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Simulating growth, development, and yield of tillering pearl millet
I. Leaf area profiles on main shoots and tillers

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Abstract

Pearl millet (*Pennisteum americanum* L.) is an essential crop in farming systems of the dry areas of the semi-arid tropics and its tillering habit is an important adaptive feature. This is the first paper in a series aiming at developing and validating a pearl millet simulation model that recognises tillers as functional entities, analogous to intercrops. The objective of this paper is to quantify the effects of total leaf number per axis (TLN), cultivar, plant density and axis number on parameters that are used to simulate potential leaf area per plant. Four cultivars with different phenology and tillering habit were grown under well-watered and well-fertilised conditions at two locations in India, covering a range of daylengths and plant densities. For selected plants, the area of fully expanded leaves was measured non-destructively. A bell-shaped function adequately described the relationship between individual leaf area and leaf position on an axis. Its shape was determined by the position (X_0) and area (Y_0) of the largest leaf and by the breadth and skewness of the leaf area profile curve. TLN affected all four parameters, although the association with Y_0 was weak. Cultivar only affected Y_0, suggesting that parameterising new cultivars is straightforward. The observed density effect confirmed that competition for light between axes started during stem elongation. The results highlighted the consistent differences between leaf area profiles of main shoots and tillers. For a high-tillering crop like pearl millet, modelling leaf area dynamics through individual leaves is justified, as this approach can potentially deal with cultivar and environmental effects on tillering. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Pearl millet; Tillering; Leaf area profiles; Leaf size; Simulation model

1. Introduction

Pearl millet is an important subsistence cereal of farming systems in the dry areas of the semi-arid tropics. The crop is often grown on sandy soils with low water retention capacity, in hot and dry environments with high vapour pressure deficits and high temporal and spatial variability in rainfall (Sivakumar, 1988; Payne et al., 1990; Sharma and Pareek, 1993). Use of inorganic fertiliser is limited, as farmers perceive that chemical amendments increase the risk of crop failure (Kollavalli, 1997). With an ever-increasing population in these dry areas, the production per capita can be maintained only by expanding the area sown to pearl millet, a situation seen in Africa (FAO and ICRISAT, 1996). However, much of this

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expansion is into even harsher environments or is achieved by reducing the fallow period, aggravating the problem of low soil fertility (Kollavalli, 1997). Soil nutrient balances (N, P, K) are negative in many African countries, including those where pearl millet is an important staple crop (Stoorvogel et al., 1993) and with the current increasing population, a trade gap for pearl millet is expected in Africa (FAO and ICRISAT, 1996). The physical environment of pearl millet-based production systems is thus very unfavourable and fragile.

The tillering habit of pearl millet is one of the key factors in its adaptation to harsh environments. The crop can compensate yield loss of the main shoot by producing additional tillers (Lambert, 1983; Mahalakshmi and Bidinger, 1986). However, high- and low-tillering cultivars adopt different adjustment strategies in response to low plant densities (Bidinger and Raju, 2000). Although both plant types respond similarly in terms of grain yield, high-tillering cultivars do so by increasing tiller number, whereas low-tillering ones adjust by increasing panicle size (Bidinger and Raju, 2000). These different adaptation mechanisms could be the reason why farmers in arid zones of India have the perception that under low-input conditions, high-tillering landraces are superior to low-tillering improved varieties, whereas this ranking reverses with increased resource availability (water, fertility). Hence, the choice of plant type (phenology, tillering ability) for a particular field or year depends to a large extent upon the farmer's expectation of that season (Kollavalli, 1997). In general, the importance to farmers of tillering increases as the timing and intensity of drought becomes more unpredictable and the role of animals in the farming system becomes more important (van Oosterom et al., 1996).

The challenge of representing tillering of a crop in a functional way in crop models is analogous to that presented by intercropping. Both must deal with competition for resources among plants and among axes within a plant in a dynamic and flexible way, and it is not surprising that both have been largely avoided by model developers. Several simulation models for pearl millet have been developed in the past, e.g. CERES-millet (ICRISAT, 1989), RESCAP (Monteith et al., 1989), CP-BFK (Verberne et al., 1995), and SARRA-millet (Affholder, 1997), but none of these considers tillering. Huda et al. (1984) perceived the tillering nature of pearl millet as a potential major bottleneck in the development of a pearl millet simulation model. The need for this functionality was one of the main incentives for the development of the Agricultural Production Systems sIMulator (APSIM) (McCown et al., 1996). The architectural change that makes simulation of competition relatively straightforward in APSIM is the making of the soil central to the system simulation. Soil state variables are dynamically influenced by weather continuously and by crops and management practices when they are present. Crop modules are "plugged in" to the soil in accordance with simulated cropping strategies, either in series (crop sequences, rotations) or in parallel (intercrops, crop + weeds, main culm + tillers). Algorithmically, crops in parallel association influence each other simply by the influence of each on the state variables of environmental resources, e.g. radiation, soil water, soil nitrate, etc., which are independently experienced by the others. This approach has been shown to deal adequately with competition among intercrops using only the crop parameters for the respective sole crops (Carberry et al., 1996). In order for this strategy to adequately simulate a tillering crop, information on differences between main shoots and tillers in parameters that determine the potential mature leaf area per axis is required, as well as the effect of cultivars on these differences. Dwyer and Stewart (1986) developed a relationship between the normalised area of individual leaves and their position on the axis. Muchow and Carberry (1990) extended this analysis to a formula that predicted individual leaf area for uniculm sorghum as a function of the total leaf number (TLN) on an axis. Carberry et al. (1993) subsequently observed for sorghum that the relationship was valid for tillers as well. Pearl millet, however, produces many more tillers than sorghum, causing inter-axis competition for resources (light) that can affect leaf area development (Maas et al., 1987). In addition, the absence of genotypic differences in the sorghum experiments of Carberry et al. (1993) might reflect limited genotypic variation in the material used in those experiments. Therefore, a need exists to quantify the effects of cultivar, density and axis on the relationship between TLN and the parameters that determine the leaf area profile.

This is the first paper in a series that aims at documenting the physiology of pearl millet in order to develop a model that simulates the growth and development of pearl millet axes. The aim of this paper is to quantify the effects of leaf number, cultivar, plant density and axis on parameters that determine the leaf area profile of individual leaves on an axis, in order to simulate maximum leaf area per axis. In the second paper of this series (van Oosterom et al., 2001), these parameter estimates are combined with estimates of leaf and tiller appearance, leaf senescence and tiller death, in order to simulate leaf area index (LAI) of pearl millet throughout the cropping season. The ultimate aim of the series is to present and validate the APSIM-millet module.

2. Materials and methods

This paper reports on data collected on four cultivars of pearl millet, grown across a range of plant densities and photoperiods (Table 1).

2.1. Cultivars

The four cultivars included in the experiments were selected to represent different combinations of phenology and plant type:

WRajPop. Population derived from landrace accessions from the arid zones of western Rajasthan (India). It is medium early, high tillering and has relatively small panicles.

RCB-IC 911. Open-pollinated variety based on germplasm from Togo. It has a similar phenology to WRajPop, but is very low tillering and has large panicles.

HHB 67. Single cross hybrid (843A × H 77/833-2). This is a very early hybrid, but has a tillering capacity comparable to WRajPop.

BJ 104. Single cross hybrid (MS 5141A × J104). This is a control cultivar on which much of the early physiological work was undertaken. The phenology and plant type are similar to WRajPop.

