

Predicting plant leaf area production: shoot assimilate accumulation and partitioning, and leaf area ratio, are stable for a wide range of sorghum population densities

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Abstract

Predicting plant leaf area production is required for modelling carbon balance and tiller dynamics in plant canopies. Plant leaf area production can be studied using a framework based on radiation intercepted, radiation use efficiency (RUE) and leaf area ratio (LAR) (ratio of leaf area to net above-ground biomass). The objective of this study was to test this framework for predicting leaf area production of sorghum during vegetative development by examining the stability of the contributing components over a large range of plant density. Four densities, varying from 2 to 16 plants m⁻², were implemented in a field experiment. Plants were either allowed to tiller or were maintained as unicum by systematic tiller removal. In all cases, intercepted radiation was recorded daily and leaf area and shoot dry matter partitioning were quantified weekly at individual culm level. Up to anthesis, a unique relationship applied between fraction of intercepted radiation and leaf area index, and between shoot dry weight accumulation and amount of intercepted radiation, regardless of plant density. Partitioning of shoot assimilate between leaf, stem and head was also common across treatments up to anthesis, at both plant and culm levels. The relationship with thermal time (TT) from emergence of specific leaf area (SLA) and LAR of tillering plants did not change with plant density. In contrast, SLA of unicum plants was appreciably lower under low-density conditions at any given TT from emergence. This was interpreted as a consequence of assimilate surplus arising from the inability of the plant to compensate by increasing the leaf area a culm could produce. It is argued that the stability of the extinction coefficient, RUE and plant LAR of tillering plants observed in these conditions provides a reliable way to predict leaf area production regardless of plant density. Crown Copyright © 2002 Published by Elsevier Science B.V. All rights reserved.

Keywords: Sorghum plant density; Tillering; Intercepted radiation; Extinction coefficient; Radiation use efficiency; Shoot assimilate partitioning; Specific leaf area; Leaf area ratio

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1. Introduction

Plant leaf area is a key determinant of the carbon balance of a plant during vegetative development. In early crop development, plant leaf area is the only supplier of, as well as the main sink for, carbohydrates and can be highly influenced by tillering (Hammer et al., 1987). Tiller production is thought to be mainly driven by plant carbon balance via assimilate availability, as observed in wheat, rice, barley, ryegrass and sorghum (Friend, 1965; Honda and Okajima, 1970; Kirby and Faris, 1972; Ong and Marshall, 1979; Gerik and Neely, 1987), even though light quality was reported to affect duration of tiller emergence (Casal et al., 1986; Gautier et al., 1995). It appears that this response to light quality acts mostly as an early perception of assimilate shortage (Deregibus et al., 1985; Ballaré et al., 1987). So, a tiller is likely to emerge and develop in conditions of assimilate surplus and to cease development and senesce under conditions of assimilate shortage. Accordingly, the ability to reliably estimate the assimilate supply available for plant leaf area development, depending on growing conditions and plant developmental stage, is essential for a modelling approach to tiller production.

Assimilate supply available for plant leaf area can be estimated by adapting existing predictive frameworks for crop yield. Monteith (1977) has provided a framework for the analysis of variation in crop yield in terms of three easily measurable factors: the amount of radiation intercepted, the efficiency of its use in net above-ground biomass production and the proportion of the net above-ground biomass partitioned to grain. During vegetative development, this framework could be adapted to leaf area if the third factor became the proportion of net above-ground biomass partitioned to leaf area, i.e. the leaf area ratio (LAR). This kind of framework has been used in crop production modelling and its ability to predict leaf area and crop yield over a range of conditions has been demonstrated for maize, sorghum, rice and wheat (Maas, 1993; Hammer and Muchow, 1994; Bastiaans et al., 1997; Jamieson et al., 1998). However, these models do not take into account morphological plasticity of the plant in response to agronomic manipulations as they usually consider a population formed by homogeneous culms. This implies in particular that partitioning of net above-ground biomass to leaf area is similar at plant level regardless of tiller number on the plant. In this

study, the validity of this framework to estimate reliably leaf area production at plant level from the three factors mentioned above was tested in a wide range of sorghum population densities.

The first factor, the amount of radiation intercepted by a crop, is known to be a function of its leaf area index (LAI), its extinction coefficient (k) and the incident radiation (Clegg et al., 1974; Muchow et al., 1982; Squire et al., 1984). The proportion of incident radiation that is intercepted increases with LAI and can reach a maximum of 0.9–1.0 in several crops. This method at whole canopy level assumes, however, that leaf angle distribution is common throughout the canopy and that radiation is diminished uniformly as it passes through the canopy leaf area according to Lambert's law. It does not take account of detailed canopy architecture, angular distribution of the incident radiation and spectral properties of leaves, which are main determinants of the amount of intercepted radiation (Campbell, 1986). These determinants can affect the value calculated for k at different stages of canopy development and in different population densities or plant configurations (Zaffaroni and Schneiter, 1989).

The second factor, the efficiency of use of intercepted radiation in producing net above-ground biomass (radiation use efficiency, RUE), is assumed to be stable and cultivar dependent (Muchow and Davis, 1988; Kiniry et al., 1989; Rosenthal et al., 1993). It is known to be a key determinant of yield differences between species (Muchow, 1989; Pengelly et al., 1999). This stability of RUE implies, however, that above-ground weight loss due to respiration is proportional to above-ground weight gain due to photosynthesis and that light saturation of photosynthesis observed for isolated leaves does not occur for leaf canopies even under high plant density. It further implies that photosynthesis and respiration are related similarly at differing developmental stages and with various plant density conditions. It is known that these implications do not hold under all conditions. Decreasing values of RUE were observed with increasing biomass, due to more rapid increase in respiration than photosynthesis (McCree, 1983), and increasing values of RUE were found with decreasing levels of radiation (Hammer and Wright, 1994).

The third factor, the LAR, was commonly used in growth analysis and studies involving allometric relationships among organs (Williams et al., 1965; Radford, 1967). LAR is the product of two components,

the leaf weight ratio (LWR), which is the ratio of leaf dry weight to net above-ground dry weight, and the specific leaf area (SLA), which is the ratio of leaf area to leaf dry weight (Bruggink and Heuvelink, 1987; Poorter and Remkes, 1990). Hence, the LAR may mask differences in partitioning and in leaf thickness even if it is stable across various growing conditions. The robustness of the stability of LAR in a wide range of assimilate availability depends therefore on the stability at plant level of both the LWR and the SLA. But this stability is questioned since these factors may vary in conditions associated with changes in assimilate balance in the plant. Fischer and Wilson (1975) for sorghum, Azam-Ali et al. (1984) for millet and Dingkuhn and Sow (1997) for rice noted some variation with plant density in shoot assimilate partitioning at plant level during grain filling. Heuvelink and Buiskool (1995) measured a decrease in SLA of tomato plants when assimilate demand was reduced. And Bruggink and Heuvelink (1987) showed that plant LAR of vegetable species decreased with increasing light intensity.

