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Dry matter accumulation and distribution in five cultivars of maize (*Zea mays*): relationships and procedures for use in crop modelling

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Abstract. The ability to predict accurately dry matter (DM) accumulation, partitioning, and thus final grain yield is crucial in crop simulation models. The objectives of the study were to measure radiation interception and radiation use efficiency, to quantify the distribution of DM among the various plant parts, and to develop improved methods of modelling DM accumulation and partitioning among plant parts.

Five cultivars of maize differing widely in maturity and adaptation were planted in October 1993 in south-eastern Queensland, and grown under non-limiting conditions of water and plant nutrient supplies. Data on DM accumulation, light interception, and canopy development were collected. The light extinction coefficient (k) did not differ among the cultivars. Radiation use efficiency was constant in each cultivar until close to physiological maturity, when a small decline was observed.

Partitioning of DM between leaves and stems (until 90% of leaf tips had appeared) was described by a linear relationship between the proportion of DM allocated to leaves and the number of leaves present. Ear growth was described by a thermal-time-dependent equation from 150 degree-days (base temperature 8°C) before silking to 115 degree-days after silking. Predictions of accumulation of grain yield by either components of yield (grain number per plant and individual grain weight) or daily increase in harvest index were assessed, but neither was entirely satisfactory, the former because of inaccurate prediction of grain number per plant, and the latter because of differences among cultivars in the daily increase in harvest index and terminal harvest index. Thus, the use of genotype-specific coefficients remains necessary. Throughout crop life, DM in stems can be predicted by difference, once DM is allocated to other plant parts. The relationships presented where leaf number mediates DM partitioning before silking simplify modelling of DM accumulation and partitioning in maize.

Additional keywords: components of yield, harvest index, yield.

Introduction

Crop models are used to predict crop development, canopy production, total dry matter (DM), and crop yield in diverse environments, for diverse genotypes, and to carry out risk analysis. Models may be either 'empirical', in that simple equations are used to describe plant processes, without necessarily being based on the processes themselves, or 'mechanistic', where the equations used are based on the mechanisms of processes that occur in plants. However, since it is not possible to describe every process that occurs in equations, models must use empirical equations for processes occurring at a level of resolution more detailed than that for which process-based relationships are available.

Total plant growth is the result of interception of radiation by leaves, the efficiency of utilisation of intercepted radiation (RUE), and the duration of radiation interception.

Duration of interception is determined by maturity type, and instantaneous interception by the amount of green leaf area present. Cumulative interception of radiation depends on leaf area index (LAI), the time (days) over which radiation is intercepted, and total incident solar radiation. Two models of maize, AUSIM-Maize (Carberry and Abrecht 1991), which was derived from CERES-Maize (Jones and Kiniry 1986), and that of Muchow *et al.* (1990) (referred to as the Muchow–Sinclair model in this paper), did not accurately simulate DM yield and partitioning when assessed against experimental data for diverse cultivars and environments (Birch 1996a, 1996b). A sensitivity analysis on input variables or parameters showed that predicted DM and grain yield were most sensitive to values for parameters that described phenological development of genotypes and rates of leaf initiation and appearance, and thus radiation intercep-

tion (Birch 1996a, 1996b). This paper addresses factors influencing radiation interception and radiation use efficiency by maize, and partitioning of DM among plant parts, and seeks to derive improved relationships for use in crop modelling.

Radiation interception

The fraction of radiation that is intercepted (RI) is usually described by Beer's Law:

$$RI = 1 - e^{-k \cdot LAI} \quad (1)$$

where k is the radiation extinction coefficient, and LAI the green leaf area index.

The k value for maize has been reported to range from 0.38 to 0.98 (Stapper and Arkin 1980). The relationship between estimated fraction of radiation intercepted and LAI shows that estimated radiation interception is sensitive to the value of k if LAI is <3.0 and/or k is <0.7. Since most reported values of k for maize are <0.7, and LAI is <3.0 for a significant part of the pre-silking period in maize, accurate values of k are needed. Values of k have been related to row spacing by Flenet *et al.* (1996), who reported lower k values as row spacing increased in a range of crops; this factor needs to be included in crop models.

Radiation use efficiency

Radiation use efficiency is defined as the amount of DM (g) accumulated per MJ of photosynthetically active radiation (PAR). In maize, RUE has ranged from 2 to 3.4 g/MJ, depending on genotypes, N supply conditions, and environments, from tropical to cool temperate (Table 1). There are some differences in RUE among cultivars, but differences are relatively minor among modern hybrids (Major *et al.* 1991). Tollenaar and Aguilera (1992) reported, however, that RUE of a modern hybrid was higher than that of an early hybrid. Temperature and N supply appear to be more important determinants of RUE than genotype but the possibility of variation in RUE among genotypes remains. There was considerable variation in RUE between high temperature conditions at Katherine (Muchow 1989a) and low temperature conditions in Ontario (Tollenaar and Aguilera 1992), Alberta (Major *et al.* 1991), and Argentina (Andrade *et al.* 1992, 1993), but Duncan and Hesketh (1968) found little difference in rate of photosynthesis between 20 and 40°C. Muchow and Davis (1988) related RUE to specific leaf N (SLN) (0.5–1.6 g N/m² of leaf) for grain sorghum and maize. Although, theoretically, there must be a point beyond which further increase in SLN leads to no further increase in RUE, there was no such indication in the results of Muchow and Davis (1988), and the highest RUE in their study was close to the highest in Table 1.