2.2. Experimental details

The two main experiments were carried out at Patancheru, India (17°45′ N, 78°16′ E), during the dry season (Experiment 1) and rainy season (Experiment 2) of 1996 on an alfisol (clayey-skeletal mixed isohyperthermic Udic Rhodustalf). The experiments contained four plant densities: 4, 11, 16 and 20 plants m^{-2}. Densities were obtained through different combinations of row spacing (100, 60, 50, and 50 cm, respectively) and plant-to-plant spacing within a row (25, 15, 12.5, and 10 cm, respectively). Planting geometry was such that the ratio of row spacing to plant-to-plant spacing was 4:1, except at the highest density, where it was 5:1 for logistical reasons. Plots

Table 1
Experiment (preceded by experiment number), daylength at emergence, plant density and the number of plants for each cultivar on which observations on individual leaf size were made

Experiment	Daylength emergence (h)	Plant density (plants m^{-2})	Cultivar			
			BJ 104	HHB 67	RCB-IC 911	WRajPop
Low plant density (<5 plants m^{-2})						
5-Patancheru rainy season 1997	14.9	2.5	10	10	10	10
1-Patancheru dry season 1996	12.5	4.0	6	6	6	6
2-Patancheru rainy season 1996	14.0	4.0	12	12	12	12
Medium plant density (5–12 plants m^{-2})						
4-Patancheru dry season 1997	14.7	8.9	5	5	5	5
1-Patancheru dry season 1996	12.5	11.1	6	–	6	6
3-Jodhpur rainy season 1996	14.6	11.1	–	–	–	15
High plant density (>12 plants m^{-2})						
1-Patancheru dry season 1996	12.5	15.0	6	6	5	6
2-Patancheru rainy season 1996	14.0	15.0	12	12	12	12
1-Patancheru dry season 1996	12.5	20.0	6	–	6	6

contained between six and nine rows of 4 m length. The experiments were laid out as a split plot design with three replications, with plant density as the main block. Because of restrictions imposed by the size of the field and the equipment used, there were some restrictions on the randomisation of the main blocks. In the dry season, HHB 67 was not part of the experiment, but was sown as a border around the experiment.

Experiment 1 (dry season) was sown on 29 February 1996 and emerged on 5 March 1996 after irrigation. A basal fertiliser dose of 150 kg ha^{-1} di-ammonium phosphate was applied before planting and a top dressing of 100 kg ha^{-1} urea was applied on 25 March 1996. The crop was sprinkler irrigated once or twice a week to avoid drought stress. Experiment 2 (rainy season) was sown on 26 June 1996 and emerged 2 days later. Fertiliser applications were the same as in the dry season. Because of a dry start of the season, the crop received two light irrigations just after emergence. Otherwise, the crop was rainfed, as rainfall throughout the season (240 mm between emergence and anthesis and 470 mm between anthesis and maturity) was sufficient to avoid any significant effect of drought stress on leaf growth.

Plants were thinned to the desired density at around 10 days after emergence. Directly afterwards, three representative plants that were well bordered were selected from each plot in two replications for all densities in the dry season and in only two densities in the rainy season (Table 1). These plants were used for the observations on individual leaf area.

In addition to the above experiments, data were collected from selected plants in experiments conducted during 1996 and 1997. In the rainy season of 1996, a split-plot experiment with two replications was conducted adjacent to Experiment 2, including the same four cultivars and two plant densities (4 and 15 plants m^{-2}). Management practices in this experiment were the same as for Experiment 2. For each cultivar × density combination, six plants were selected for observations on individual leaf area. In order to collect data from plants with more leaves per axis, observations were also done on plants selected in experiments conducted under longer daylength. Experiment 3 was sown on 1 July 1996 at Jodhpur, India (26°30′ N, 73°02′ E) on a sandy soil (Psamment). The experiment was laid out as a randomised complete block design with three replications. Each plot consisted of 20 rows of 8 m long with a row spacing of 60 cm and a plant density of 9 plants m^{-2}. At sowing, the crop was fertilised with 20 kg ha^{-1} P, applied as single super phosphate and with 0, 20, or 40 kg ha^{-1} N, applied as calcium ammonium nitrate. The experiment included two cultivars, but data from only one of them (WRajPop) are considered here. For each N-treatment, individual leaf area was measured for the main shoot of five plants. As there was no effect of N-treatment on leaf size, all data were included in the analyses. Experiments 4 and 5 were conducted at Patancheru during the dry season and rainy season of 1997, respectively, on an alfisol under extended daylength. Both experiments were well fertilised and were either irrigated or received sufficient rainfall to avoid any significant effect of drought on leaf growth. Experiment 4 contained only one replication, whereas Experiment 5 was laid out as a randomised block design with three replications.

Across all experiments, the daylength at emergence ranged from 12.5 to 14.9 h (Table 1). This provided a range in leaf numbers from 11 to 27 for main shoots and from 6 to 20 for tillers. Plant densities were classified into low (<5 plants m^{-2}), medium (between 5 and 12 plants m^{-2}), and high (>12 plants m^{-2}) (Table 1).

2.3. Measurement of individual leaf area

For each selected plant, the leaves of each axis were numbered from 1 through to the flag leaf. Tillers were numbered according to the main shoot leaf axil from which they appeared. In general, tillering started from the axil of Leaf 3, making Tiller 3 (T3) the first tiller to appear.

Our experiments included a landrace population (WRajPop) and an open-pollinated variety (RCB-IC 911) and thus we expected variation in TLN per axis within plots. Since individual leaf area was expected to be a function of TLN (Carberry et al., 1993; Keating and Wafula, 1992), leaf area measurements had to be done non-destructively. Therefore, we measured the length and maximum breadth of fully expanded leaves and calculated individual leaf area as

$$\text{Individual leaf area} = \text{leaf length} \times \text{leaf breadth} \times \text{leaf shape factor} \qquad (1)$$

Data on the leaf shape factor have been published for many crops. For pearl millet, Payne et al. (1991) reported a factor of 0.68 for cultivar ICTP 8203. Unpublished data collected at Patancheru (M.V. Potdar, personal communication) indicated that fertiliser application and cultivar had no effect on the shape factor and if the regression of leaf area on length × breadth was forced through the origin, the factor in that experiment ranged from 0.64 to 0.73 ($n = 74$ or 75) for individual cultivars. Eight of 12 cultivars had a shape factor in the range 0.68–0.70, whereas the value for ICTP 8203 was 0.66. The leaf shape factor, therefore, appears to be conservative. However, the effect of leaf shape (length/breadth ratio) was not considered in these experiments, neither across leaves within plants (flag leaves tend to have a lower length/breadth ratio than other leaves) nor across cultivars (leaves of WRajPop tend to have a high length/breadth ratio). Therefore, we obtained values for the leaf shape factor in the dry season of 1996 for the following leaf classes of each cultivar: (1) small leaves that expanded during the vegetative phase of the apex; (2) larger leaves that expanded during the generative phase of the apex; (3) flag leaves.

2.4. Data analysis

A bell-shaped function was used to relate the area of an individual leaf to its ordinal position on an axis (Carberry et al., 1993):

$$Y = Y_0 \exp(a(X - X_0)^2 + b(X - X_0)^3) \tag{2}$$

where X_0 is the position of the largest leaf, Y_0 the mature area of the largest leaf, a the empirical constant determining the breadth of the bell-shaped curve, b the empirical constant determining the skewness of the bell-shaped curve. More negative values for a result in a sharper peak of the function. Negative values for b result in the curve being skewed towards the left and positive values result in the curve being skewed towards the right. Reduced skewness is generally associated with a broader peak of the curve.

For each axis that produced a flag leaf, the non-linear procedure in the statistical package SAS (SAS, 1985) was used to fit the above function through the observed leaf areas. The fitted values for X_0, Y_0, a, and b that we thus obtained were then regressed on TLN to quantify the effects of cultivar, density and axis on this relationship.

The values for the parameters were finally used to estimate the area of each individual leaf that was used in the analysis. As a measure for the accuracy of the estimation, the residual mean square difference (RMSD) was calculated as

$$\mathrm{RMSD} = \sqrt{\sum \frac{(\text{observed} - \text{estimated})^2}{n - 1}} \tag{3}$$

The RMSD was calculated on a leaf, axis and plant basis. In the case of missing data, leaf areas were estimated through linear interpolation or extrapolation of the previous and successive leaf, to enable calculations on an axis or plant level. To quantify the effects of cultivar, density and axis on the accuracy of the estimations, scenario's using different estimates of the parameters X_0, Y_0, a, and b were used.

3. Results

3.1. Leaf shape factor

The small leaves that were produced just after emergence (leaves 1–3 on the main shoot) had an average shape factor of 0.67 ($n = 48$). No attempt was made to identify differences between cultivars, as the small individual leaf size did not allow very accurate estimates of the shape factor.

For the large leaves which were produced during stem elongation, we observed consistent effects of cultivar and leaf type (flag leaf versus non-flag leaf) on the leaf shape factor. For both the flag leaves and non-flag leaves, WRajPop had the lowest shape factor (Table 2). For the other three cultivars, the leaf shape factor of the non-flag leaves was close to 0.68 as reported by Payne et al. (1991). The similarity in shape factor between the small early leaves and the large non-flag leaves suggest that the shape factor is not significantly affected by leaf size. It was, however, affected by leaf type, as flag leaves consistently had lower shape factors than the large non-flag leaves in the upper layers of the canopy (Table 2).

