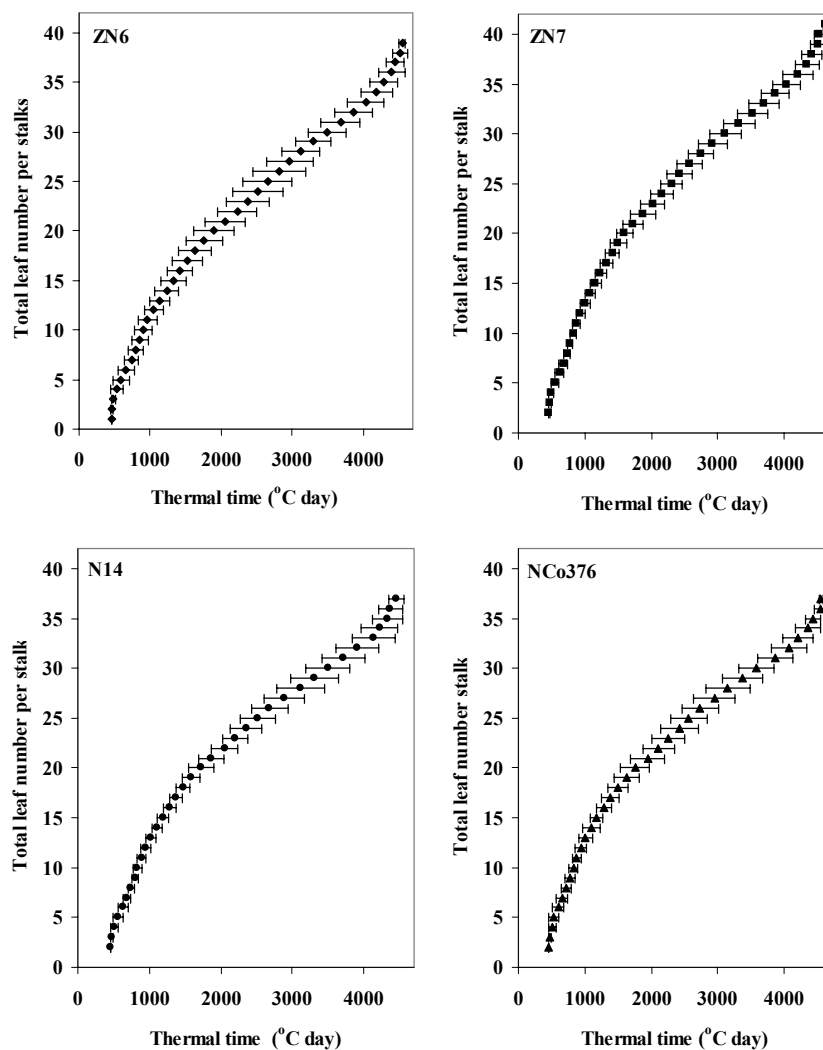


Figure 1. Total leaf number per stalk in relation to thermal time with base temperature of 10°C for cultivars ZN6, ZN7, N14 and NCo376. The horizontal bars denote one standard deviation.

Leaf appearance

Leaf appearance as a function of thermal time is shown in Figure 1. Results suggested that the conventional 'broken stick' approach to the phyllochron concept (Inman-Bamber, 1994) would not adequately explain leaf appearance. The phyllochron intervals increased with each successive leaf and, after reaching a peak, decreased with subsequent leaves (Figure 2). The maximum phyllochron and the leaf number where this maximum occurs could be considered as a reference point for future modelling of leaf appearance. From Figure 2, it would appear that cultivars ZN6 and ZN7 have faster rates of leaf appearance (higher phyllochrons) than cultivars N14 and NCo376.

Results for the 'broken stick' approach to the phyllochron concept are given in Table 4. Inman-Bamber (1994) reported a higher value for TTL1 (109 °C.day) and a lower value for TTL2 (169 °C.days) for a ratoon crop of cultivar NCo376 than the values arrived at in this study.