There are numerous reports of lower RUE after silking than before (Bonhomme *et al.* 1982; Muchow 1989a; Muchow and Sinclair 1994), but Major *et al.* (1991) argued

that RUE was constant for the whole crop cycle under non-stressed conditions. Also, Muchow (1994) and Andrade (1995) found no reduction in RUE at least until just before physiological maturity. Thus, RUE appears to be constant until close to physiological maturity for crops grown under non-limiting conditions, but may decline under inadequate supply of, for example, nitrogen.

As most values of RUE were calculated from above-ground DM, they must be higher when root DM is included. The proportion of total DM allocated to roots is rarely reported, but Tollenaar (1989) reported that it was 47% at the 4-leaf stage, 40% (8 leaf), and 30% (12 leaf), and Fairey and Daynard (1978) reported that the allocation to root DM was 16% at silking and 13% 2 weeks after silking. Because of the need to allocate DM to roots in models such as CERES-Maize and AUSIM-Maize, RUE must be adjusted accordingly.

Dry matter partitioning

Leaf and stem dry weight

Tollenaar (1989) proposed both a shoot partitioning coefficient to calculate distribution of DM to stems of maize plants with up to 12 leaves, and a leaf area partition coefficient (cm²/g increase in plant dry weight) and specific leaf area (SLA) (cm²/g new leaf) to partition DM increase to leaves. Specific leaf area (cm²/g leaf) can be used to calculate leaf weight, when leaf area is known, or leaf area when leaf weight is known. However, SLA is the likely consequence of leaf area expansion and DM accumulation in leaves, rather than a factor that determines distribution of DM among plant parts. Further, the use of SLA in models assumes that leaf area is known or accurately predicted, and that SLA is constant or has a well-defined relationship with another plant characteristic.

Assimilate is withdrawn from stems after silking (Fischer and Palmer 1984; Lorens *et al.* 1987), the withdrawal implying that there is a remobilisable pool of assimilate stored temporarily in the stems. The loss in stem weight after silking varies from 0 to 21% of the stem weight (Jurgens *et al.* 1978; Cooper 1979; Fischer and Palmer 1984; Muchow 1989b, Kiniry *et al.* 1992b). In modelling, a variable for this pool would be more biologically sound than setting limits to the proportion of assimilate that can be withdrawn.

Grain yield

There are 2 common approaches to predicting grain yield, one which uses components of yield (grain number per plant and individual grain weight), and a second that uses the increase in harvest index during grain filling.

Number of grains per plant. Grain number per plant (GPP) has been related to average daily photosynthesis from silking to the start of linear grain filling (Edmeades and

Table 1. Selected reports of radiation use efficiency (expressed as RUE, g/MJ photosynthetically active radiation) in studies covering a range of environmental and crop cultural conditions

RUE	Location	Experimental conditions	Time, other notes	Author
2.10–2.24	3 sites, Kenya	Altitude 1268–2250 m, mean temp. 14.8–22.3°C, nutrients non-limiting	18th visible leaf to 50% tasselling (total 29–43 days, depending on location)	Cooper (1979)
2.00–3.20	Katherine, NT, Australia	Water non-limiting, N supply varied	Based on specific leaf N (g N/m ² leaf)	Muchow and Davis (1988)
2.70–3.08 2.02–2.32	Katherine	N, water non-limiting, F ₁ hybrids	Emergence to silking; silking to physiological maturity	Muchow (1989a)
2.07–2.44	Lethbridge, Alberta	10 hybrids of varying maturity, all adapted to temperate environ.	Whole crop cycle, small differences among hybrids	Major <i>et al.</i> (1991)
2.27–3.17	Balcarce, Argentina	Cool area, average temp. during vegetative growth 15–18°C	Whole crop cycle, RUE same b/f and after silking	Andrade <i>et al.</i> (1992)
2.24 1.95 3.08 2.78 3.78 2.41	Elora, Ontario ,, ,, ,, ,,	Pioneer 3902, 8 plants/m ² Pride 5, 7 plants /m ² Pioneer 3902, 8 plants/m ² Pride 5, 7 plants /m ² Pioneer 3902, 8 plants/m ² Pride 5, 7 plants /m ²	Silk–2 weeks after silk Silk–2 weeks after silk 2–4 weeks after silk 2–4 weeks after silk 4–6 weeks after silk 4–6 weeks after silk	Tollenaar and Aguilera (1992)
3.00–3.40	Redland Bay, Qld, Australia	Field	21–43 and 43–61 days after sowing	Watiki <i>et al.</i> (1993)
3.22	Katherine; Gatton, Qld	Maximum RUE, 240 kg N/ha, Gatton (4), Katherine (3) experiments	Period of maximum RUE, stable across location and planting date	Muchow (1994)
2.32–3.34	,,	Average RUE, 240 kg N/ha, Gatton (4), Katherine (3) experiments	From sowing to maturity, varied with planting date	
2.77	Balcarce	7.8–9.1 plants/m ²	Whole crop cycle	Andrade (1995)