Because of the effect of cultivar (WRajPop versus others) and of leaf type (flag leaf versus non-flag leaves), the values in Table 2 were used as shape

Table 2
Leaf shape factors and the number of observations from which they are derived, for non-flag leaves and flag leaves, obtained from the 1996 dry season experiment at Patancheru[a]

Cultivar	Non-flag leaf		Flag leaf	
	n	Factor	*n*	Factor
BJ 104	18	0.68 (0.03)	4	0.60 (0.02)
HHB 67	9	0.66 (0.03)	3	0.61 (0.04)
RCB-IC 911	12	0.67 (0.04)	4	0.57 (0.77)
WRajPop	52	0.62 (0.05)	13	0.54 (0.04)

[a] Values in parentheses are standard deviations. Non-flag leaf data include only observations on large leaves which expanded during the generative phase of the apex.

factors to derive leaf area from leaf length × leaf breadth measurements.

3.2. Leaf area per leaf

Leaf area profiles on individual axes were in general well described by the bell-shaped function (Fig. 1). We obtained leaf area profiles for 887 axes, out of which five had to be omitted because bell-shaped curves could not be fitted properly. All R^2-values were ≥ 0.90, with a median R^2 of 0.99.

3.2.1. Position of the largest leaf (X_0)

The position of the largest leaf on an axis (X_0) was a linear function of TLN (Fig. 2, Table 3). The effect of cultivar on the relationship was minor and inconsistent, and will not be considered any further. There was, however, a consistent effect of axis. For a given TLN, the value for X_0 was highest for the main shoot and gradually declined for later tillers (Fig. 2). Within the range of observed TLN, the expected values for X_0 for a given TLN were significantly higher ($P < 0.05$) for the main shoot than those for each of the tillers (data not presented). Among tillers, the expected values for X_0 were in most cases also significantly different ($P < 0.05$).

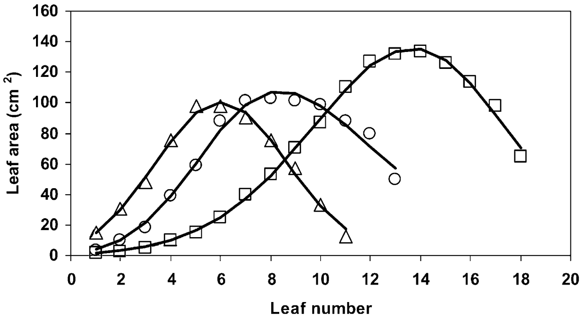

Fig. 1. Individual leaf area as a function of leaf position for the main shoot (□), Tiller 3 (○), and Tiller 6 (Δ) for a plant of WRajPop, grown at Patancheru in the rainy season of 1996 at a density of 4 plants m^{-2}.

Across all axes, the relationship between X_0 and TLN was very strong ($R^2 = 0.87$, $n = 882$, Table 3). However, the slope of the regression line of this combined analysis was considerably higher than if individual axes were considered. In the analysis across axes, X_0 increased by about 0.8 for each additional leaf, whereas for individual axes, this increase was only 0.5–0.6 (Table 3). This difference was due to the fact that the overall analysis fitted a regression through a group of essentially parallel lines.

Plant density had a minor effect on X_0. The relationships between X_0 and TLN for the main shoot for the three plant density classes were:

$$\leq 5\,\text{plants m}^{-2}: \quad X_0 = 4.27 + 0.58\,\text{TLN}, \quad n = 109, \quad R^2 = 0.80 \tag{4}$$

$$5-12\,\text{plants m}^{-2}: \quad X_0 = 4.10 + 0.57\,\text{TLN}, \quad n = 52, \quad R^2 = 0.68 \tag{5}$$

$$\geq 12\,\text{plants m}^{-2}: \quad X_0 = 4.10 + 0.55\,\text{TLN}, \quad n = 87, \quad R^2 = 0.72 \tag{6}$$

Although neither the intercepts nor the slopes were significantly different among the three classes of plant densities, the expected value for X_0 was >0.5 leaf less at the highest density as compared with the lowest density; this difference was significant at $P < 0.05$. Comparable results were observed for T3 and T4 (the first two tillers to appear).

3.2.2. Area of the largest leaf (Y_0)

The area of the largest leaf (Y_0) increased linearly with TLN. The overall relationship, however, was weak ($R^2 = 0.19$, $n = 882$), as it was affected by cultivar, plant density and axis (Table 4). For a given TLN, RCB-IC 911 tended to have larger leaves than the other three genotypes (Fig. 3). High plant densities tended to reduce the area of the largest leaf (Table 4). Within plants, tillers tended to have larger leaves for a

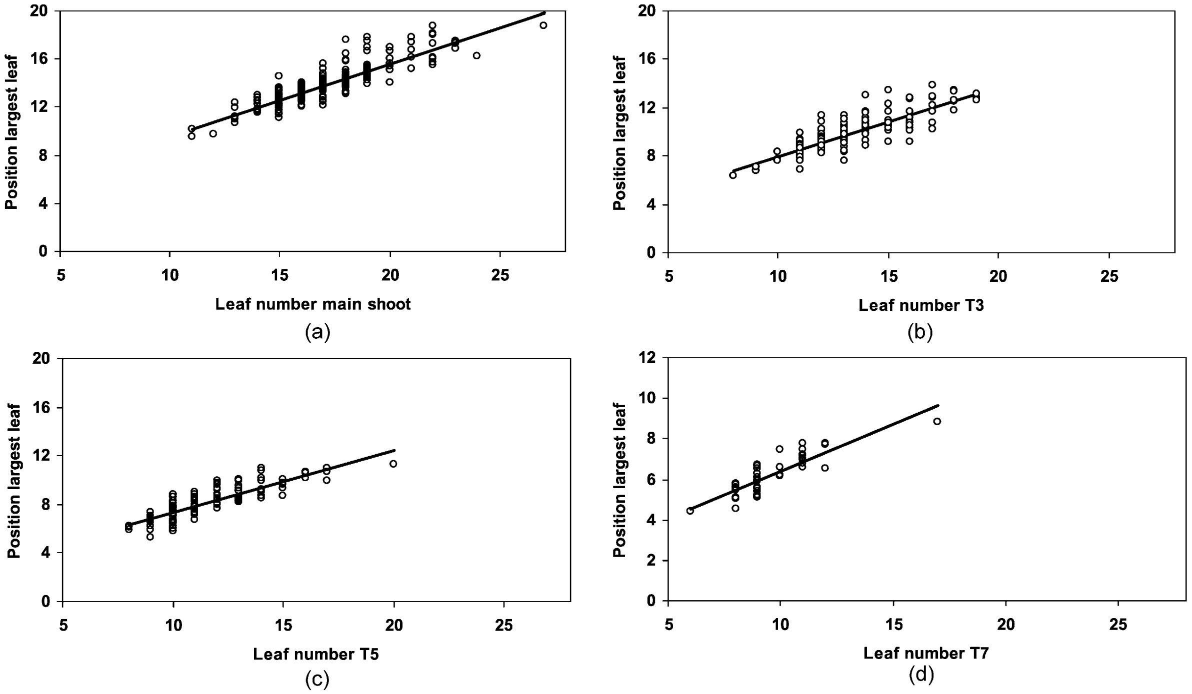

Fig. 2. Observed (○) and fitted (—) values for the regression of the position of the largest leaf (X_0) on TLN for (a) main shoot, (b) Tiller 3, (c) Tiller 5, and (d) Tiller 7. For equations of the fitted regression lines, see Table 3.

given TLN than main shoots. Although tillers produced at least 3–4 leaves less than the main shoot, their maximum leaf area was often only marginally smaller than that of the main shoot (Fig. 1).

Within cultivar × density × axis groups, the relationship between Y_0 and TLN was often still weak (Table 4), suggesting that both environmental and genotypic heterogeneity accounted for a large proportion of the variation in leaf area.