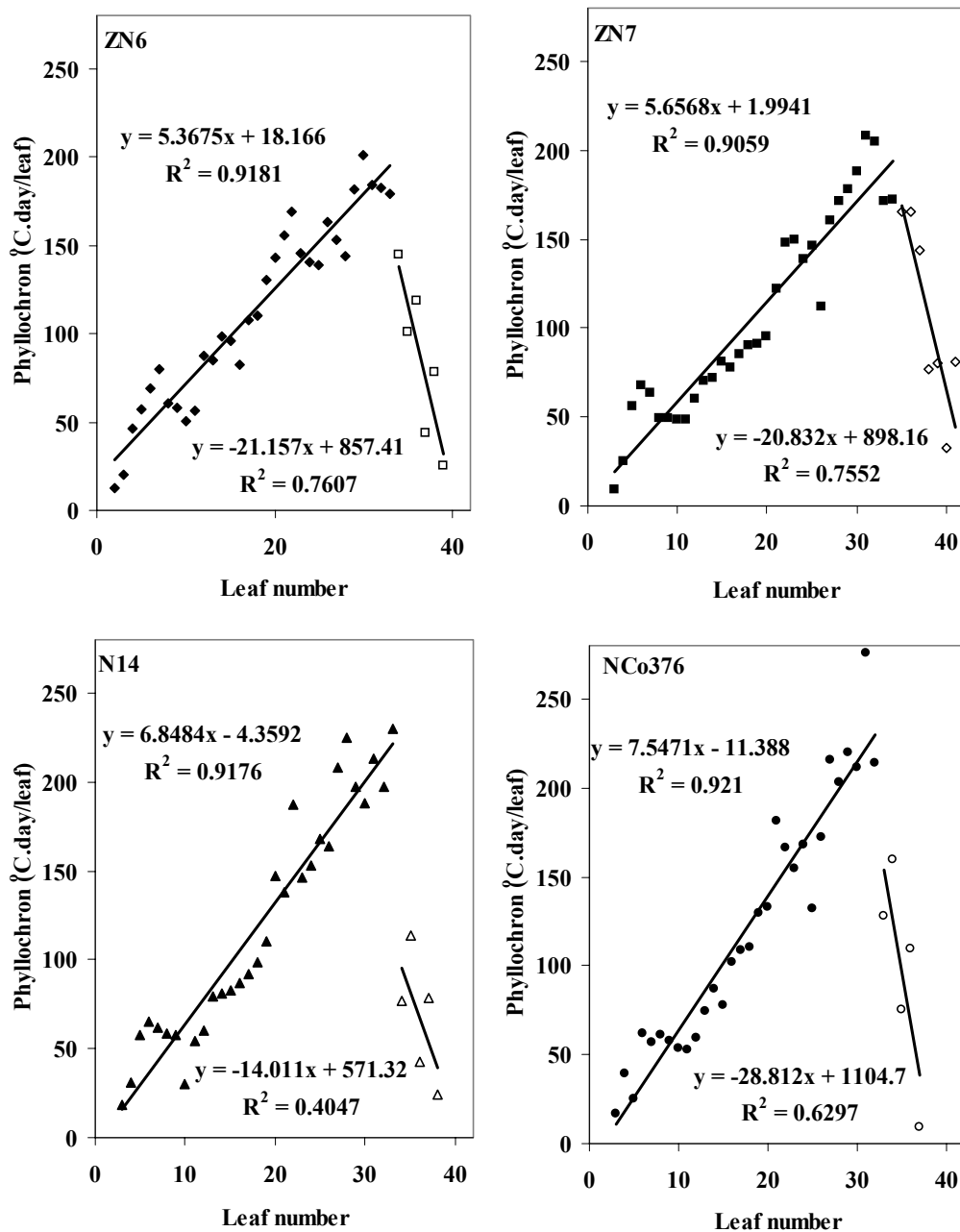


Figure 2. Phyllochron for each leaf for cultivars ZN6, ZN7, N14 and NCo376.

Table 4. Parameters for the ‘broken stick’ phyllochron concept of leaf appearance and properties of the biggest leaf for cultivars ZN6, ZN7, N14 and NCo376. Thermal time (base 16°C) to appearance of the biggest leaf was calculated from time of 50% shoot appearance.