Daynard 1979), ear weight at flowering (Fischer and Palmer 1980), plant weight at tasselling (Stapper and Arkin 1980), crop growth rates during kernel formation (Grant 1989), ear weight 10 days after silking (Aluko and Fischer 1987), and incident radiation/plant.day soon after anthesis (Kiniry and Knievel 1995). Such relationships may provide simple means to estimate grain number, if they are sufficiently robust. For example, Edmeades and Daynard (1979) proposed a hyperbolic equation:

$$GPP = 825.4 * (x - 195) / [1213.2 + (x - 195)] \quad (r^2 = 0.62) \quad (2)$$

where x is the average daily rate of photosynthesis from silking to the start of linear grain filling (g/plant.day). This equation has an asymptote of 825 grains per plant. Since it relies on photosynthesis from silking to the start of linear grain filling, it will be sensitive to incident radiation during

this period. Further, the coefficient of determination ($r^2 = 0.62$) is relatively low, and is likely to lead to substantial errors in prediction when used in crop models. Eqn 2 was used in CERES-Maize (Jones and Kiniry 1986) and retained in AUSIM-Maize, as no acceptable alternative could be found (Carberry and Abrecht 1991). A better alternative may be linear relationships between seed number and intercepted light near silking. Such linearity has been found by Kiniry and Knievel (1995) for several diverse data sets and genotypes of maize, and appears logical, in agreement with the often stated concept that it takes a certain amount of assimilate to support each seed soon after anthesis, and those that are not supported are aborted.

Individual grain weight. The final individual grain weight depends on the supply of assimilates, the number of grains to fill, the genetic limit to grain size (Fischer and

Palmer 1984), the duration of grain filling, and cumulative radiation during grain filling (Cooper 1979; Aluko and Fischer 1987). The potential rate of growth of individual grains varies among cultivars, and ranges from <6.0 mg/grain.day (Jones and Simmons 1983) to >10.0 mg/grain.day (Ritchie *et al.* 1986; Tollenaar and Bruulsema 1988). Muchow (1990a) related individual grain weight to duration (days) for grain weight to increase from 10% to 80% of final grain weight, in 3 otherwise identical trials planted at different times of the year at Katherine. This author proposed that a linear relationship between grain growth rate (mg/grain.day) (GGR) was then linearly related to mean temperature (T) during grain filling:

$$\text{GGR (mg/grain.day)} = -1.16 + 0.315 \cdot T \quad (r^2 = 0.80) \quad (3)$$

The equation was derived from a narrow range of temperatures, and extrapolation to temperatures lower than used in the development of Eqn 3 produces individual grain weights that are lower than achieved experimentally by Brooking (1993). Thus Eqn 3 has limited application. Grain growth rate and duration of grain filling were related quadratically to mean temperature during grain filling (derived from data in Fisher and Palmer 1980); the maximum grain growth rate and maximum grain size occurred at a mean temperature of 24.8°C, with a 31-day duration of grain filling. Alternatively, grain growth rate can be related to temperature (0.3 mg/grain.degree-day, $T_b = 0^\circ\text{C}$) (Tollenaar and Bruulsema 1988).

Onset and duration of grain filling. There is wide variation in reported commencement of rapid (linear) grain filling, e.g. 14 days after silking (Tollenaar and Daynard 1978), 14 days after mid-silking (Jones and Simmons 1983), 12 days after silking depending on genotype and temperature (Fischer and Palmer 1984), 3–4 days after silking (Muchow 1988), and 7 days after silking (Muchow 1990a). The variation is almost certainly due to the diversity of environments in which these studies were conducted, methods of assessment, and perhaps genotypes used, and suggests that time (days) may be a poor predictor of delay from silking to start of linear grain filling. The duration of linear grain filling depends on the mean temperature (Fischer and Palmer 1984; Muchow 1990a) and the supply of assimilates (Tollenaar and Bruulsema 1988).

Use of harvest index to estimate grain yield. Harvest index, i.e. grain as the proportion of above DM, is a useful parameter to predict grain yield (Kiniry *et al.* 1992a). However, harvest indices in tropically adapted genotypes of maize (0.3–0.4) are lower than in temperate genotypes (0.5–0.55) (Aluko and Fischer 1987; Karanja 1993). The rate of increase in harvest index as grain is filled has received less attention than terminal harvest index. Linear increase in harvest index has been used in models of maize (Muchow *et al.* 1990), sorghum (Hammer and Muchow 1991), and sunflower (Chapman *et al.* 1993), but for satisfactory use needs

to be stable or predictable. It was stable in maize and grain sorghum grown in a limited range of environments (Muchow 1990a, 1990b), but varied in sunflowers, especially when temperature was low (Bange 1995). Variations in the rate of increase in harvest index in sunflower, and in terminal harvest index in maize, are sufficient reason to question the use of these variables as predictive tools, unless they can be related to another plant characteristic, e.g. crop ontogeny.

Objectives of this study

Because of the unsatisfactory prediction of total DM and grain yield by AUSIM-Maize and the Muchow–Sinclair models, and yield of other plant parts by AUSIM-Maize, this study sought to develop improved methods of prediction of DM accumulation and partitioning among plant parts. To achieve this, a field study using 5 cultivars of maize was undertaken, radiation interception and RUE were measured, and the data were used to derive general predictive relationships.