Table 3
Fitted relationship between the position of the largest leaf (X_0) and TLN on an axis, plus the number of observation (n) on which the relationship is based and the R^2 across all axes and for individual axis

Axis	Regression	n	R^2
All	$X_0 = -1.04 + 0.83\,\mathrm{TLN}$	882	0.87^{***}
Main	$X_0 = 3.58 + 0.60\,\mathrm{TLN}$	248	0.78^{***}
T3	$X_0 = 2.18 + 0.58\,\mathrm{TLN}$	166	0.69^{***}
T4	$X_0 = 1.81 + 0.57\,\mathrm{TLN}$	187	0.76^{***}
T5	$X_0 = 2.22 + 0.51\,\mathrm{TLN}$	128	0.73^{***}
T6	$X_0 = 2.09 + 0.49\,\mathrm{TLN}$	87	0.69^{***}
T7	$X_0 = 1.72 + 0.47\,\mathrm{TLN}$	41	0.74^{***}

*** Significant at $P < 0.001$.

3.2.3. *Breadth of the leaf area curve (a)*

The value of *a* increased asymptotically with increasing TLN (Fig. 4). Cultivar and plant density had only a minor effect on this relationship, and as these effects were inconsistent across axes, they will not be considered any further. There was, however, a consistent effect of axis, with main shoots having lower values for *a* (sharper peak) for a given TLN than tillers (Figs. 1 and 4). A similar effect was observed if later tillers were compared with earlier tillers. The asymptotic relationship described the observed data well for the main shoot and first three tillers, with $R^2 > 0.60$ (Table 5). For the late tillers (T6 and T7), the fit was slightly less, but TLN still explained well over 50% of the variation in *a* (Table 5).

3.2.4. *Skewness of the leaf area curve (b)*

The relationship between *b* and TLN was also affected by axis. The effects of cultivar and plant

Table 4
Regression of area of largest leaf on an axis (Y_0) on TLN, as affected by cultivar, plant density and axis

Cultivar	Density (plants m^{-2})	Axis	n	R^2	Regression
BJ 104	<5	Main	26	0.64^{***}	$Y_0 = -123.9 + 17.1^{*}$ TLN
		All tillers	127	0.55^{***}	$Y_0 = 5.1 + 13.2^{*}$ TLN
	>5	Main	35	0.00 ns	$Y_0 = 141.3 - 0.1^{*}$ TLN
		All tillers	52	0.06^{+}	$Y_0 = 106.9 + 1.8^{*}$ TLN
HHB 67	<5	Main	28	0.04 ns	$Y_0 = 72.8 + 3.3^{*}$ TLN
		All tillers	132	0.26^{***}	$Y_0 = 34.8 + 7.4^{*}$ TLN
	>5	Main	22	0.11 ns	$Y_0 = 37.6 + 4.0^{*}$ TLN
		All tillers	45	0.43^{***}	$Y_0 = 15.7 + 7.2^{*}$ TLN
RCB-IC 911	<5	Main	28	0.23^{*}	$Y_0 = 32.0 + 12.7^{*}$ TLN
		All tillers	72	0.34^{***}	$Y_0 = 18.1 + 18.2^{*}$ TLN
	>5	Main	34	0.27^{**}	$Y_0 = 15.7 + 10.7^{*}$ TLN
		All tillers	11	0.21 ns	$Y_0 = 58.4 + 8.3^{*}$ TLN
WRajPop	<5	Main	27	0.47^{***}	$Y_0 = -83.5 + 14.3^{*}$ TLN
		All tillers	123	0.29^{***}	$Y_0 = 21.0 + 11.5^{*}$ TLN
	>5	Main	48	0.68^{***}	$Y_0 = -48.0 + 10.9^{*}$ TLN
		All tillers	72	0.55^{***}	$Y_0 = 25.5 + 8.2^{*}$ TLN

$^{+}$ Significant at $P < 0.10$.
* Significant at $P < 0.05$.
** Significant at $P < 0.01$.
*** Significant at $P < 0.001$.

density were minor and inconsistent and will not be considered any further. For the main shoot and tillers T3, T4, and T5, b tended to become less negative (reduced skewness) with increasing TLN (Fig. 5a–c), but the R^2's were relatively low, ranging from 0.35 for T5 to 0.53 for the main shoot and T3 (Table 6). For the later tillers, however, the relationship was not significant (Table 6), due to the fact that at low leaf numbers, both positive (skewed towards the left) and negative (skewed towards the right) values for b were observed (Fig. 5d). As absolute values for b in these late tillers were small compared with the other axes (Fig. 6), the results indicate a general absence of skewness in these late tillers.

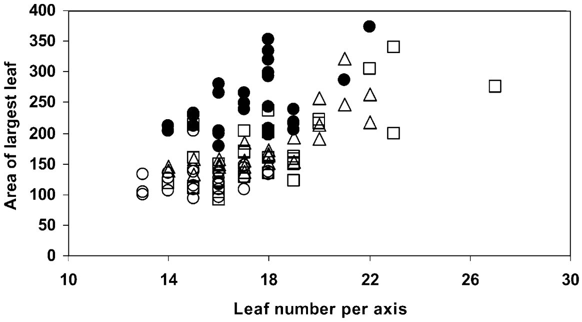

Fig. 3. Relationship between the area of the largest leaf (cm^2) and the total number of leaves on an axis for the main shoots of BJ 104 (Δ), HHB 67 (○), RCB-IC 911 (●), and WRajPop (□) for plants grown at densities of <5 plants m^{-2}.

3.3. Maximum leaf area per axis and per plant

The previous results indicated that axis had a profound effect on the relationship between TLN and each of the four parameters that determine the leaf area profile (Eq. (2)). The effects of cultivar and plant density were largely limited to an effect on the relationship between maximum leaf size and TLN, although plant density also had a minor effect on the position of the largest leaf.

To quantify the contributions of these effects to the accuracy of leaf area estimations, five methods with increasing detail in parameter estimation were used to calculate leaf area per axis and per plant. The RMSD was used as a measure of accuracy. The five methods and their order were based on the effects of

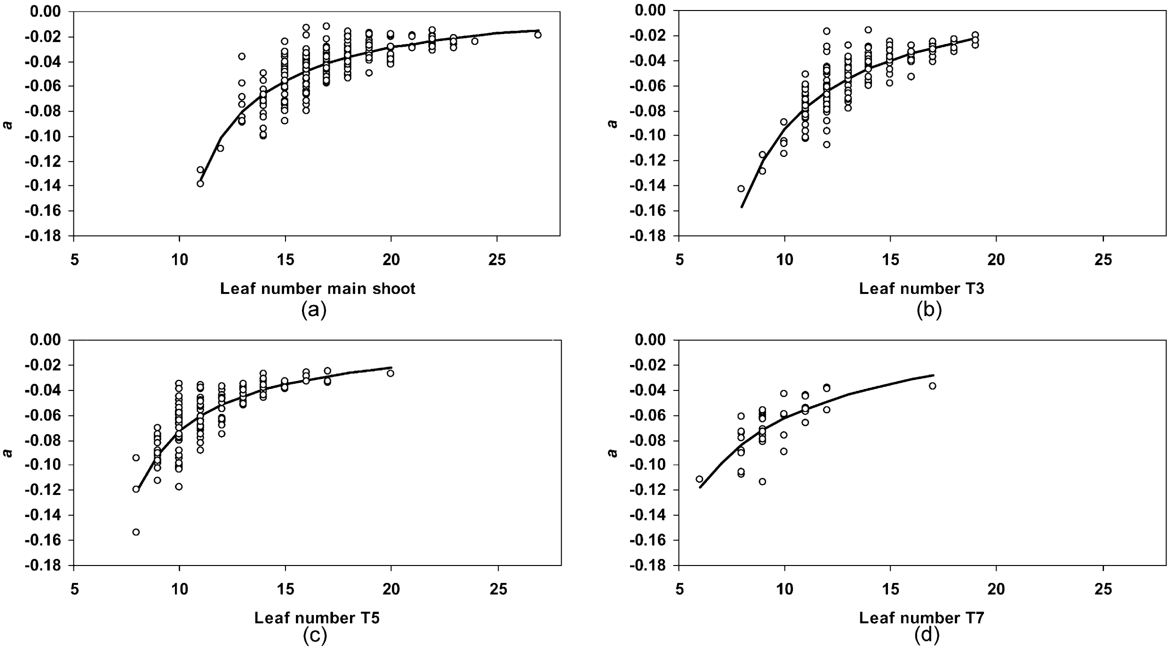

Fig. 4. Observed (○) and fitted (—) values for the regression of a (parameter describing the breadth of the peak of bell-shaped curve) on TLN for (a) main shoot, (b) Tiller 3, (c) Tiller 5, and (d) Tiller 7. For equations of the fitted regression lines, see Table 5.