Cultivar	Phyllochron switch (leaf no.)	Phyllochron 1 (°C.day)	Phyllochron 2 (°C.day)	Leaf number	Maximum leaf area (cm ²)	Thermal time to appearance of the biggest leaf (°C.day)
ZN6	21	99.01	185.19	16	422.7	641.6
ZN7	20	70.92	172.41	18	409.6	671.1
N14	17	68.03	188.68	18	457.8	724.6
NCo376	18	77.52	200.00	15	355.3	506.1

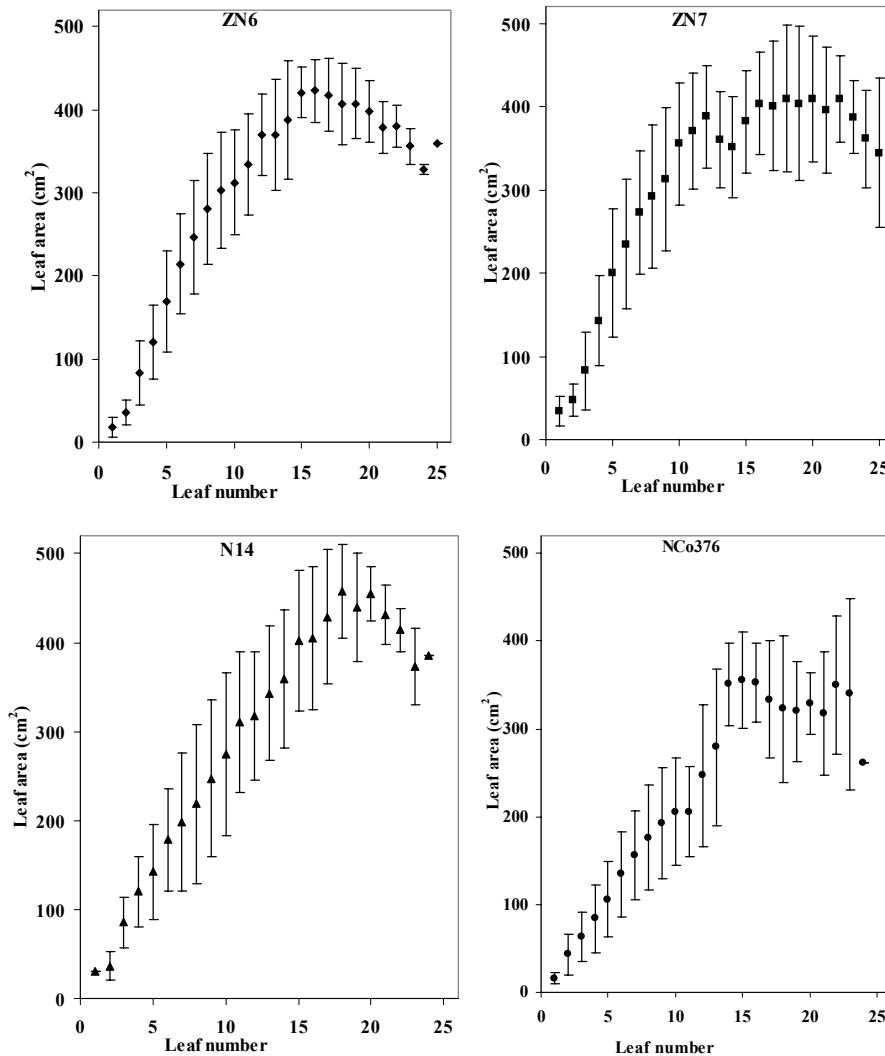


Figure 3. Leaf area (cm²) of successive leaves on stalk for cultivars ZN6, ZN7, N14 and NCo376. The vertical bars denote one standard deviation.

Leaf size

Mature leaf area increased with each successive leaf on the stalk until it reached a maximum, and then decreased (Figure 3). There were significant differences between cultivars in leaf area of the biggest leaf, and the leaf number that attained the maximum area (Table 4). Cultivar N14 had the greatest area of the biggest leaf, and cultivar NCo376 the least. Leaf area of cultivar N14 increased linearly up to the leaf number with the biggest leaf. Inman-Bamber (1994) also found linear increases in leaf area and a maximum mature leaf area of approximately 380 cm² for cultivar NCo376. The biggest leaf emerged before peak tiller population in all cultivars (Table 4).

Leaf area index

The LAI of all cultivars showed a rapid increase up to a peak and remained at around peak, only declining sharply towards the end of the season (Figure 4). The uncharacteristic decrease in LAI between 100 and 150 days after planting was due to a lack of irrigation.