The objective of this study was to examine the stability of the extinction coefficient, RUE, LWR and SLA in sorghum for a wide range of population density. This could establish the validity of this framework as a means to estimate assimilate supply available for leaf area production and, thus, underpin an approach for modelling tiller production (Lafarge and Hammer, 2002). This analysis focussed on the period up to anthesis as plant leaf area is developed, and fertile tiller number is determined, during this period (Ong, 1984). A broad range of plant density from 2 to 16 plants m^{-2} , that represented the large variation in growing conditions found in farming areas, was employed with non-limiting water and nitrogen supply conditions. A tiller removal treatment was performed in each density to ensure that the conditions encountered in the study included high assimilate supply per culm.

2. Material and methods

2.1. Plant material and growing conditions

Grain sorghum (*Sorghum bicolor* (L.) Moench) was grown under non-limiting water and nitrogen supply in a field experiment at Lawes (27.34°S, 152.20°E, 90 m

altitude a.s.l.), in southeastern Queensland, Australia. A split-plot design was set up with two tiller treatments and four planting densities in three replicates, with planting density as the first split and tiller treatment the second. The four planting densities were 2, 4, 8 and 16 plants m^{-2} , represented as D1, D2, D3 and D4, respectively in the following sections. The two tiller treatments included a tiller removal treatment, in which tillers were systematically removed as they emerged, and the natural situation. Plots were 4 m wide and comprised eight rows at 0.5 m spacing. Plot lengths were 10 m for D4, 20 m for D2 and D3, and 30 m for D1. 'Buster', a well-adapted commercial Australian dwarf hybrid with little photoperiod response (Hammer, unpublished data), was chosen for its high tillering ability. The crop was sown on 23 October 1998 at a depth of 20 mm using a coneseeder planter, at a target rate 3–5 times the required density. Plots were thinned to the required density on 8 November. Seed was dressed with Concep (Ciba Geigy, Basle; 1,3-dioxolan-2-ylmethoxy imano (phenyl) acetonitrile) at 1.25 mg g^{-1} , for protection against pre-emergence herbicides. Immediately after sowing, Dual (metolachlor) at 2.4 l ha^{-1} and Gesaprim (atrazine) at 2.4 l ha^{-1} were applied to provide good weed control. When necessary, *Heliothis armigera* and *Contarinia sorghicola* were controlled by applications of Deltamethrin at 1.25 mg m^{-2} or Endosulfan at 73.5 mg m^{-2} . Leaf rust was controlled by applications of Mancozeb at 160 mg m^{-2} . There was negligible damage to the photosynthetic leaf surface throughout growth.

The soil at the experimental site was a Lawes brown black clay loam, which is a moderately fertile deep alluvial, weakly cracking vertisol (Typic Chromustert) that was well drained. It was characterised in the upper layers (0–0.2 m) by pH of 7.2, cation exchange capacity of 31.1 meq 100 g^{-1} and electric conductivity of 0.4 dS m^{-1} , and in the deeper layers (0.4–0.6 m) by pH of 7.6, cation exchange capacity of 40.4 meq 100 g^{-1} and electric conductivity of 0.3 dS m^{-1} . Bulk density was 1.34 at 0–0.2 m, 1.30 at 0.4–0.6 m and 1.45 at 0.9–1.2 m. Fertiliser containing potassium at 9 g m^{-2} as muriate of potash, phosphorous at 2.5 g m^{-2} , copper sulphate and zinc sulphate at 0.3 g m^{-2} as single superphosphate with copper and zinc was applied before sowing. A broadcast application of 24 g m^{-2} nitrogen as urea was made at sowing with additional applications of 6 g m^{-2} at initiation and anthesis. The site had a cover crop of oats

(2.5 g m⁻² applied N), which was removed in September 1998. Before sowing, soil nitrogen rating was 6.4 mg kg⁻¹ soil at 0–0.2 m, 1.4 at 0.4–0.6 m and 0.1 at 0.9–1.2 m. At maturity, it was 2.1 mg kg⁻¹ soil at 0–0.2 m, 1.5 at 0.4–0.6 m and 2.7 at 0.9–1.2 m. Overhead irrigation was applied to keep the soil water profile at full water potential.

2.2. Climatic measurements and calculations

Incident solar radiation (I_0 , Li 200S, Li-Cor, Lincoln, Nebraska, USA) and air temperature (108-L6, Campbell Scientific, Shepshed, Leicestershire, UK) in a ventilated cylinder were measured 1.5 m above soil level. Data were stored hourly in a datalogger (CR10, Campbell Scientific, Shepshed, Leicestershire, UK) and, with addition of minimum and maximum temperature, averaged daily. Variation of daily temperature during the plant cycle (data not shown) was 12 °C (from 18 to 30 °C). Two thermal periods were distinguished, one up to 400 °C days after emergence with daily temperature around 21 °C and the other subsequently, with daily temperature around 25 °C.

Daily thermal time (δ TT) was calculated from a broken linear function of the mean air temperature, depending on three parameters, base, optimum and maximal temperatures, respectively, 11, 30 and 42 °C, as reported by Hammer et al. (1993). Thermal time (TT) was then calculated by accumulating δ TT from seedling emergence. The base temperature used was derived from studies on leaf appearance rate of 12 sorghum hybrids (Hammer et al., 1993) and was similar to that determined by Lafarge et al. (1998), 10.8 °C, using leaf appearance and leaf elongation rates analysed for different leaf positions and different growing periods at two different locations. Lafarge et al. (1998) highlighted the role of meristem temperature on plant growth and development. Meristem temperature was not essential in the present study, however, as plant measurements were performed for a single growing period at a weekly interval at plant level and with the general goal to compare density treatments rather than analyse temperature effects. Lafarge et al. (1998) also proposed to calculate TT with a base temperature only, providing a correction of plant variables with vapour pressure deficit of the air. In this study, TT was simply calculated from three temperature parameters that took into account the

detrimental effect of vapour pressure deficit by its correlation with high temperature. Such conditions occurred rarely in this study.

Radiation interception was measured by placing a 1 m long tube solarimeter (Type TSL, Delta-T Devices, Cambridge, UK) at ground level in each plot. The radiation transmitted to the soil through the crop canopy in the range 0.35–2.5 μ m was recorded using the data collection system described by Muchow and Davis (1988). Before being installed, the tubes were cleaned with vinegar, levelled by use of built-in levelling bubble and gassed using compressed industrial nitrogen to free them from condensation. They were calibrated by positioning on a rack in an area free from shading, choosing one of them as a reference and determining correction factors for the others. Tubes were placed 0.05 m above ground level and diagonally across the two inner rows of each plot so that the ends of the tube were both midway between rows. Dead leaves were removed weekly from plants around the tube solarimeters, so that the radiation intercepted by green leaf only was recorded. Using a single solarimeter per plot gives rise to an issue of representativeness, especially in the low-density treatment where shadow originated mainly from one or two plants. This issue was mostly resolved, however, when observations from the three replicates studied in this experiment were analysed and the extent of any error quantified. The reference tube solarimeter was placed above the crop, and orientated the same way as the tubes in the plot, to record incident radiation. Readings from the solarimeters were recorded every 5 min using a CR10 datalogger and the values averaged to an hourly reading. The fraction of incident radiation intercepted in the plot x (F_{i_x}) was determined hourly by dividing the value transmitted to the tube (R_{t_x}), modified with its correction factor (C_{f_x}), by the value intercepted by the reference tube (R_t), and by subtracting the resulting value from 1:

$$F_{i_x} = 1 - \frac{R_{t_x} C_{f_x}}{R_t} \quad (1)$$

The amount of radiation intercepted in the plot x (S_{i_x}) was calculated daily as the cumulative product of the fraction intercepted and the solar incident radiation:

$$S_{i_x} = \sum F_{i_x} I_0 \quad (2)$$

It was then calculated on a per plant basis by dividing S_{ix} by the plant density. From seedling emergence up to the stage of five fully expanded leaves on the main culm (just before emergence of first tillers), accurate readings from solarimeters were not possible due to the small plant size. As a consequence, daily intercepted radiation during this period was calculated as the cumulated product of hourly incident radiation by plant leaf area calculated on that day, that was determined as the sum of the area of all individual leaves of the plant that had appeared. This method assumed that all expanded leaf area of the plant on that day was intercepting light and that the effect of the leaf zenith angle on the interception was negligible at such early plant stages.