TLN, cultivar, density and axis on the parameter estimates:

Method 1. Effect of only TLN on all parameters.
Method 2. Effect of TLN on all parameters, plus cultivar effect on Y_0.
Method 3. Effect of TLN on all parameters, plus cultivar and density effects on Y_0.
Method 4. Effect of TLN on all parameters, plus cultivar and density effects on Y_0, plus axis effect on X_0, Y_0, a, and b (main shoot versus pooled tillers).
Method 5. Effect of TLN on all parameters, plus cultivar and density effects on Y_0, plus axis effects on X_0, Y_0, a, and b (main shoot and individual tillers).

If only an effect of TLN on parameter estimates was considered, the RMSD was about 38% of the mean, both on an axis and plant basis (Table 7). Taking into account the effect of cultivar on leaf area (Method 2) reduced the RMSD to 34% of the mean (Table 7). This was entirely due to an improved accuracy in the

Table 5
Fitted relationship between the parameter determining the breadth of the peak of the bell-shaped curve (a) and TLN on an axis, plus the number of observation (n) on which the relationship is based and the R^2 across all axes and for individual axis

Axis	Regression	n	R^2
All	$a = 0.01549 + (75.5947/(1 - 83.4078\,\mathrm{TLN}))$	882	0.55^{***}
Main	$a = 0.00955 + (0.0608/(1 - 0.1293\,\mathrm{TLN}))$	248	0.62^{***}
T3	$a = 0.02491 + (0.1714/(1 - 0.2431\,\mathrm{TLN}))$	166	0.70^{***}
T4	$a = 0.01715 + (0.1479/(1 - 0.2447\,\mathrm{TLN}))$	187	0.73^{***}
T5	$a = 0.00321 + (0.0806/(1 - 0.2060\,\mathrm{TLN}))$	128	0.66^{***}
T6	$a = 0.00792 + (0.2431/(1 - 0.4411\,\mathrm{TLN}))$	87	0.60^{***}
T7	$a = 0.02004 + (546.56/(1 - 660.90\,\mathrm{TLN}))$	41	0.57^{***}

*** Significant at $P < 0.001$.

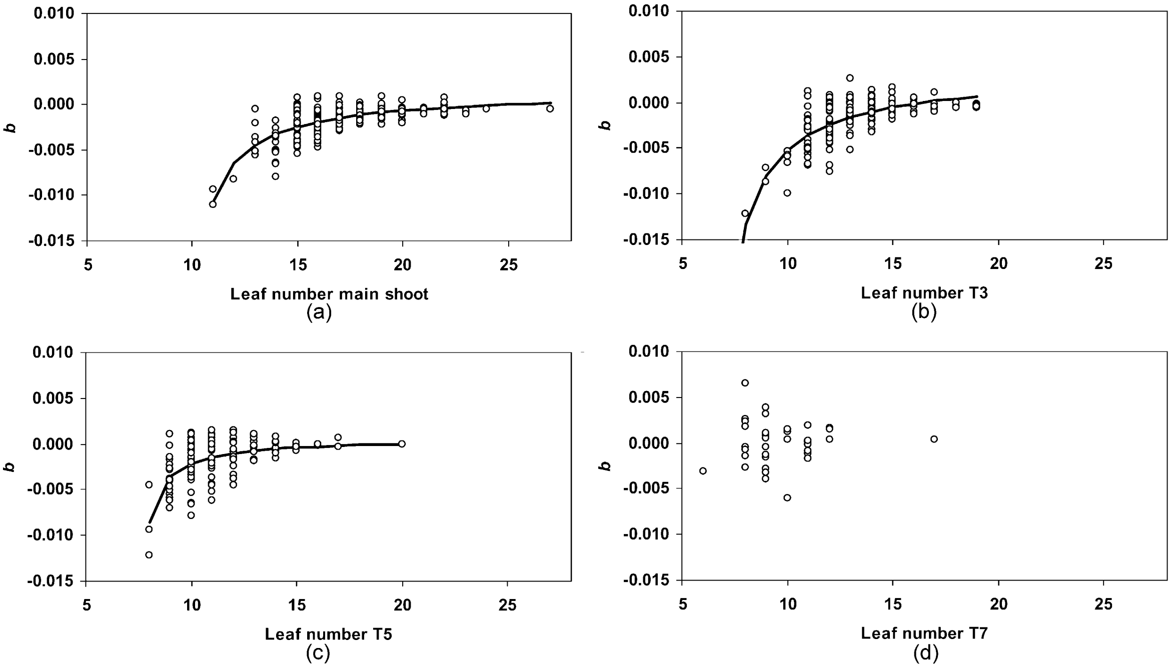

Fig. 5. Observed (○) and fitted (—) values for the regression of *b* (parameter describing the skewness of bell-shaped curve) on TLN for (a) main shoot, (b) Tiller 3, (c) Tiller 5, and (d) Tiller 7. For equations of the fitted regression lines, see Table 6.

estimation of leaf area for HHB 67 and RCB-IC 911 (Table 8), the two cultivars with the smallest and largest leaves, respectively (Fig. 3). Adding the effect of plant density on leaf area (Method 3) reduced the RMSD further to 27–28% of the mean; gains were primarily achieved through improved accuracy at higher plant densities (Table 8). Incorporating the effect of density on the position of the largest leaf had no effect (data not presented). Distinguishing between main shoot and tillers reduced the RMSD to 23% of the mean (Table 4), primarily due to improved accuracy in the estimation of main shoot leaves (Table 8). Taking into account the differences between tillers had only a minor effect (Table 7), although it resulted in more homogeneous RMSD estimates between tillers (Table 8). For both axes and plants, the accuracy in Methods 4 and 5 improved 40% as compared with Method 1.

Table 6
Fitted relationship between the parameter determining the skewness of the bell-shaped curve (*b*) and TLN on an axis, plus the number of observations (*n*) on which the relationship is based and the R^2 across all axes and for individual axis

Axis	Regression	*n*	R^2
All	$b = 0.00046 + (1.64865/(1 - 61.7930\,\mathrm{TLN}))$	882	0.05***
Main	$b = 0.00144 + (0.0025/(1 - 0.1100\,\mathrm{TLN}))$	248	0.53***
T3	$b = 0.00335 + (0.0061/(1 - 0.1706\,\mathrm{TLN}))$	166	0.53***
T4	$b = 0.00287 + (0.0059/(1 - 0.1861\,\mathrm{TLN}))$	187	0.44***
T5	$b = 0.00058 + (0.0011/(1 - 0.1394\,\mathrm{TLN}))$	128	0.35***
T6	$b = -0.00013 + (0.0003/(1 - 0.1578\,\mathrm{TLN}))$	87	0.04 ns[a]
T7	$b = -0.00045 - (0.0002/(1 - 0.1518\,\mathrm{TLN}))$	41	0.06 ns

[a] Not significant at $P < 0.05$.
*** Significant at $P < 0.001$.

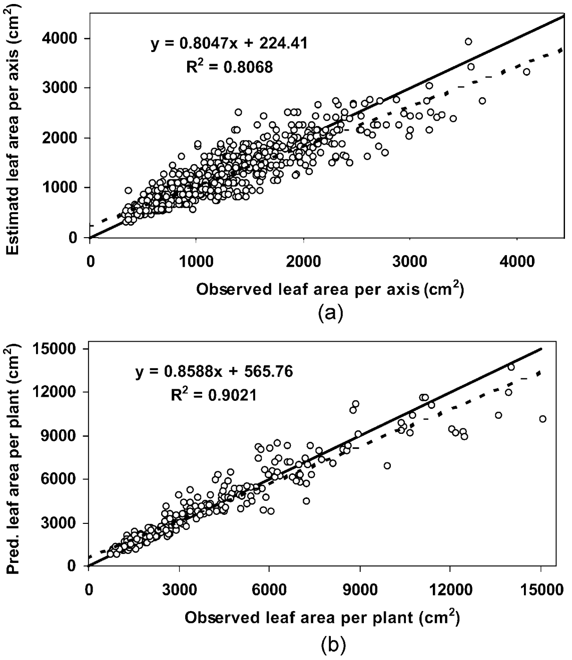

Fig. 6. Relationship between predicted and observed leaf area (a) per axis and (b) per plant, using parameter estimates for the leaf area profile curve based upon Method 4 (effect of TLN on all parameters, plus cultivar and density effect on Y_0, plus axis effect (main shoot versus pooled tillers) on X_0, Y_0, a, and b). Dotted line is fitted regression, solid line is 1:1 line.