There was a marked difference in LAI between cultivars. Cultivars ZN6 and ZN7 achieved peak LAI earlier, but their peak LAI was lower than that of cultivars N14 and NCo376. Cultivar N14 had the greatest LAI, and ZN7 the least. Cultivars achieved peak LAI around 2500 °C.days from planting (Tbase = 10°C).

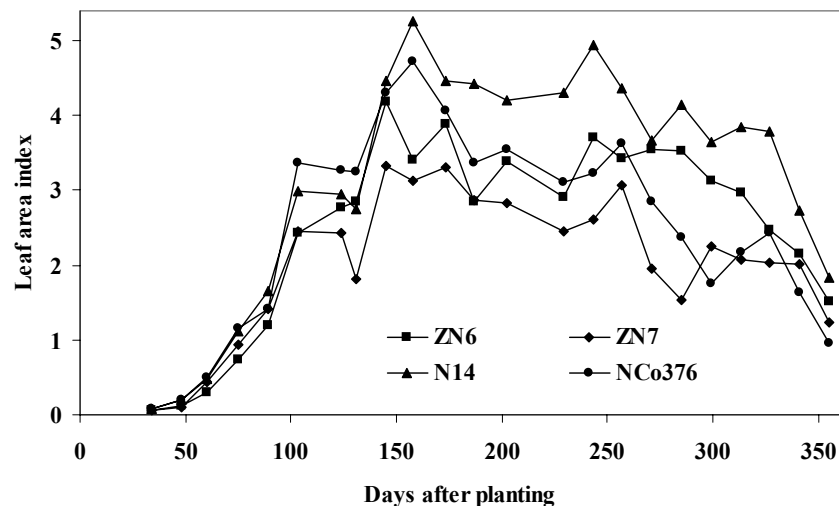


Figure 4. Development of leaf area index in cultivars ZN6, ZN7, N14 and NCo376 as a function of days after planting.

Table 5. Canopy extinction coefficients for cultivars ZN6, ZN7, N14 and NCo376 at different times after planting.

Days after planting	ZN6	ZN7	N14	NCo376
87	0.447	0.478	0.471	0.482
95	0.430	0.424	0.409	0.426
102	0.493	0.497	0.488	0.502
109	0.559	0.571	0.582	0.584
116	0.675	0.640	0.597	0.662
124	0.539	0.699	0.537	0.562
131	0.588	0.607	0.571	0.609

PAR interception

Interception of PAR by the canopy is modified by the architecture of the canopy as represented by the extinction coefficient (k). There were no significant differences in k between cultivars at the 5% level of statistical significance (Table 5). The data showed that there was an increase in extinction coefficients for all cultivars with increasing crop age. This is in agreement with trends found by Inman-Bamber (1994).