2.3. Phenological measurements and calculations

Seedling emergence was scored daily on 2 m of row (4 m for the highest density) in each plot until emergence ceased. Emergence was considered to have occurred when the plant could be seen above the soil surface. The date of 50% emergence, which occurred 5 days after sowing, was defined as the first day on which at least 50% of the final day count plants had emerged. Floral initiation of the main culm was measured under a binocular microscope (SZ 6045 TR, Olympus Optical, Tokyo, Japan) by dissecting three plants from each plot, collected from the guard rows every day. Initiation was deemed to have occurred when the first row of floral primordia was visible on the shoot apex. Anthesis was noted by scoring five adjacent tagged plants in the inner rows of each plot. Each head was rated every second day by assessing how far down the head anthers were observed, in increments of 5%. Date of anthesis was determined in each plot when the average of 50% of exerted anthers was reached. Physiological maturity was noted on 10 plants, the five used for assessment of anthesis plus another five in an adjacent row. Each head was rated every second day by assessing the presence of black layer on individual grains. The attachment point at the seed base, through which plants translocate assimilates to the grain, turns black when the grain is mature (Eastin et al., 1973). Grains on individual heads were assessed in quartiles from the tip down. If five or more grains from 10 sampled had reached black layer in the first quartile, the head was

physiologically mature to that quartile, and was rated as 25% mature. Date of maturity was determined in each plot when the average value of 90% mature was reached on the 10 main culm heads observed. In each case, the mean over the three replicates provided the value for each treatment.

The production of fully expanded leaves on the main culm was recorded weekly by noting ligule appearance on the five tagged plants in each plot until ligule appearance of the final leaf. A ligule was counted once it was visible above the enclosing sheath of the previous leaf. When ligule appearance of the final leaf was approaching, observations were made every day and date of ligule appearance of the final leaf was then determined. Tiller emergence was observed weekly on the five tagged plants in each plot. The origin of each emerged tiller, defined by the main culm node from which it developed and sheath from which it emerged, was written on one of the tiller's leaves. For example, T3 was for a tiller that developed from node 3 of the main culm and so emerged from sheath of leaf 3. The production of fully expanded leaves was recorded for all emerged tillers on the tagged plants in the same manner as for main culms, and ligule appearance of the final leaf and anthesis were noted. Data from the tagged plants in each plot were averaged to derive plant variables for data analysis.

2.4. Destructive morphological measurements and calculations

Biomass accumulation was determined by sampling plants in each plot every 7 days from time of thinning to anthesis, and at mid-grain filling and maturity. At each harvest, plants were cut at ground level from the four inner rows of each plot in a 4 m² quadrat in D1, a 2 m² quadrat in D2 and D3, and a 1 m² quadrat in D4. A minimum of 0.5 m was left between each harvest area. For each sample, main culms and tillers were separated and numbered systematically. Tillers were regularly identified and labelled in the field, close to their date of emergence, to avoid any confusion at harvest time. However, some difficulties in identifying tillers towards the end of the plant cycle may have introduced minor error in tiller number associated with each tiller origin. Moreover, subsequent measurements have included senescent tillers during destructive harvests as it was not practical to separate senescent tillers

from others with the same node of origin. For each culm at each harvest, biomass was separated into four components: green and dead leaves, stems (which comprised sheaths and internodes) and heads (when present). Net above-ground biomass per unit area was obtained for each component after drying the samples at 80 °C until there was no further weight loss (6–7 days). Shoot dry weight of any culm (g) was calculated as the sum of dry weight of leaves, stems and heads. LWR was calculated as the ratio of leaf dry weight to total shoot dry weight. A sub-sample of green leaves from each type of culm (roughly one-third of the collected area, but the total area if dry weight samples were lower than 10 g) was isolated systematically before drying. The area of these leaves was measured with a leaf area meter (Mk2, Delta-T Devices, Cambridge, UK) and their dry weight determined. For each type of culm, SLA ($\text{cm}^2 \text{g}^{-1}$) was calculated by dividing leaf area by leaf dry weight. Total green leaf area (GLA) (cm^2) for the harvest area was determined from the product of total green leaf dry weight and SLA. LAI was calculated as the total GLA divided by the harvest area of each plot. LAR ($\text{cm}^2 \text{g}^{-1}$) was calculated as the product of SLA and LWR. All measurements were determined on a per plant basis by dividing each variable by the plant number per plot. Green leaves of each type of culm were analysed for N concentration at anthesis and maturity using method 7A1 for total nitrogen analysis (Bremner, 1965). Tissue nitrogen concentrations (2.96% in main culm green leaves at anthesis and 1.93% at maturity) indicated that non-limiting conditions were achieved for nitrogen.

Development of fertile main culms and tillers was observed and compared. All main culms of tillering and unculm plants in all plant densities produced grain at maturity (data not shown). The tiller type that was the most productive was T3 (i.e. the tiller that developed from node 3 of the main culm). T3 was fully fertile in D1 and D2, but some senescence was observed in D3 and considerable senescence occurred in D4 (data not shown). The analysis presented here concerned only main culms of tillering and unculm plants and T3. Because of differences in their timing of emergence and in their duration up to maturity, development of all tillers, while being quicker than that of main culms, was slightly later. To compare dry matter partitioning of T3 and main culms at the same developmental stage, this effect was taken into account by considering the TT for

T3 at each harvest time in a manner that was consistent to that for main culms. Emergence of T3 was estimated as the x -intercept of the regression of fully expanded leaf number on TT and ligule appearance of its final leaf was noted in the field. To achieve this comparison with the main culm, duration of the period from emergence to last ligule appearance was obtained for main culms and T3, and the ratio of the duration for main culms to that for T3 was calculated. Emergence of T3 was then considered to be simultaneous to that of main culms and TT of each subsequent measurement on T3 was modified by a factor corresponding to the ratio of the durations. This also facilitated estimation of timing of floral initiation for T3.

2.5. Architectural and physiological analysis

The extinction coefficient, k , and the maximal fraction of intercepted radiation, LI_{max} , were determined by fitting:

$$\frac{\text{LI}}{I_0} = \text{LI}_{\text{max}}(1 - e^{-k\text{LAI}}) \quad (3)$$

where LI and I_0 (MJ m^{-2}) are the intercepted and incident radiation, respectively, and LAI the leaf area index. RUE (g MJ^{-1}) was calculated as the slope of the linear relation between shoot dry weight (g m^{-2}) and intercepted radiation accumulated from emergence (MJ m^{-2}).