Materials and methods

Experimental design and cultural conditions

A field experiment was conducted at The University of Queensland, Gatton College (27°33'S, 152°20'E), on a moderately fertile, deep alluvial vertisol (Typic Chromustert) (Powel 1982) that has moderate water-holding capacity and is well drained. Five cultivars of maize (Hycorn 42, DK529, XL82, Hycorn 83, and Barker) were planted 5 cm deep on 24 October 1993, after routine land preparation, and thinned to 70 000 plants/ha at 1 week after emergence. Based on the American Eastern States Relative Maturity System, these cultivars represented relative maturities of 98 days (Pacific Hycorn 42, De Kalb DK529), 113 days (De Kalb XL82), 128 days (Hycorn 83), and >135 days (Barker). The genetic background and cultivar characteristics are described in Birch *et al.* (1998a). Plots were 20 m long and consisted of 8 rows 0.75 m apart. The outer 2 rows were guard rows, the other 6 rows were used for data collection. Three replicates were used in a randomised complete block design.

Irrigation and nutrients were applied at rates to ensure that non-limiting conditions were maintained. Nitrogen was applied at 150 kg N/ha as ammonium nitrate immediately after planting and at 50 kg N/ha (as urea or ammonium nitrate) 4 and 7 weeks after planting and incorporated by irrigation. Zinc was applied as a foliar spray of 1 kg ZnSO₄·7H₂O in 100 L H₂O/ha at 2, 4, and 6 weeks after emergence. The soil was well supplied with all other nutrients (Anon. 1983). Irrigation was scheduled by the WATERSCHED (Department of Primary Industries 1993) technique, and applied by sprinkler when the accumulated deficit reached, at most, 50 mm. Irrigation was more frequent during and immediately after tasselling and silking, because of high temperatures from late December 1993 to mid January 1994. The sprinklers were mounted above the crop canopy on risers to ensure satisfactory water distribution. Insects were controlled by chemicals, and weeds chemically or by removal by hand.

Meteorological data were collected at a nearby automatic weather station (Figs 1 and 2). Thermal time was calculated using the base, optimum, and maximum temperatures of 8, 34, and 40°C before silking and 0, 34, and 40°C after silking (Birch *et al.* 1998a).

Dry matter and leaf area

Ten plants were removed from adequately bordered linear quadrats 1.9 m long (1.42 m²) in each plot on 10–14-day intervals until silking, and

7–10-day intervals after silking. At each sampling, 2 of the 10 plants were randomly selected and the leaf length and width (at the widest point) of each leaf measured. Leaves of these plants were dried separately and used for calculation of specific leaf area (SLA, cm^2/g) and specific leaf weight (SLW, g/cm^2). The remaining plant parts were partitioned into stem (including leaf sheath), husk, and ear, as appropriate, dried, and weighed. After drying, ears were partitioned into grain and pith, and dry weights of each recorded. At physiological maturity, determined by the presence of black layers at the base of the grains, after which no further accumulation of grain mass is possible (Daynard and Duncan 1969), individual grain weight (GRWT) and number of grains per plant (GPP) were determined. Harvest index (HI) was calculated for all samplings when grain was present, as the ratio of grain DM to total above-ground DM.

Leaf area of individual leaves on the 2 randomly selected plants referred to above (LALF) was determined as:

$$\text{LALF (cm}^2\text{)} = 0.79 * \text{LL} * \text{LW} \quad (4)$$

with the constant (0.79) having been established by Birch *et al.* (1998b).

Total green leaf area per plant was calculated by summing individual LALF for all green leaves on a plant. This was then used to estimate the green leaf area index (LAI), from total green leaf area per plant and plant population, on each sampling date.

Radiation interception and radiation use efficiency

At 24 days after emergence, 1 tube solarimeter per plot (Type TSL, Delta-T Devices, Cambridge, England; adsorption band 0.35–2.5 μm), which had been calibrated against an absolute reference Kipp pyranometer, was placed in each plot of 2 replicates. The solarimeters were placed near ground level across 2 rows, as described by Monteith (1993), to measure transmitted radiation. One was placed outside the trial area, as a reference solarimeter, to measure total incident radiation. All were connected to a data logger (Type DT-100F, Datataker, Melbourne, Australia) programmed to record hourly average radiation transmission. The solarimeters remained in place until 1 week before physiological maturity (PM) of the latest maturing hybrid. To ensure that the measured radiation represented that remaining after interception by green leaves, senesced leaves (<50% of the leaf area

green) were removed from plants surrounding the solarimeters at approximately 7-day intervals. The data were used to calculate the radiation extinction coefficient (k) and RUE, using SOLINTDT (Davis 1995), a computer program for processing radiation data.

Radiation use efficiency ($\text{g}/\text{MJ PAR}$) was calculated as the slope of the regression of accumulated above-ground DM yield against cumulative intercepted PAR, assuming that 50% of incident radiation is PAR (Monteith 1977). RUE was determined for crop growth before and after silking, for the whole crop cycle, and for additional intervals during the grain fill period.

Statistical procedures

All statistical procedures were carried out using SYSTAT (Wilkinson 1990), using MGLH (Multiple General Linear Hypothesis), for analysis of variance and regression, STATISTICS (for Root Mean Square Deviation), and NONLIN (nonlinear estimation), for estimation of coefficients in non-linear and broken linear relationships.