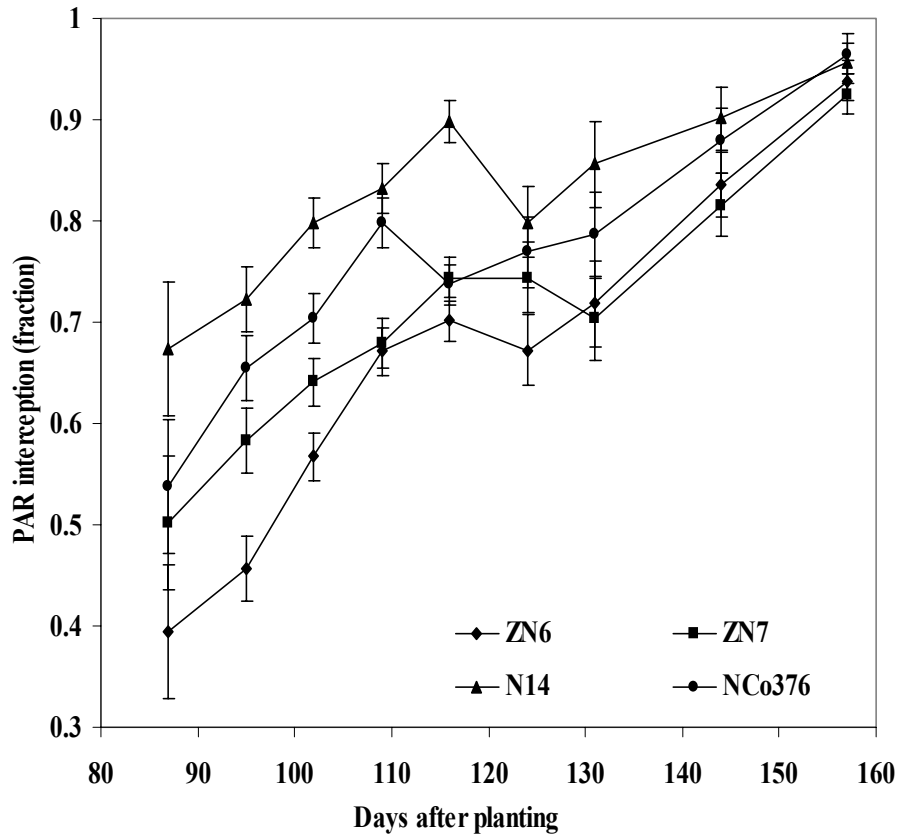


Figure 5. Fraction of intercepted PAR as a function of days after planting for cultivars ZN6, ZN7, N14 and NCo376. Bars denote one standard deviation.

Intercepted PAR increased with crop age for all cultivars (Figure 5). There were significant differences ($P=0,05$) among cultivars in PAR intercepted. The data showed that the high stalk population cultivars N14 and NCo376 intercepted more PAR than the low stalk population cultivars ZN6 and ZN7. The high stalk population cultivars had greater LAI, and therefore more leaf surface to intercept PAR (Figure 4).

Discussion

Biomass production is dependent on the amount of PAR intercepted by the canopy (Singels and Donaldson, 2000). Therefore cultivars that can intercept more PAR should have a yield advantage. Cultivars N14 and NCo376 intercepted more PAR than cultivars ZN6 and ZN7. The major difference in canopy development between these cultivars was that N14 and NCo376 produced more tillers than ZN6 and ZN7. The fact that cultivar NCo376 intercepted so much PAR despite having the smallest leaves, could mean that leaf size is less important than tiller population for PAR interception. This suggests that selecting for high tiller population in breeding programmes could be the key to achieving high yields.

In most sugarcane breeding programmes, high sucrose content is the main criteria for selection, with visual estimates of yield being used only during the early stages because of cost limitations (Skinner *et al.*, 1987). Tiller population could be assessed in the early stages of selection, as it is an inexpensive measurement. High density planting aimed at increasing tiller population is an alternative way of increasing PAR interception in inherently low population cultivars. Work done in Australia by Bull and Bull (1996) showed that cane yield could be increased by using high density planting. Cultivars with high PAR transmission thresholds are unlikely to produce a yield response to high density planting, and *vice versa*.

From the analysis of physiological parameters for canopy development, cultivar N14 emerged as the most efficient cultivar in terms of PAR interception. Planted eyes of this cultivar emerged faster and achieved the highest percentage emergence of planted eyes, and that was desirable for cane establishment. It also achieved the greatest leaf area of individual leaves, which was desirable for increased PAR interception and photosynthetic capacity. The high leaf appearance rate early on increased photosynthetic area and PAR interception, and shaded out weeds, while leaf emergence slowed later, with the plant concentrating resources for sucrose accumulation. Its tillers only started senescing at low transmitted PAR values and therefore produced a higher stalk population. A lower extinction coefficient meant that PAR was well distributed, increasing photosynthetic capacity in the canopy.

Conclusions

Various parameters for simulating cultivar-specific canopy development were determined for two Zimbabwean and two South African bred cultivars. Cultivars had similar values of thermal to leaf emergence and the parameter was stable across environments, indicating that it could be a useful method of simulating shoot emergence. There were marked cultivar differences in parameters tiller appearance rate per unit of thermal time and light transmission threshold for tiller production. These parameters hold promise for simulating cultivar-specific environmental control of tiller population. Tiller survival rate had similar values for all cultivars and could be used to predict stalk population, given peak tiller population.

Maximum leaf area captures the clear genotypic control of leaf size. The 'broken stick' approach to the phyllochron concept did not adequately capture temperature control of leaf appearance. The phyllochron interval appears to increase with successive leaves, reach a maximum and then decrease thereafter. The maximum phyllochron and its corresponding leaf number are suggested as parameters for simulating leaf appearance.