2.6. Statistical analysis

Fitting of non-linear relationships and parameter estimation were carried out using the least squares method (GRG2 algorithm, Excel, Microsoft). Differences in relationships among plant density treatments were tested using analysis of covariance. The residual sum of squares for a relationship fitted to a specific density treatment was compared to the residual sum of squares for the same relationship fitted to data from all density treatments.

3. Results

The relationship between fraction of intercepted radiation and LAI was observed between emergence and anthesis for all plant density and tillering treatments (Fig. 1). Data collected after anthesis were not

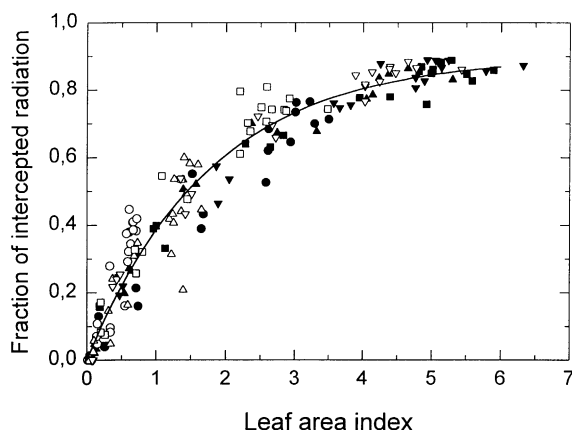


Fig. 1. Relationship between the fraction of intercepted radiation and LAI for tillering (closed symbols) and unicum (open symbols) plants at 2 plants m^{-2} (\bullet), 4 plants m^{-2} (\blacktriangle), 8 plants m^{-2} (\blacksquare) and 16 plants m^{-2} (\blacktriangledown). Data were calculated weekly between emergence and anthesis. Solid line is the non-linear regression, $LI/I_0 = LI_{\max} (1 - e^{-kLAI})$, with $LI_{\max} = 0.9$ and $k = 0.56$, fitted for all plant densities and tillering treatments.

taken into account to avoid any confounding effects of senescent leaves on the measurement of interception. An exponential model (Eq. (3)) was fitted separately to all treatments except D1, where the limited range of variation in LAI (<1 for unicum plants and <3.5 for tillering plants) prevented reliable fitting. Fitted models did not differ significantly among the remaining three plant density treatments within tillering plants. Differences among density treatments within unicum plants and between tillering treatments were, however, statistically significant ($P = 0.05$) but small in magnitude. Accordingly, a single model was fitted for all plant density and tillering treatments. The extinction coefficient and maximal fraction of light interception were fitted at 0.56 and 0.9, respectively.

The relationship between shoot dry weight and accumulated intercepted radiation per unit area was observed between emergence and anthesis for all plant density and tillering treatments (Fig. 2). Data collected after anthesis were not taken into account to avoid any confounding effects of senescent leaves on the measurement of interception. A linear regression was fitted separately to all treatments except D1, where the limited range of variation in intercepted radiation prevented reliable fitting. The fitted linear regressions did not differ significantly among the remaining three

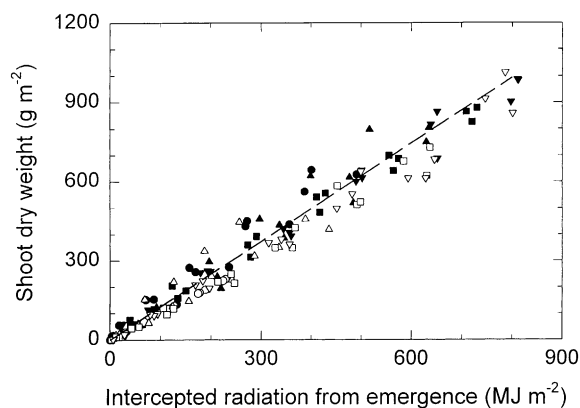


Fig. 2. Relationship between shoot dry weight and intercepted radiation. Symbols as in Fig. 1. Data were calculated weekly between emergence and anthesis. Solid line is the linear regression fitted using only data from tillering plants. The slope is the RUE, which was 1.24 g MJ^{-1} .

plant density treatments within each tillering treatment. The model did, however, differ significantly between the two tillering treatments ($P < 0.001$): biomass of emerged tillers removed weekly to obtain unicum plants was not included in this analysis and most likely explains this difference. Consequently, a unique linear model was fitted for all plant density treatments using only data from tillering plants. This model was valid for intercepted radiation up to 800 MJ m^{-2} and shoot dry weight up to 1000 g m^{-2} . Accordingly, the resultant slope of the model, i.e. RUE which was determined as 1.24 g MJ^{-1} , was assumed to apply to all plant density treatments.

The same pattern with TT in dynamics of leaf, stem and head dry weights was observed at plant level for tillering plants in the four density treatments (Fig. 3). In D1, leaf and stem dry weights increased similarly until $600 \text{ }^\circ\text{C}$ days after emergence, which corresponded to ligule appearance of the final leaf on the main culm (Fig. 3a). After $600 \text{ }^\circ\text{C}$ days, head dry weight increased rapidly up to 550 g , whereas leaf dry weight remained fairly constant at 120 g and stem dry weight increased for a while and then tended to remain constant at 160 g . Organ dry weights differed greatly among treatments, but relative differences among organs within a treatment were similar in D2, D3 and D4 to that found in D1 (Fig. 3a–d). Leaf, stem and head dry weights at maturity were 120 , 160 and 550 g in D1; 65 , 90 and 290 g in D2; 35 , 50 and

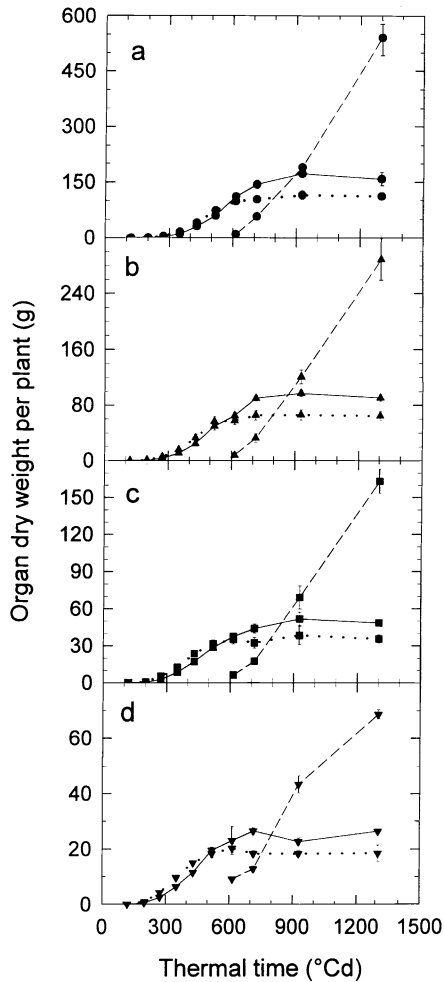


Fig. 3. Change with TT from emergence in organ dry weight for tillering plants at 2 plants m^{-2} (a, ●), 4 plants m^{-2} (b, ▲), 8 plants m^{-2} (c, ■) and 16 plants m^{-2} (d, ▼). In a–d, the dotted line is for leaf dry weight, solid line for stem dry weight and dashed line for head dry weight. Vertical lines represent the standard error of the mean of three replications.