Results

Temperatures gradually increased until late January and decreased thereafter (Fig. 1). Daily solar radiation was highly variable, with monthly maxima of 24–36 $\text{MJ}/\text{m}^2.\text{day}$ for November–January, and 20–25 $\text{MJ}/\text{m}^2.\text{day}$ for February and March (Fig. 2).

Whereas dates of silking and maturity followed the expected trends with maturity type, the ranges were less than indicated by the relative maturity ratings of individual cultivars. For example, silking for the first 4 cultivars ranged over only 4 days, and 3 of the 5 reached physiological maturity over 9 days.

LAI values were fairly similar until 30 days after emergence, then began to diverge (Fig. 3). Maximum LAI ranged from 4.5 for DK529 to 6.8 for Barker. Though maximum LAI values followed the expected trend with later maturity,

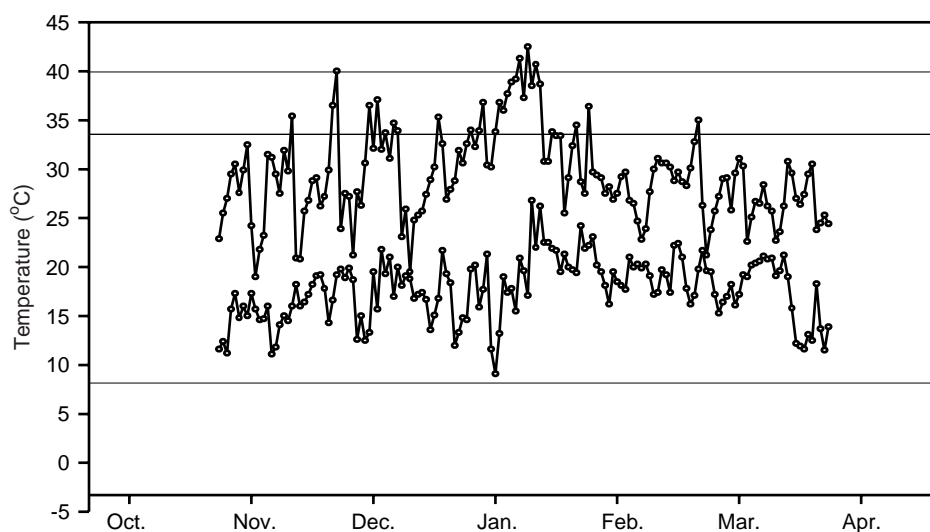


Fig. 1. Daily maximum and minimum temperatures at Gatton from 24 October 1993 to 15 March 1994. (Months are shown on the first day of the month.) Horizontal lines are at 8, 34, and 40°C: the base, optimum, and maximum temperatures for calculation of thermal time.

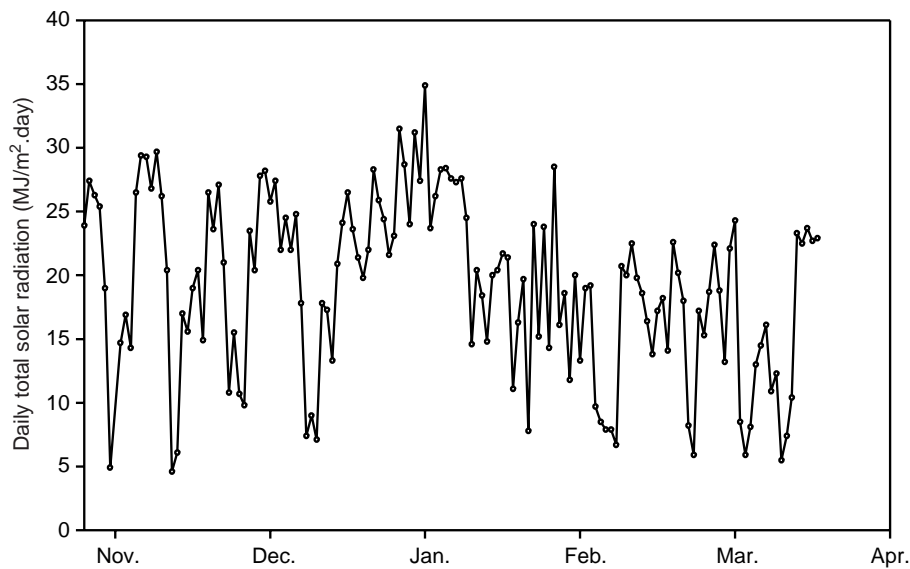


Fig. 2. Daily total radiation ($\text{MJ}/\text{m}^2\cdot\text{day}$) at Gatton from 2 October 1993 to 15 March 1994. (Months are shown on the first day of the month.)