Future work would need to focus on measuring the parameters defined here for more cultivars, in more environments and for ratoon crops. It is believed that some of these parameters are well correlated, and data will be investigated for these links. For example, the commencement of tiller senescence and stalk elongation could coincide, while characteristics such as tillering proficiency and leaf size could also be linked. An attempt could also be made to categorise cultivars in groups with sets of similar parameters, and identify easily recognisable morphological or physiological attributes for each category. Categorisation of cultivars has been attempted by Inman-Bamber (1994).

Acknowledgements

The authors would like to thank Chiredzi Research Station, Chiredzi, Zimbabwe for allowing the use of their Delta-T leaf area meter used for leaf area measurements, and Professor JR Milford,

Physics Department, University of Zimbabwe, for the loan of the SunScan ceptometer used for PAR measurements. Dr MA Smit and Mr CN Bezuidenhout are thanked for their inputs and suggestions. The authors would also like to thank the Board of Directors of ZSAES for financing this study, and the Directors of South African Sugar Association Experiment Station and Zimbabwe Sugar Association Experiment Station, who approved the project. Thanks go also to staff at ZSAES who helped with data collection.

REFERENCES

- Barnes AC (1964). *The Sugar Cane. Botany, Cultivation and Utilization*. World Crops Books. Nescience Pub. 456 pp.
- Boote KJ, Jones JW and Pickering NB (1996). Potential uses and limitations of crop models. In: Use and abuse of crop simulation models. *Agron J*. 88: 704-716.
- Boote KJ, Knopff MJ and Bindraban PS (2001). Physiology and modelling of traits in crop plants: implications for genetic improvement. *Agricultural Systems* 70: 395-420.
- Bull TA and Bull JK (1996). Increasing sugarcane yields through higher planting density – preliminary results. pp 166-168 In: JR Wilson, DM Hogarth, JA Campbell and AL Garside (Eds) *Sugarcane: Research Towards Efficient and Sustainable Production*. CSIRO Division of Tropical Crops and Pastures, Brisbane, Australia.
- Campbell GS and Norman JM (1998). *An Introduction to Environmental Biophysics*. Second Edition. Springer. New York pp 26-36.
- Cock JH (2001). Sugarcane growth and development. *Sugarcane International* August 2001: 5-15.
- Hay KM and Walker AJ (1989). *An Introduction to the Physiology of Crop Yield*. Longmans, London. 292 pp.
- Inman-Bamber NG (1991). A growth model for sugarcane based on a simple carbon balance and CERES-Maize water balance. *S Afr J Plant Soil* 8: 93-99.
- Inman-Bamber NG (1994). Temperature and seasonal effects on canopy development and light interception of sugarcane. *Field Crops Res* 36: 41-51.
- King NJ, Mungomery RW and Hughes SG (1965). *Manual of Cane Growing*. Elsevier, USA. 375 pp.
- Monteith JL and Unsworth MH (1990). *Principles of Environmental Physics*. Second Edition. Edward Arnold, London.
- O’Leary GJ and Kiker GA (2000). Workshop Summary. pp 2-3 In: GJ O’Leary and GA Kiker (Eds) *Proceedings of the First International Workshop on the CANEGRO Sugarcane Model*. South African Sugar Association Experiment Station, Mount Edgecombe, South Africa.
- Ong CK and Monteith JL (1985). Response of pearl millet to light and temperature. *Field Crops Res* 11: 141-160.

- Singels A and Donaldson RA (2000). A simple model of unstressed sugarcane canopy development. *Proc S Afr Sug Technol Assoc* 74: 151-154.
- Skinner JC, Hogarth DM and Wu KK (1987). Selection methods, criteria and indices. pp 409-453 In: DJ Heinz (Ed) *Sugarcane Improvement Through Breeding*. Elsevier, USA.
- van Dillewijn C (1952). *Botany of Sugarcane*. Waltham, Mass, USA. 371 pp.
- White JW (1998). Modelling and crop improvement. pp 179-188 In: GY Tsuji, G Hoogenboom and PK Thornton (Eds) *Understanding Options for Agricultural Production*. Kluwer Academic Publishers, New York, USA.