165 g in D3; and 18, 26 and 68 g in D4. A similar pattern in dynamics of organ dry weight with TT was observed at culm level for T3 and for main culms of tillering and unicum plants for the four plant densities tested (Fig. 4). Although organ dry weights differed among culms and densities, relative differences among organs were similar within density treatments for each culm type. Organ dry weight of main culms of tillering plants at maturity increased with decreasing plant density, from 14.7 to 23.2 g for leaf (Fig. 4b),

23.0 to 28.3 g for stem (Fig. 4e) and 63 to 117 g for head (Fig. 4h). For unicum plants, it increased with decreasing plant density from 17.5 to 32.1 g for leaf (Fig. 4c), 23.8 to 53.1 g for stem (Fig. 4f) and 83 to 193 g for head (Fig. 4i). And for T3, it increased between D2 and D1 (where these tillers were all fertile) from 13.6 to 23.1 g for leaf (Fig. 4a), 20.2 to 32.2 g for stem (Fig. 4d) and 62 to 113 g for head (Fig. 4g). Values for T3 were appreciably lower in D3 and mainly in D4 as they included senescent tillers (see Section 2). The amplitude of variation of organ dry weight, however, differed between culm types. Dry weights of leaf, stem and head at maturity were similar in D4 for main culm of tillering and unicum plants, whereas they were significantly higher in lower densities for unicum plants than for tillering plants. Organ dry weights were also similar for main culm and T3 in D1 of tillering plants, whereas they were significantly higher for main culm in D2.

A disparity in the patterns in dynamics of main culm dry weight was observed, however, between anthesis and maturity. In the case of tillering plants in D1 and D2 (Fig. 4b and e), stem dry weight decreased slightly during this period. In the case of tillering plants in D3 and D4 (Fig. 4b and e) and of unicum plants in D4 (Fig. 4c and f), stem dry weight decreased strongly between anthesis and mid-grain filling, then increased until maturity, and leaf dry weight was relatively constant during this whole period (any decrease was likely due to leaf loss). In the case of unicum plants in D1, D2 and D3 (Fig. 4c and f), stem dry weight decreased strongly until mid-grain filling, then increased until maturity, and leaf dry weight increased from anthesis to maturity.

Leaf dry weight increased linearly with shoot dry weight at the time of panicle initiation for all the fertile culms studied in Fig. 4, i.e. the eight main culms of tillering and unicum plants in the four plant densities and the two tillers for T3 in D1 and D2 (Fig. 5a). Similar linear relationships between leaf and shoot dry weights, that were independent of culm type, were also observed at time of ligule appearance of the final leaf (Fig. 5b), anthesis (Fig. 5c) and maturity (Fig. 5d). These linear relationships were maintained over the large range in shoot dry weight per culm observed in this study, from 4 to 6 g at panicle initiation, 25 to 60 g at last ligule appearance, 40 to 90 g at anthesis and 100 to 275 g at maturity. The slope of the fitted regressions

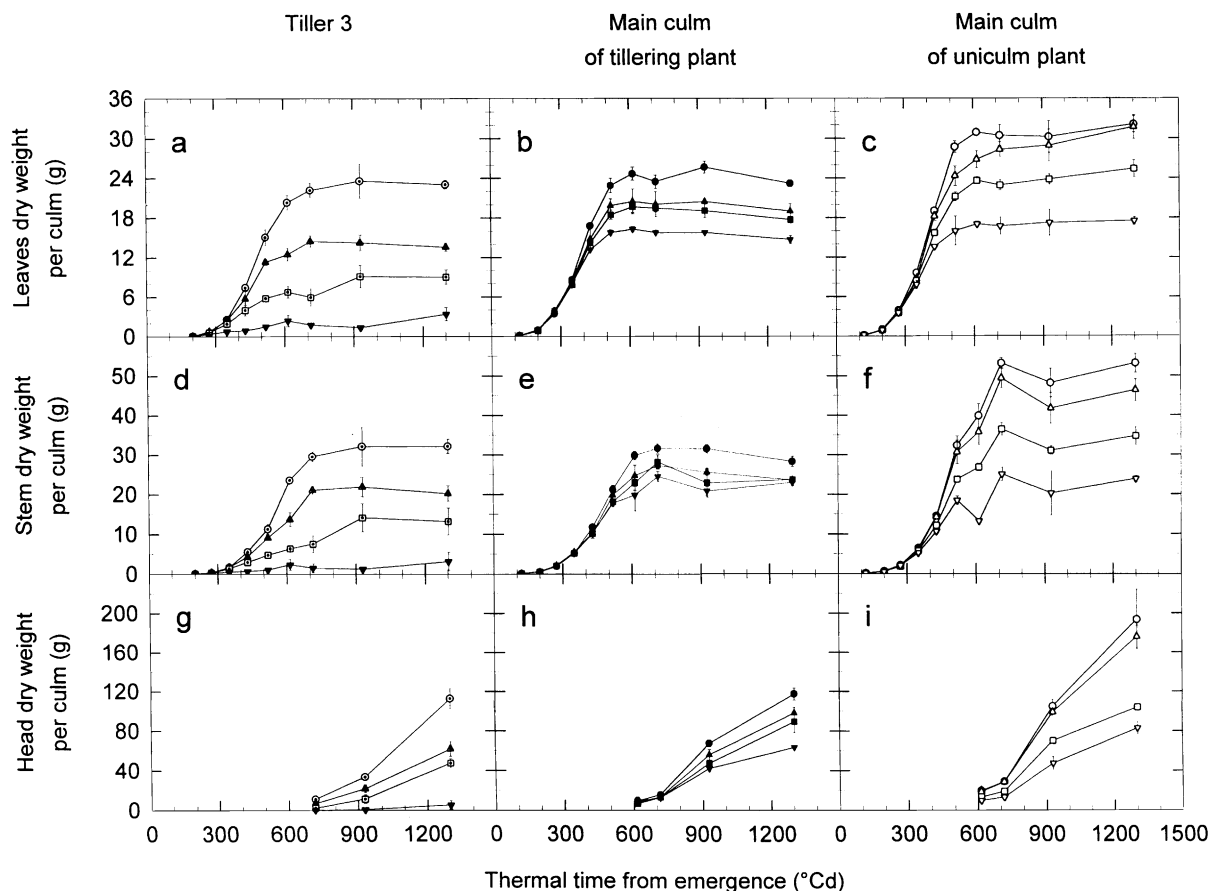


Fig. 4. Change with TT from emergence in leaf (a–c), stem (d–f) and head (g–i) dry weight, for tiller 3 (a, d, g, dotted symbols), main culm of tillering plants (b, e, h, closed symbols) and main culm of unicum plants (c, f, i, open symbols) grown at densities of 2 plants m⁻² (●), 4 plants m⁻² (▲), 8 plants m⁻² (■) and 16 plants m⁻² (▼). Vertical lines represent the standard error of the mean of three replications.