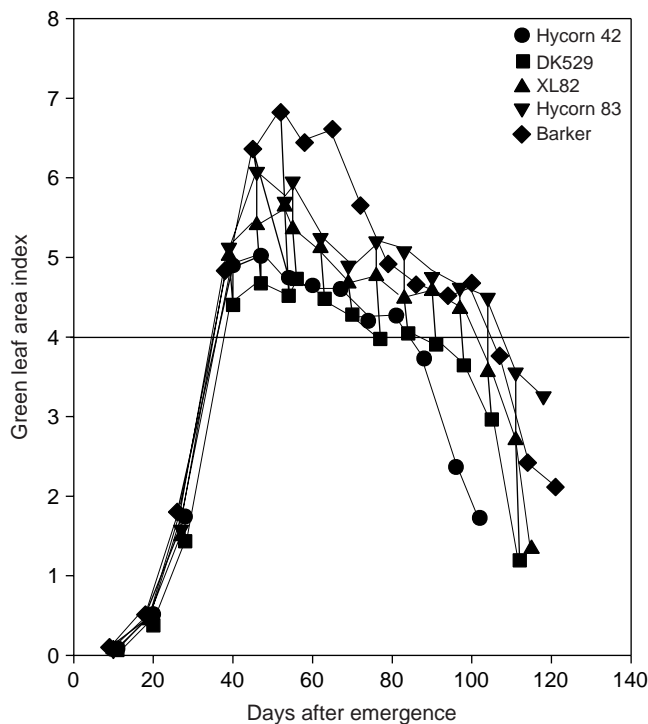


Fig. 3. Green leaf area index (LAI) in 5 cultivars of maize from emergence to physiological maturity.

different rates of senescence caused some shifts in the order late in grain filling.

There were few differences among cultivars in total DM accumulation per m^2 until silking of Hycorn 42 (Fig. 4). Hycorn 83 and Barker had higher final DM yield than the other cultivars. DK529 had the lowest final DM accumula-

tion. The beginning of linear grain filling was within 1 week of silking in all cultivars used.

Radiation interception

Interception of radiation followed generally similar patterns for each cultivar until LAI reached 3.5–4.0. Maximum radiation interception persisted for longer in the cultivars with longer crop duration (Fig. 5). In all cultivars, maximum radiation interception exceeded 85% for a period from before silking to near the end of grain filling. As the maximum proportion of radiation that could be intercepted was unity in all cultivars, there appeared to be no reason to add a factor for maximum interception, as suggested by Milthorpe and Moorby (1988). Recalculation of k values according to Eqn 1 produced a k value of 0.46 for all cultivars. This agrees closely with the expected value of 0.43, predicted for 0.75-m rows of maize (Flenet *et al.* 1996).

Radiation use efficiency

Total DM increased linearly with accumulated PAR until just before physiological maturity in all cultivars, after which there was a reduction. The reduction commenced, on average, 240 degree-days (base = 0°C) before physiological maturity, with RUE only half of that earlier in crop life. No difference in the time of the commencement of this reduction was found. RUE for the whole crop cycle (to 240 degree-days before physiological maturity) was marginally higher in Barker than in Hycorn 42, XL82, and Hycorn 83, and significantly lower in DK529 (Table 2). When calculated for before and after silking and from silking to 240 degree-days (base = 0°C) before physiological maturity, there was a small, on average 9%, reduction in RUE after silking (Table 2).