In general, Method 4 adequately estimated leaf area per axis and plant, although there was a slight tendency to underestimate leaf area at high values, as the slope of the regression of estimated on observed leaf area was significantly smaller than 1 (Fig. 6). As the intercept was significantly greater than zero, the underestimation occurred especially at the higher end of the observed range and was mainly due to some plants with very large leaves in the rainy season experiment of Patancheru 1997.

4. Discussion

This paper describes a method to simulate the potential leaf area per axis for pearl millet as a function of TLN per axis and uses a bell-shaped function to express individual leaf area as a function of the ordinal position of the leaf on the axis. The four parameters required to describe the bell-shaped function (position (X_0) and area (Y_0) of the largest leaf and the breadth (a) and skewness *(b)* of the function) are all a function of TLN. Because TLN itself is a function of daylength (Muchow and Carberry, 1990; van Oosterom et al., 2001), the parameter estimates should be applicable across a range of latitudes. The concept we used has been used successfully to simulate leaf area of non-tillering maize and sorghum (Carberry and Abrecht, 1991; Keating and Wafula, 1992) and of tillering sorghum (Carberry et al., 1993). The method is also not very different to the approach which uses a logistic function of thermal time to simulate total leaf area per axis as developed for wheat (Meinke et al., 1998) and sorghum (Hammer et al., 1993). In that approach, the parameters determining the inflection point and steepness of the curve are related to the position of the largest leaf (X_0) and the area of the largest leaf (Y_0), respectively. Although Carberry et al. (1993) concluded for sorghum that the parameter estimates were very similar across main shoots and tillers, our more comprehensive analysis of pearl millet data indicates consistent differences in the parameter estimates among axes, justifying the use of axis-specific parameters in a leaf area module.

Table 7
Mean leaf area per axis and per plant (cm^2) plus RMSD for the estimates of leaf area per axis and per plant (cm^2) using bell-shaped functions with parameter estimates derived by five methods with increasing detail in parameter estimates[a]

Level	Observed mean area (cm^2)	RMSD				
		Method 1[b] (cm^2)	Method 2 (cm^2)	Method 3 (cm^2)	Method 4 (cm^2)	Method 5 (cm^2)
Axis	1154	444 (38)	390 (34)	323 (28)	261 (23)	251 (22)
Plant	4028	1556 (39)	1375 (34)	1103 (27)	919 (23)	910 (23)

[a] Values in parentheses express RMSD as a percentage of the mean.

[b] For description of the five methods, see text.

Table 8
Mean leaf area per axis (cm^2) plus RMSD using bell-shaped functions with parameter estimates derived by five methods with increasing detail in parameter estimates, stratified by cultivar, plant density and axis[a]

Level	n	Observed mean area (cm^2)	RMSD				
			Method 1[b] (cm^2)	Method 2 (cm^2)	Method 3 (cm^2)	Method 4 (cm^2)	Method 5 (cm^2)
Cultivar							
BJ 104	242	1235	438 (35)	436 (35)	336 (27)	255 (21)	242 (20)
HHB 67	228	719	320 (44)	164 (23)	147 (20)	134 (19)	128 (18)
RCB-IC 911	145	1628	643 (40)	508 (31)	414 (25)	327 (20)	320 (20)
WRajPop	272	1193	410 (34)	409 (34)	363 (30)	305 (26)	294 (25)
Plant density							
Low (<5 plants m^{-2})	567	1251	480 (38)	413 (33)	374 (30)	302 (24)	290 (23)
Medium	128	1216	373 (31)	323 (27)	233 (19)	197 (16)	194 (16)
High (>12 plants m^{-2})	192	823	374 (45)	359 (44)	186 (23)	145 (18)	140 (17)
Axis type[c]							
Main shoot	251	1343	499 (37)	440 (33)	360 (27)	259 (19)	259 (19)
T3	168	1142	424 (37)	349 (31)	271 (24)	252 (22)	236 (21)
T4	187	1117	448 (40)	384 (34)	318 (28)	253 (23)	251 (22)
T5	128	1096	453 (41)	401 (37)	343 (31)	273 (25)	256 (23)
T6	87	1062	424 (40)	412 (39)	352 (33)	290 (27)	260 (24)
T7	41	806	224 (28)	226 (28)	206 (26)	174 (22)	166 (21)

[a] Values in parentheses express RMSD as a percentage of the mean.

[b] For description of the five methods, see text.

[c] Observations do not add up to 887, because there were a few other tillers (T2, T8, T9).

4.1. Effects of TLN

TLN had a linear effect on the position of the largest leaf (X_0) and the slope of the relationship was well below unity. This observation was in accordance with the results obtained for sorghum (Muchow and Carberry, 1990; Carberry et al., 1993) and maize (Keating and Wafula, 1992). Within the range of observed TLN, the relationship between X_0 and TLN (across axes) that was reported for sorghum (Muchow and Carberry, 1990; Carberry et al., 1993) yielded virtually identical values for X_0 at a given TLN as our relationship across all axes (Eq. (4)). Similarly, the regression reported for the main shoot of maize by Keating and Wafula (1992) gave values for X_0 similar to T3 in our experiment. The available data thus suggest that in cereals the position of the largest leaf gradually shifts away from the flag leaf if TLN increases.

Estimates for a and b increased curvilinearly with TLN (except estimates for b of late tillers), in a similar fashion as reported for maize by Keating and Wafula (1992). The relationships they reported, yielded within the range of observed TLN, values for a and b that were comparable to our results for the main shoot. Carberry et al. (1993), however, reported for the main shoot of sorghum a linear relationship with TLN for both the parameters a and b, rather than a curvilinear relationship. It is very likely that the curvilinear nature of the relationships was not revealed in these sorghum experiments because of a narrow range in observed leaf numbers for the main shoot. As values for a approach zero, the leaf area profile loses its bell shape, making a linear relationship between a and TLN a mathematical impossibility. Although our curvilinear function for a is not asymptotic to zero, the current parameterisation only affects the bell shape of the leaf area function if leaf number is about 35. According to the results of the next paper in this series (van Oosterom et al., 2001), such high leaf numbers are only expected if the time to panicle initiation is about 900°C day. This is well beyond the maximum time to panicle initiation of about 600°C day, observed under a daylength beyond the ceiling photoperiod for the cultivars included in this study (van Oosterom et al., 2001). The increase in a and b with increasing TLN gives the leaf area profile a broader peak and makes it less skewed towards the left. This effect corroborates the observations on the position of the largest leaf (X_0), which moves away from the flag leaf as TLN increases, also resulting in making the leaf area curve less skewed.

The heterogeneity of pearl millet was especially evident in the poor association between the area of the largest leaf (Y_0) and TLN. This association was much weaker than that reported for sorghum (Carberry et al., 1993) and maize (Keating and Wafula, 1992). A reason for this difference is that pearl millet, unlike sorghum and maize, is a cross-pollinating crop. Although this heterogeneity appears to be a major weakness for any approach to model leaf area at an individual leaf level, the high number of plants measured in this study should ensure that the average plant size in the sample of observed plants closely represents the average plant size in the crop.

4.2. *Effects of cultivar*

The magnitude of the smallest RMSD in our experiments, about 23% of the mean observed leaf area if axis-specific parameter estimates were used (Method 4 or 5), was only marginally higher than that observed for sorghum (Carberry et al., 1993) in a comparable analysis. The size of the RMSD (using Method 4) varied by cultivar, ranging from 26% of the mean observed leaf area for the heterogeneous landrace WRajPop to 19% for the single cross hybrid HHB 67. The slightly higher RMSD in our study can thus be partly attributed to the heterogeneous nature of pearl millet as compared to sorghum.