(LWR) decreased with developmental stage, from 0.64 at panicle initiation to 0.47 at ligule appearance of the final leaf (i.e. shoot dry weight was nearly equally divided between leaf and stem (sheath + internode) at this time) and to 0.13 at maturity. This slope decreased with TT from emergence to maturity for all the culms analysed in this study (Fig. 6). It did not vary appreciably among plant densities or in relation to culm type or culm number per plant. TT for tillers was here modified according to their delay in development to facilitate comparison between main culms and tillers (see Section 2). Head dry weight at maturity also increased linearly with shoot dry weight (Fig 5d, inset).

GLA on the main culm of tillering plants in D4 increased up to a maximum of 2816 cm² at 500 °C

days after emergence (Fig. 7a), when leaf senescence was still insignificant (Fig. 7a inset), and then decreased slowly until maturity. Meanwhile, SLA of the same culm decreased from 355 to 181 cm² g⁻¹ at 500 °C days and then decreased more slowly until maturity (Fig. 7c). In D1 at 500 °C days, GLA on the main culm of tillering plants reached a maximum at 3448 cm² (Fig. 7a), whereas SLA of that culm at that time was 154 cm² g⁻¹ (Fig. 7c). Consequently, at 500 °C days, the 22% increase in GLA (i.e. bigger leaves) and the 15% decrease in SLA (i.e. thicker or more dense leaves) for main culm leaves of tillering plants measured in D1 compared to D4, explained the extra 7.1 g in leaf dry weight measured in D1 (Fig. 4b). In D4, the dynamics observed for the main culm of

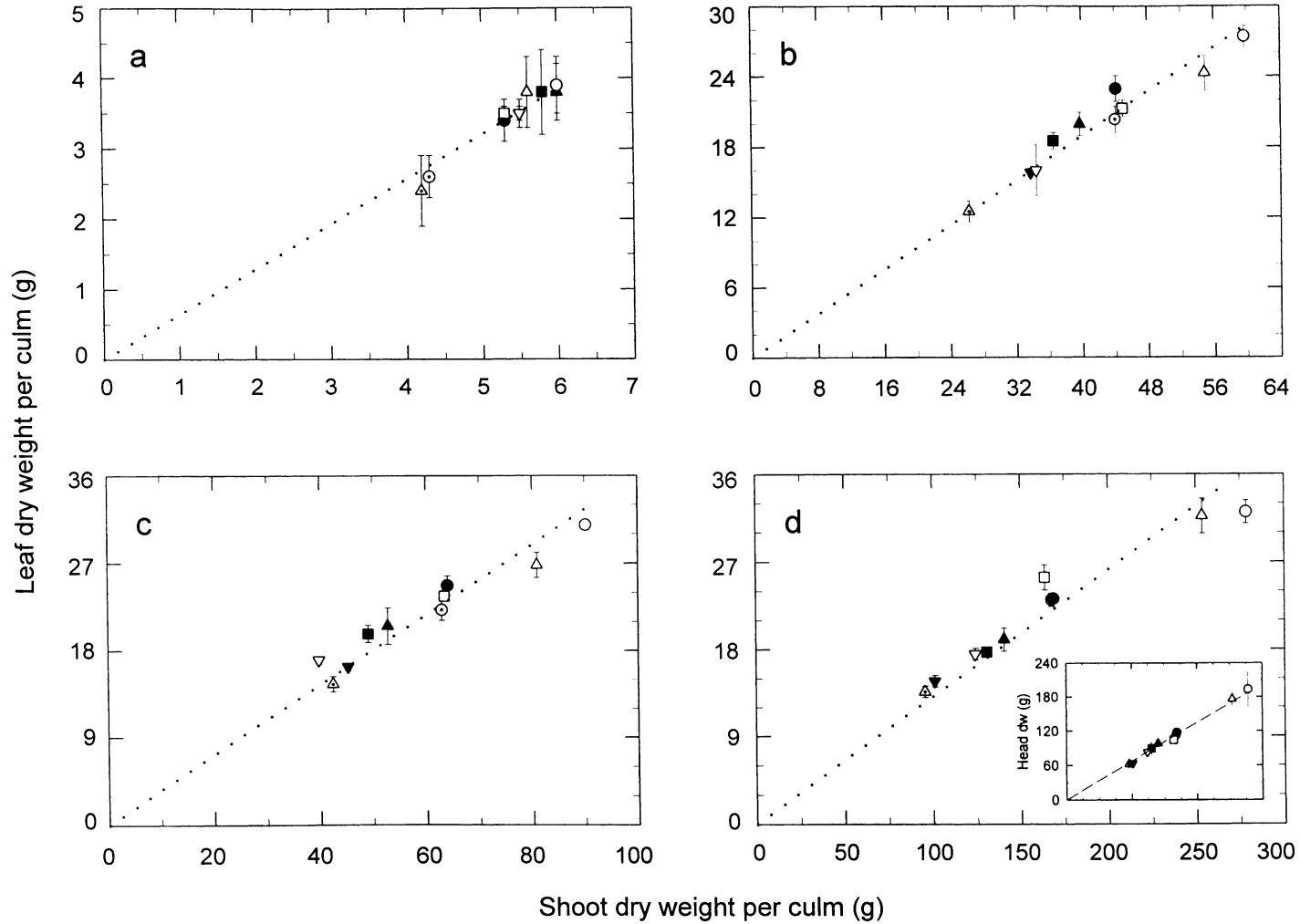


Fig. 5. Relationship between leaf dry weight and shoot dry weight at panicle initiation (a), ligule appearance of the final leaf (b), anthesis (c) and maturity (d) for fully fertile culms from tiller 3 (dotted symbols), main culms of tillering plants (closed symbols) and main culms of unicum plants (open symbols), grown at density of 2 plants m⁻² (●), 4 plants m⁻² (▲), 8 plants m⁻² (■) and 16 plants m⁻² (▼). Dotted lines are the corresponding linear regressions, with slopes of 0.64, 0.47, 0.36 and 0.13 in a, b, c and d, respectively. The inset in d shows the relationship between head dry weight and shoot dry weight at maturity and the dashed line is the corresponding linear regression with slope of 0.67. Vertical lines represent the standard error of the mean of three replications.