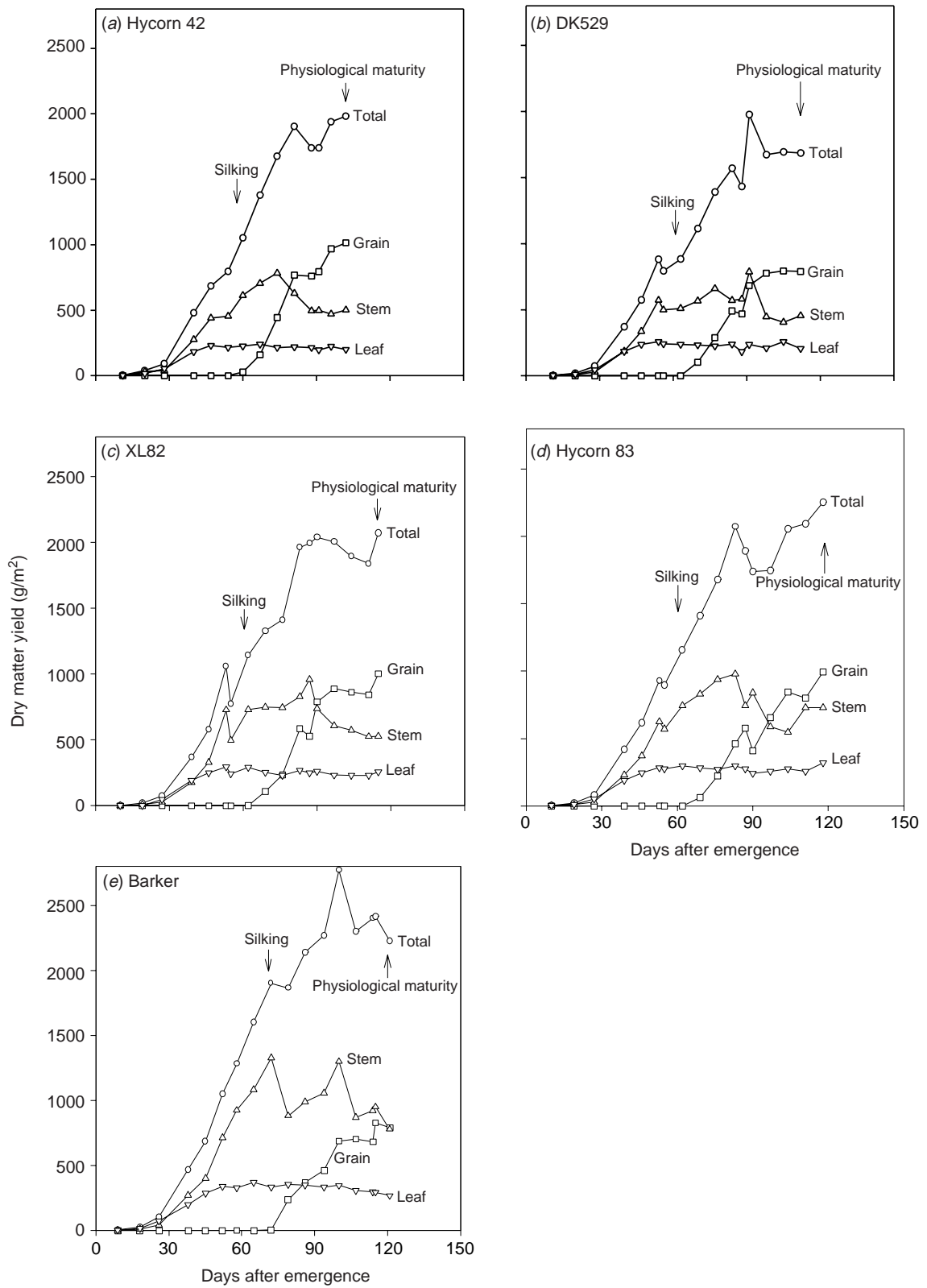


Fig. 4. Dry matter accumulation and distribution (g/plant) from emergence to physiological maturity in 5 cultivars of maize.

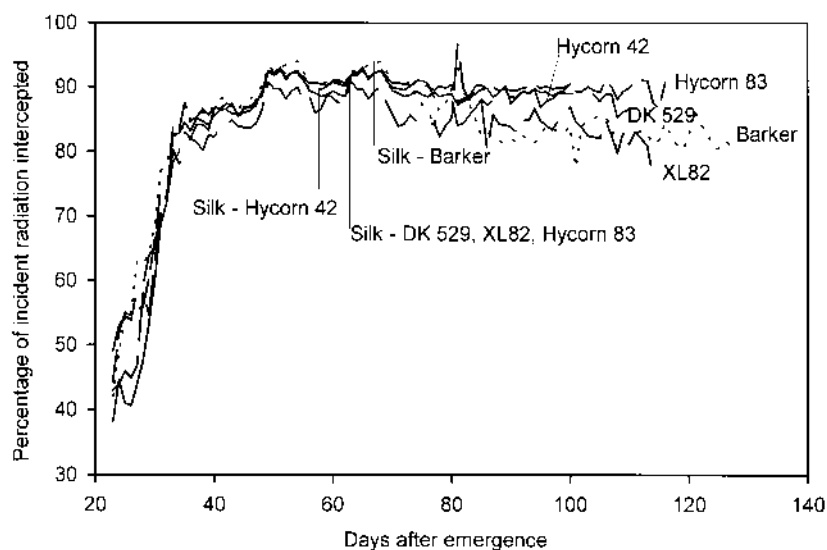


Fig. 5. Radiation interception (%) by 5 cultivars of maize from 24 days after emergence to physiological maturity (except in Barker, 1 week before physiological maturity).

Table 2. Radiation use efficiency (g DM/MJ photosynthetically active radiation) for the whole crop cycle, before silking, and after silking in five cultivars of maize, calculated by regression of dry matter accumulation on intercepted photosynthetically active radiation

Cultivar	Whole crop cycle ^A		Before silking		After silking ^A	
	RUE	s.e.	RUE	s.e.	RUE	s.e.
Hycorn 42	3.06	0.08	3.00	0.16	2.90	0.12
DK529	2.48	0.30	2.38	0.30	2.48	0.08
XL82	3.00	0.12	2.78	0.08	2.98	0.18
Hycorn 83	3.06	0.10	3.12	0.12	2.90	1.14
Barker	3.42	0.12	3.46	0.18	3.16	0.14
All	3.00	0.09	3.08	0.14	2.94	0.08
All except DK529 ^A	3.10	0.06	3.32	0.10	3.00	0.08

^ATo 240 degree-days (base 0°C) before physiological maturity.

Dry matter partitioning

Leaf dry weight

Maximum total leaf dry weight (leaf blades only) and maximum dry weight of green leaves occurred at silking in all 5 cultivars. Leaf DM was a declining proportion of total and of incremental DM as the number of leaves increased. The relationship between percentage of above-ground DM present as leaf (%DML) and the percentage of total leaf tips that had appeared (%TLNO) at individual samplings was highly significant (Fig. 6), and did not differ among cultivars, although total leaf number varied from 18 to 23. The equation was:

$$\%DML = 81.8(\pm 1.4) - 0.45(\pm 0.045) * \%TLNO \quad (r^2 = 0.77, n = 75) \quad (5)$$

Thus, the leaf declined from 82% of DM early in crop growth

to 40% just before the end of leaf growth, and fell to about 20% as the last leaf unfurled (Fig. 6).