The effect of cultivar on the leaf area profiles was limited to leaf size. Although inclusion of cultivar-specific values for Y_0 reduced the RMSD for leaf area estimation by only 10%, the importance of such an inclusion extends beyond improving the accuracy of leaf area estimations. Leaf size has an effect on tillering, as larger leaves on the main shoot cause more shading for the tiller leaves that are expanding lower in the canopy. As a result, the expansion of leaves on tillers will sooner become limited by carbon supply as main shoot leaves get larger, resulting in increased death of tillers. In our experiments, the cultivar with the largest leaves, RCB-IC 911 (Fig. 3, Table 4) was also the one with the lowest rate of tiller survival during stem elongation (van Oosterom et al., 2001). Tillering ability is an important feature of the adaptation of pearl millet to harsh environments with unpredictable occurrence of stress and genotypic differences in the ability to compensate losses in the main shoot through tillering have been reported (Mahalakshmi and Bidinger, 1986; Bidinger and Raju, 2000). Similarly, the reduction in panicle bearing tillers as daylength increases (Craufurd and Bidinger, 1988) can be attributed to the increased number of leaves on the main shoot under long daylength, which results in larger leaves and more shading. Inclusion of genotypic differences in individual leaf area into APSIM-millet allows simulation of the different tillering habits of contrasting plant types through simulation of differences in inter-axis competition.

Genotypic differences in leaf area profiles are a potential drawback for the wide applicability of an individual leaf approach to modelling, if parameterisation of new cultivars becomes cumbersome. In our study, cultivars affected only leaf size and their effect on the other three parameters (X_0, a, and b) was minor. Although the number of cultivars in this study was small, they did represent a range of genetic backgrounds, including Indian (WRajPop) and West African (RCB-IC 911). In addition, the close agreement between our results and those for sorghum (Carberry et al., 1993) and maize (Keating and Wafula, 1992) confirms that the robust relationships of X_0, a and b with TLN that we observed across cultivars within pearl millet are also valid in other cereals. This indicates that differences in leaf area profiles across species are mainly associated with differences in individual leaf size. Parameterisation of new cultivars only involves obtaining a relationship between area of the largest leaf and TLN. The logistics of that are straightforward, as Y_0 for an axis can easily be obtained at the flag leaf stage by measuring the area of the last few leaves, preferably at low plant densities under non-limiting conditions. This can greatly enhance the potentially wide applicability of the individual leaf approach to modelling leaf area.

4.3. *Effects of density*

Plant density had its main effect on the area of the largest leaf, but also a minor effect on its position. Our data did not allow a quantification of the effect of plant density on Y_0, but Maas et al. (1987) observed for sorghum that this effect is most dramatic at low plant densities, and becomes relatively small at densities >10 plants m^{-2}. In our experiment, we put the distinction at 5 plants m^{-2}, but since the lowest density in the high density group was 8.9 plants m^{-2}, our grouping was consistent with the results of Maas et al. (1987). If density would have had an effect only on Y_0, increasing plant density would reduce the area of all leaves on an axis by the same proportion (Eq. (2)). The effect of considering the shift in the position of the largest leaf as a response to increased plant density is illustrated in Fig. 7, which uses parameter estimates for a main shoot of WRajPop with 21 leaves, grown either at low (<5 plants m^{-2}) or high (>15 plants m^{-2}) plant densities. Early in the season, differences in leaf area are negligible, but the effect of density becomes apparent at the 12–13 leaf stage during stem elongation, when tillers stop growing and inter-plant competition for resources (light) increases under high plant density (van Oosterom et al., 2001). The decline in size of the upper leaves on an axis has been attributed to increased inter-plant competition (Maas et al., 1987). An effect of plant density on X_0 is consistent with this, as it causes leaf size to decline at an earlier stage under high plant density as compared to low plant density (Fig. 7). This shift in the peak of the leaf area curve has only a minor effect on total leaf area per axis or plant (and hence on the RMSD). However, it affects the distribution of leaf size on the axis as it results in a larger size for the early leaves and a smaller size for the later ones. This can affect the competitive strength of an axis and can hence affect tiller survival in the simulation model.

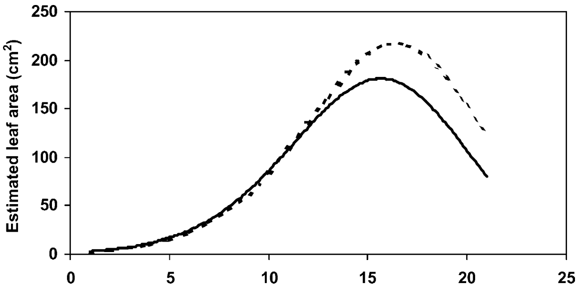

Fig. 7. Predicted leaf area profile for a main shoot of WRajPop with 21 leaves, using density-specific parameter estimates for X_0 and Y_0. Dotted line: <5 plants m^{-2}, solid line: >15 plants m^{-2}.

4.4. Effects of axis

The consistent differences in leaf area profiles between different axes that we observed reflect differences in phenology, but are also a result of increased competition for resources. The effect of axis on the estimates of parameters X_0, a, and b indicate that for any given number of leaves, the peak of the leaf area profile is broader and less skewed in tillers than in main shoots. Hence, the position of the largest leaf is shifted away from the flag leaf in tillers as compared with the main shoot (Fig. 1). This shift continues, although less pronounced, with each successive tiller. The differences in the position of the largest leaf between axes reflect the fact that late tillers experience more inter-axis competition than the main shoot and earlier developing tillers, resulting in a relatively earlier decline in leaf size (Maas et al., 1987). The differences between axes in breadth and skewness of the leaf area curve, however, are rather a result of phenological differences. In cereals, a sharp increase in the size of successive leaves has been associated with the transition of the growing point of the axis from its vegetative to its generative stage (Peacock, 1976; van Oosterom and Acevedo, 1993). In pearl millet, the time from appearance of an axis to panicle initiation is considerably shorter for tillers than for the main shoot. Craufurd and Bidinger (1988) reported that for T3, the duration of the period from appearance to panicle initiation is circa 100°C day shorter than for the main shoot, whereas for T5 this period takes about 150°C day less than the main shoot. With a phyllochron interval close to 36°C day per leaf (van Oosterom et al., 2001), this represents a difference of 3–4 leaves. This confirms data of Fig. 1, which indicate that leaf size increases rapidly after Leaf 5 in the main shoot, but already after Leaf 2 in T3 and even directly after Leaf 1 in T6. The consistent effect of axis that we observed does not support the conclusion of Carberry et al. (1993) for sorghum that the differences between main shoots and tillers are largely a result of differences in TLN between axes. A reason for this discrepancy might be the fact that the results for sorghum were biased by the large difference in TLN between main shoots and tillers, relative to the range in TLN within each of these two groups. The difference in phenology between main shoots and tillers as observed in pearl millet explains why the RMSD of main shoots is reduced if separate parameter estimates for main shoots versus all tillers were used.

The analysis of RMSD suggested that there is little merit in using axis-specific parameter estimates for tiller leaf area profiles. However, consistent differences in the area of the first leaves of successive tillers were observed. The size of each of the first four leaves, averaged across cultivars and densities, increased linearly from T3 to T7 (data not presented). Although differences in parameter estimates for individual tillers were small, their combined effect mimics this difference in size of the first leaves. The absence of any positive effect of axis-specific parameter estimates (compare Method 4 with Method 5) could be attributed to the fact that axis-specific parameter estimates affect individual leaf area estimates, but have little effect on the total leaf area per axis. Using parameter estimates that are pooled across axes will therefore give the early tillers (T3), a comparative early advantage in the simulation model, and the late tillers (T6) a comparative disadvantage. These early and late tillers were also the ones where RMSD was most reduced in Method 5 as compared with Method 4, with a reduction >6% for T3 and even >10% for T6. Ignoring these differences amongst tillers can affect tiller survival in the simulations and hence yield estimates.

5. Conclusions

The area of individual leaves on an axis could be adequately described by a bell-shaped function that was determined by parameters representing the position (X_0) and area (Y_0) of the largest leaf and the breadth (a) and skewness (b) of the leaf area profile curve. The relationships of TLN with three of the parameters were robust, not affected by cultivars and close to those reported for maize and sorghum. This suggests that these parameter estimates may have an applicability that goes well beyond the cultivars used in this study. This would greatly facilitate a wider applicability of the individual leaf area approach towards modelling leaf area dynamics. The results highlighted the consistent differences between main shoots and tillers in the leaf area profile. The parameters derived in this paper need to be combined with simulations of TLN, the appearance rate of leaves and tillers, and the rates of leaf senescence and tiller death, to simulate crop LAI throughout the growing season. This will be the subject of the next paper (van Oosterom et al., 2001). An individual leaf area approach to modelling crop LAI potentially offers the flexibility to simulate genotypic differences in LAI and tillering, which can result in cultivar × environment interactions for panicle number.