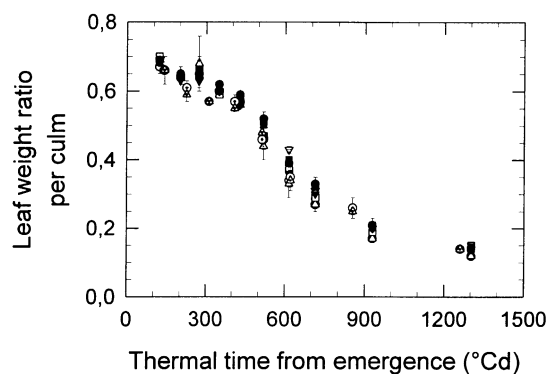


Fig. 6. Change with TT from emergence in LWR (leaf dry weight divided by shoot dry weight) per fully fertile culm. Same symbols as in Fig. 5. Vertical lines represent the standard error of the mean of three replications.

uniculm plants was similar to that for tillering plants: GLA reached 2818 cm² at 500 °C days (Fig. 7b) before any leaf senescence (Fig. 7b inset) and SLA decreased from 347 to 178 cm² g⁻¹ at 500 °C days and then decreased more slowly until maturity (Fig. 7d). However, in D1 at 500 °C days, although GLA of the main culm was similar for unicum and tillering plants (3386 cm² for unicum plants, Fig. 7b), SLA was significantly lower in unicum plants, 119 cm² g⁻¹, than in tillering plants (Fig. 7d). Consequently, at 500 °C days, the larger difference in leaf dry weight of unicum plants between D1 and D4 (12.7 g, Fig. 4c) than that for tillering plants was mostly explained by the 33% decrease in SLA from D4 to D1. Indeed, the increase in GLA from D4 to D1 (20%, Fig. 7b) was close to that observed for main culms on tillering plants. In the same way, at maturity, SLA for main culms of tillering plants decreased 12% from D4 to

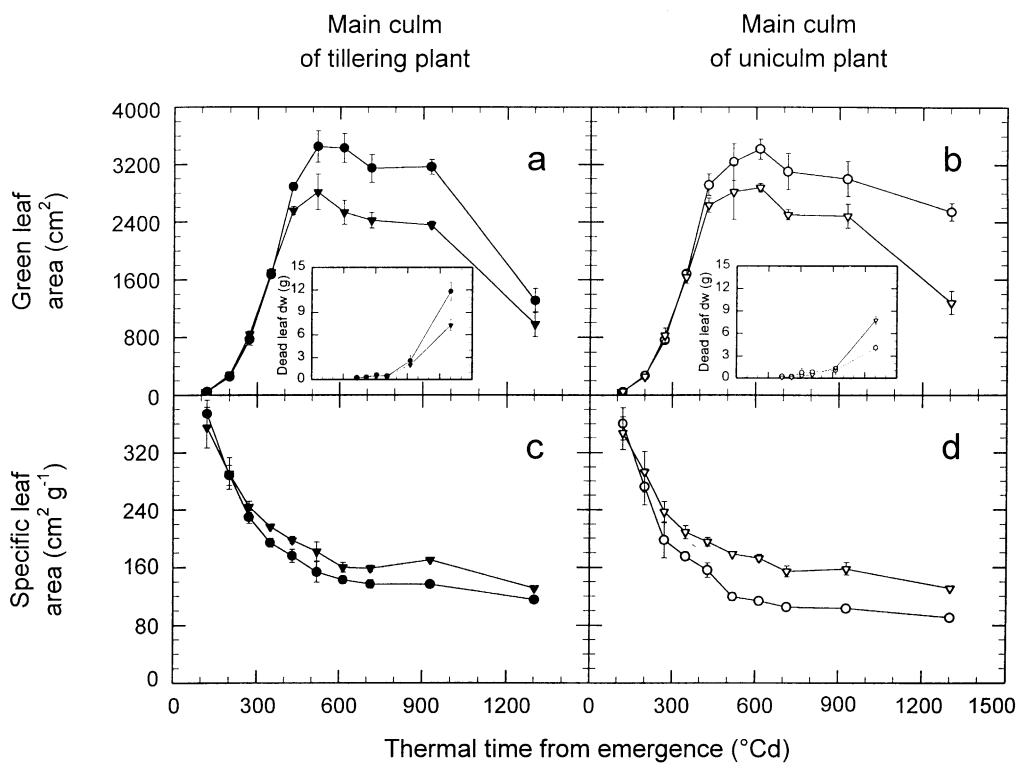


Fig. 7. Change with TT from emergence in GLA (a and b) and SLA (leaf area divided by leaf dry weight, c and d) for main culms of tillering (a and c) and unicum (b and d) plants grown at density of 2 plants m⁻² (●) and 16 plants m⁻² (▼). The insets in a and b show the relationship between dead leaf dry weight and TT for main culm of tillering (a) and unicum (b) plants grown at density of 2 plants m⁻² (●) and 16 plants m⁻² (▼). Vertical lines represent the standard error of the mean of three replications.

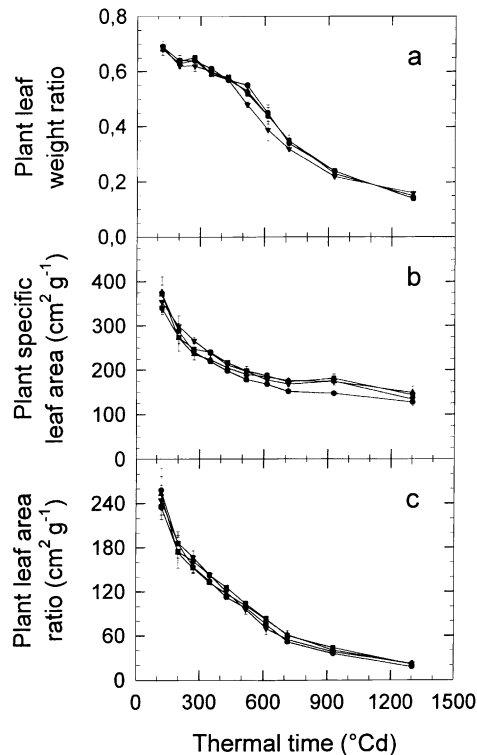


Fig. 8. Change with TT from emergence in plant LWR (leaf dry weight divided by shoot dry weight, a), plant SLA (leaf area divided by leaf dry weight, b) and plant LAR (leaf area divided by shoot dry weight, c), for tillering plants grown at density of 2 plants m^{-2} (●), 4 plants m^{-2} (▲), 8 plants m^{-2} (■) and 16 plants m^{-2} (▼). Vertical lines represent the standard error of the mean of three replications.

D1, from 131 to 115 $cm^2 g^{-1}$, whereas SLA for unicum plants decreased 31%, from 131 to 91 $cm^2 g^{-1}$. Rate of leaf senescence at maturity was similar in D4 for main culms of tillering and unicum plants (Fig. 7a and b). In contrast in D1, 62% of leaf area on main culms of tillering plants was dead at maturity, whereas it was only 26% for unicum plants.

LWR of tillering plants decreased with TT from emergence in a similar manner regardless of plant population, not only at culm level (Fig. 6a), but also at plant level (Fig. 8a). It decreased from 0.68 at 100 °C days to 0.15 at maturity. No significant difference among densities was observed, except between 500 and 700 °C days for plants growing in D4. A similar stability among densities was observed at plant level for SLA of tillering plants, except for values measured

in D1 that became slightly lower as the crop progressed (Fig. 8b). Plant LAR, as the product of LWR and SLA, was also stable regardless of plant density (Fig. 8c). It decreased from 250 to 20 $cm^2 g^{-1}$ from 100 °C days after emergence to maturity. Exponential models fitted on LAR against TT did not differ significantly across plant densities so that the parameters fitted using all data could be used to determine LAR at any developmental stage regardless of plant density. The model of LAR on TT, $LAR = a e^{-bTT} + c$, was fitted with parameter values $a = 307$, $b = 0.0026$ and $c = 11$. Although SLA was determined from GLA only, the resultant LAR could be applied to total leaf area, during vegetative development since no senescence was observed before 500 °C days, but also until maturity since SLA was almost stable from the time when leaves started to senesce.

4. Discussion

The adequacy of a general framework for predicting leaf area production of sorghum during vegetative development was examined in this study over a diverse range of population density. This range resulted from variation in either plant density imposed at time of thinning (2–16 plants m^{-2}) or culm density imposed throughout the crop life cycle (uniculm and tillering plants). A level of stability across the density treatments was observed in the extinction coefficient, in the RUE and in the relationship of LAR with TT from emergence. The stability of these factors supports use of this framework for predicting leaf area growth during vegetative development and allows robust prediction independently of stage of plant development and plant density. In particular, the range in plant density resulted in plants varying significantly in tillering (from 0.2 to 4.7 tillers per plant at maturity), yet the partitioning of net above-ground biomass to leaf area among culms remained stable across these plant types. This was a consequence of the stability of the underlying shoot dry matter partitioning and SLA. Similarly, a unique relationship showing the decrease of LAR with TT was observed by O'Leary et al. (1985) for two wheat cultivars measured over eight growing seasons. These results indicate that, regardless of plant density, the increase in plant leaf area could be predicted from knowing only the current LAI, the daily

incident radiation and the thermal conditions. Six parameters are sufficient to facilitate this prediction: the extinction coefficient, the maximal fraction of intercepted radiation, the RUE and the three parameters defining the dynamics of LAR with TT. It could be possible then to derive methods to predict tiller dynamics when this framework is combined with estimates of potential plant leaf area growth according to environmental conditions and patterns of tiller development (Lafarge and Hammer, 2002).

The extinction coefficient and the RUE did not differ significantly among tillering canopies as long as plant density was high enough to generate sufficiently large values of LAI at anthesis. Previous studies that have measured the extinction coefficient of sorghum before anthesis (Muchow and Davis, 1988; Rosenthal et al., 1993), have found values of 0.42 and 0.51, compared with the value of 0.56 found here. In those studies, the maximal fraction of intercepted radiation was fixed at 1, which introduces some bias to the value of the extinction coefficient. The maximal fraction of intercepted radiation fitted in this study was 0.9. When the data from this study were fitted so that this maximal value was fixed at 1, the value obtained for the extinction coefficient was 0.44, which was similar to that reported in the previous studies. The stability of the RUE of sorghum with plant density was also reported by Rosenthal et al. (1993) over a range of plant density from 5 to 26 plants m^{-2} . The significant difference between tillering and unicum plants found in this study would likely have been removed if tiller removal had been more frequent (e.g. daily), but this would have required high labour input. The value of RUE of 1.24 $g MJ^{-1}$, fitted in this study, was close to the efficiencies calculated for sorghum by Muchow and Davis (1988), 1.25 $g MJ^{-1}$, and by Kiniry et al. (1989), 1.26 $g MJ^{-1}$. The constancy of RUE for shoot biomass across treatments and over time from emergence to anthesis suggested that production of root biomass was a constant proportion of total biomass for this diverse range of conditions.

Partitioning of shoot dry matter in the plant up to anthesis did not differ among plant density and tillering treatments as the plant LWR decreased with developmental stage in the same manner for all treatments. This finding was also observed by Goldsworthy (1970), Tetio-Kagho and Gardner (1988) and Wu et al.

(1998) for sorghum, maize and rice, respectively. Dry matter partitioning to leaf, stem and head up to anthesis was also stable among individual culms regardless of plant density, provided the culm developed to become fertile and produce grain. This finding was valid for a wide range of culm dry weight at maturity (from 96 to 279 g). This suggests that both leaf and stem were probably used as assimilate stock organs (particularly for unicum plants), with no priority assigned between them. The constancy of RUE combined with this finding on LWR suggests also that any upper limit of storage capacity or organ dry weight was not reached in this study, even for unicum plants at low density.

Variation in partitioning of shoot assimilate between leaf and stem was observed, however, during grain filling among plant density treatments. This appeared to be related to the manner in which assimilate demand of the developing panicle was satisfied by sources of assimilate availability. Between anthesis and mid-grain filling, in the higher plant densities for tillering treatments and at all densities for unicum treatments, stem dry weight of main culms decreased in favour of the developing head, probably due to the inability of current assimilation to meet head demand in these conditions. Similar findings were reported by Goldsworthy (1970) and Fischer and Wilson (1975) for sorghum, Azam-Ali et al. (1984) for millet and Wu et al. (1998) for rice. Leaf dry weight did not vary significantly during this period, highlighting that the stem was the major provider of stored assimilate to developing grain, as also observed by Fussell et al. (1980). Between mid-grain filling and maturity, head demand in unicum plants was probably not high enough to consume all current assimilation, allowing leaf and stem dry weight to increase. Similar behaviour has been reported at the plant level for rice and also attributed to sink limitations (Dingkuhn and Sow, 1997). This could also be the case for the main culms of tillering plants in the two highest densities, although leaf dry weight decreased during this period. Another hypothesis is that the stem of these culms was not strong enough to support the potential increase in head dry weight, leading to current assimilate partitioning between stem and head. Despite these differences during grain filling, no significant variation in dry matter partitioning was observed among plant density treatments at maturity.

SLA of tillering plants did not differ significantly among plant density treatments. It was also similar among plant density treatments for main culms of tillering plants, whereas it differed substantially across densities for unicum plants. Systematic tiller removal in the low-density treatment led to an increase in plant leaf dry weight but not in plant leaf area. This removal promoted a significant decrease in SLA with decreasing density, as the plant was unable to compensate by producing bigger leaves. In the same way, Heuvelink and Buiskool (1995) measured a decrease in SLA of tomato plants when assimilate demand, but not assimilate supply, was reduced by fruit and truss pruning. Hence, increase of assimilate availability in the mother culm was likely a trigger for tiller production. So, SLA of the culm responded as a consequence of the culm carbon budget. Similarly, at the leaf level, Tardieu et al. (1999) reported that SLA decreased when environmental conditions had a greater depressive effect on elongation rate than on photosynthesis and increased for the converse. The range in values found for SLA in this study for the same type of culm growing in contrasting conditions (main culm of tillering plants in high density conditions and main culm of unicum plants in low-density conditions) indicates the degree of plasticity of leaf area growth. Two components determine SLA (Wilson et al., 1999): leaf thickness and dry matter content (tissue density). It is likely that the assimilate surplus found in the leaves of unicum plants in this study, that was predisposed to tiller production, contributed to the pool of soluble carbohydrates that increased tissue density of the leaf rather than to structural carbohydrates that increased leaf size or thickness.

Further experimentation is required, however, to determine whether the level of stability of LAR would persist for other genotypes and environments, which might differ in temperature, photoperiod, and incident radiation. Nonetheless, when this stability was combined with similar level of stability for the extinction coefficient and RUE, this study indicated that this framework provided a reliable way to predict leaf area production for a wide range of population densities. This can be used to estimate assimilate supply required for leaf area production and, hence, any available surplus, which provides a basis for modelling the dynamics of tillering (Lafarge and Hammer, 2002).

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