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References

Affholder, F., 1997. Empirically modelling the interaction between intensification and climatic risk in semiarid regions. Field Crops Res. 52, 79–93.

Bidinger, F.R., Raju, D.S., 2000. Mechanisms of adjustment by different pearl millet plant types to varying plant populations. J. Agric. Sci. Camb. 134, 181–189.

Carberry, P.S., Abrecht, D.G., 1991. Tailoring crop models to the semiarid tropics. In: Muchow, R.C., Bellamy, J.A. (Eds.), Climatic Risk in Crop Production: Models and Management for the Semiarid Tropics and Subtropics. CAB International, Wallingford, UK, pp. 157–182.

Carberry, P.S., Muchow, R.C., Hammer, G.L., 1993. Modelling genotypic and environmental control of leaf area dynamics in grain sorghum. II. Individual leaf level. Field Crops Res. 33, 311–328.

Carberry, P.S., Adiku, S.G.K., McCown, R.L., Keating, B.A., 1996. Application of the APSIM cropping systems model to intercropping systems. In: Ito, O., Johansen, C., Adu-Gyamfi, J.J., Katayama, K., Kumar Rao, J.V.D.K., Rego, T.J. (Eds.), Dynamics of Roots and Nitrogen in Cropping Systems of the Semi-Arid Tropics. Proceedings of the International Workshop, held at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, India, November 21–25, 1994. Japan International Research Center for Agricultural Sciences (JIRCAS), International Agriculture Series No. 3. JIRCAS, Japan, pp. 637–648.

Craufurd, P.Q., Bidinger, F.R., 1988. Effect of duration of the vegetative phase on shoot growth, development and yield in pearl millet (*Pennisetum americanum* (L.) Leeke). J. Exp. Bot. 39, 124–139.

Dwyer, L.M., Stewart, D.W., 1986. Leaf area development in field grown maize. Agron. J. 78, 334–343.

FAO and ICRISAT, 1996. The World Sorghum and Millet Economies. Facts, Trends and Outlook. Food and Agriculture Organization (FAO) of the United Nations, Via delle Terme di Caracalla, Rome, Italy, and International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, India, 68 pp.

Hammer, G.L., Carberry, P.S., Muchow, R.C., 1993. Modelling genotypic and environmental control of leaf area dynamics in grain sorghum. I. Whole plant level. Field Crops Res. 33, 293–310.

Huda, A.K.S., Sivakumar, M.V.K., Alagarswamy, G., Virmani, S.M., Vanderlip, R.L., 1984. Problems and prospects in modelling pearl millet growth and development: a suggested framework for a millet model. In: Virmani, S.M., Sivakumar, M.V.K. (Eds.), Agrometeorology of Sorghum and Millet in the Semi-arid tropics. Proceedings of the International Symposium, 15–20 November, 1982. ICRISAT, Patancheru, Andhra Pradesh, India.

ICRISAT, 1989. Modelling the growth and development of sorghum and pearl millet. Research Bulletin No. 12. In: Virmani, S.M., Tandon, H.L.S., Alagarswamy, G. (Eds.), International Crops Research Institute for the Semi Arid Tropics, Patancheru, Andhra Pradesh, India, 43 pp.

Keating, B.A., Wafula, B.M., 1992. Modelling the fully expanded area of maize leaves. Field Crops Res. 29, 163–179.

Kollavalli, S., 1997. Water and nutrient management: farmers' practices, perceptions, and researchable issues. In: Seeling, B., Joshi, N.L. (Eds.), From Research Station to Farmer's Fields: Nutrient Management Research for Millet-based Cropping Systems of Western Rajasthan. Proceedings of a Planning Workshop, 20–22 May, 1996, Jodhpur, India. International Crops Research Institute for the Semi-arid Tropics, Patancheru, Andhra Pradesh, India and Central Arid Zone Research Institute, Jodhpur, Rajasthan, India, pp. 71–77.

Lambert, C., 1983. Influence de la précocité sur le développement du mil (*Pennisetum typhoides* Stapf et Hubbard) en conditions naturelles. II. Elaboration du rendement. Agron. Trop. 38, 7–15.

Maas, S.J., Arkin, G.F., Rosenthal, W.D., 1987. Relationships between the areas of successive leaves on grain sorghum. Agron. J. 79, 739–745.

Mahalakshmi, V., Bidinger, F.R., 1986. Water deficit during panicle development in pearl millet: yield compensation by tillers. J. Agric. Sci. Camb. 106, 113–119.

McCown, R.L., Hammer, G.L., Hargreaves, J.N.G., Holzworth, D.P., Freebairn, D.M., 1996. APSIM: a novel software system for model development, model testing, and simulation in agricultural systems research. Agric. Syst. 50, 255–271.

Meinke, H., Hammer, G.L., van Keulen, H., Rabbinge, R., 1998. Improving wheat simulation capabilities in Australia from a cropping systems perspective. III. The integrated wheat model (I-WHEAT). Eur. J. Agron. 8, 101–116.

Monteith, J.M., Huda, A.K.S., Midya, D., 1989. RESCAP: a resource capture model for sorghum and pearl millet. In: Virmani, S.M., Tandon, H.L.S., Alagarswamy, G. (Eds.), Modelling the Growth and Development of Sorghum and Pearl Millet. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Research Bulletin No. 12. Patancheru, Andhra Pradesh, India, pp. 30–34.

Muchow, R.C., Carberry, P.S., 1990. Phenology and leaf-area development in a tropical grain sorghum. Field Crops Res. 23, 221–237.

Payne, W.A., Wendt, C.W., Lascano, R.J., 1990. Root zone water balances of three low-input millet fields in Niger, West Africa. Agron. J. 82, 813–819.

Payne, W.A., Wendt, C.W., Hossner, L.R., Gates, C.E., 1991. Estimating pearl millet leaf area and specific leaf area. Agron. J. 83, 937–941.

Peacock, J.M., 1976. Temperature and leaf growth in four grass species. J. Appl. Ecol. 13, 225–232.

SAS, 1985. SAS User's Guide: Statistics, Version 5. SAS Institute Inc., Cary, NC.

Sharma, P.C., Pareek, R.S., 1993. Variability of southwest monsoon in west Rajasthan during last two decades. Mausam 44, 389–391.

Sivakumar, M.V.K., 1988. Predicting rainy season potential from the onset of rains in southern Sahelian and Sudanian climatic zones of west Africa. Agric. For. Meteor. 42, 295–305.

Stoorvogel, J.J., Smaling, E.M.A., Janssen, B.H., 1993. Calculating soil nutrient balances in Africa at different scales. I. Supranational scale. Fert. Res. 35, 227–235.

van Oosterom, E.J., Acevedo, E., 1993. Leaf area and crop growth in relation to phenology of barley in Mediterranean environments. Plant and Soil 148, 223–237.

van Oosterom, E.J., Whitaker, M.L., Weltzien Rattunde, E., 1996. Integrating genotype × environment analysis, characterisation of drought patterns, and farmer preferences to identify adaptive plant traits for pearl millet. In: Cooper, M., Hammer, G.L. (Eds.), Plant Adaptation and Crop Improvement. CAB International/IRRI/ICRISAT, pp. 383–402.

van Oosterom, E.J., Carberry, P.S., Hargreaves, J.N.G., O'Leary, G.J., 2001. Simulating growth, development, and yield of tillering pearl millet 2. Simulation of canopy development. Field Crops Res. 72, 67–91.

Verberne, E., Dijksterhuis, G., Jongschaap, R., Bazi, H., Sanou, A., Bonzi, M., 1995. Simulations des cultures pluviales au Burkina faso (CP-BKF3): sorgho, mil et mais. Nota 18, DLO Institute for Soil Fertility and Agroecological Research, Oosterweg 92, PO Box 129, 9750 AC Haren, The Netherlands, 53 pp. plus appendices.