Stem dry weight

There was an approximately linear increase in stem dry weight from tassel initiation (assumed to be at the same thermal time after emergence as in maize planted at a similar time in a companion study; Birch *et al.* 1998a) until about 2 weeks after silking (Fig. 4). In all except Barker, stem dry weight then declined for 2–3 weeks to 80–90% of the dry weight of stem at silking, after which no further decline, or a small increase, occurred. There was no distinct pattern in Barker.

Since robust relationships for %DML (Eqn 5) and ear growth before silking (Eqn 6, below) were developed, stem growth before and after silking can be predicted by the dif-

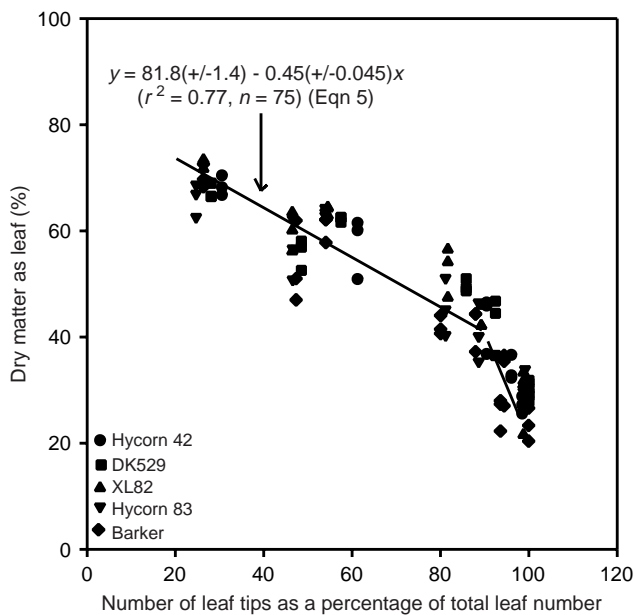


Fig. 6. Relationship between the percentage of dry matter present as leaf and the number of leaf tips that have appeared expressed as a percentage of total leaf number.

ference between total daily growth and allocation to other plant parts.

Ear growth before the start of linear grain filling

Ears were evident about 10 days (average 150 degree-days, base temperature 8°C) before silking in all cultivars. There were no differences among cultivars in the relationship between ear weight (EARWT) (g/m²) and accumulated thermal time (TT) from the start of ear growth to the start of linear grain filling, which occurred 4–7 days after silking (86–166 degree-days, base temperature = 0°C; Birch 1996a) (Table 3). The equation was:

$$\text{EARWT (g/m}^2\text{)} = 1.29(\pm 0.14) * \text{TT} \quad (r^2 = 0.83, n = 34) \quad (6)$$

The frequency of sampling was insufficient to explore relationships based on translocation of assimilate from a reserve pool, or direct allocation of photosynthate from current photosynthesis to ears, and thus Eqn 6 was retained.

Differences among cultivars in the delay from silking to the start of linear grain filling were small (Table 3), so an average thermal duration of the delay of 115 degree-days (base temperature 0°C) was considered appropriate for all cultivars.

Components of yield

Number of grains per plant, individual grain weight, and grain growth rate

There were no obvious trends of later maturing cultivars having more grains per plant (GPP) or greater individual

grain weight (Table 3). DK529 and Barker produced fewer grains per plant than other cultivars, but individual grain weight was larger.

Table 3. Mean number of grains per plant and individual grain weight (mg/grain) in five cultivars of maize

Cultivar	Grains per plant	Individual grain weight
Hycorn 42	534	248
DK529	445	268
XL82	569	252
Hycorn 83	577	242
Barker	401	270
l.s.d. ($P = 0.05$)	92	12

Grain growth rates (mg/grain.day) were calculated for the period of linear grain filling (i.e. 10% to 80% of grain yield having accumulated). These were 7.0(±0.9), 6.6(±0.8), 5.8(±0.8), 5.1(±0.7), and 6.4(±0.8) mg/grain.day for Hycorn 42, DK529, XL82, Hycorn 83, and Barker, respectively, all with coefficient of determination >0.80.

Harvest index

Harvest indices decreased with increasing maturity type. Final harvest indices at PM were Hycorn 42 (0.51), DK529 (0.47), and XL82 (0.49), but lower in Hycorn 83 (0.40) and Barker (0.38) (l.s.d. ($P = 0.05$) = 0.045). Harvest index was also calculated for individual samplings during which grain mass accumulation increased from 10% to 80% of maximum grain yield, as in Muchow (1990a) (Fig. 7). The rates of increase in harvest index (δ HI) were similar in Hycorn 42, DK529, and XL82, but lower (and similar) in Hycorn 83 and Barker (Table 4).

Discussion

Leaf area index and radiation interception

Leaf area index increased rapidly from 25 to 40 days after emergence, and interception increased from 30–40% to 80–85% in all cultivars. Leaf area index remained above 3.5 and radiation interception above 80% until close to PM. The k value (0.46) is in the lower end of the range for maize given by Stapper and Arkin (1980), and refers to the whole crop cycle, rather than being for specific canopy conditions and structure, which may vary through crop life. Lack of differences among cultivars means that the value of 0.46 can be used with confidence with a wide diversity of cultivars. Also, since this value of k is similar to those used in the model evaluations in Birch (1996a, 1996b), errors of prediction in DM yield should not be due to an inappropriate radiation extinction coefficient.

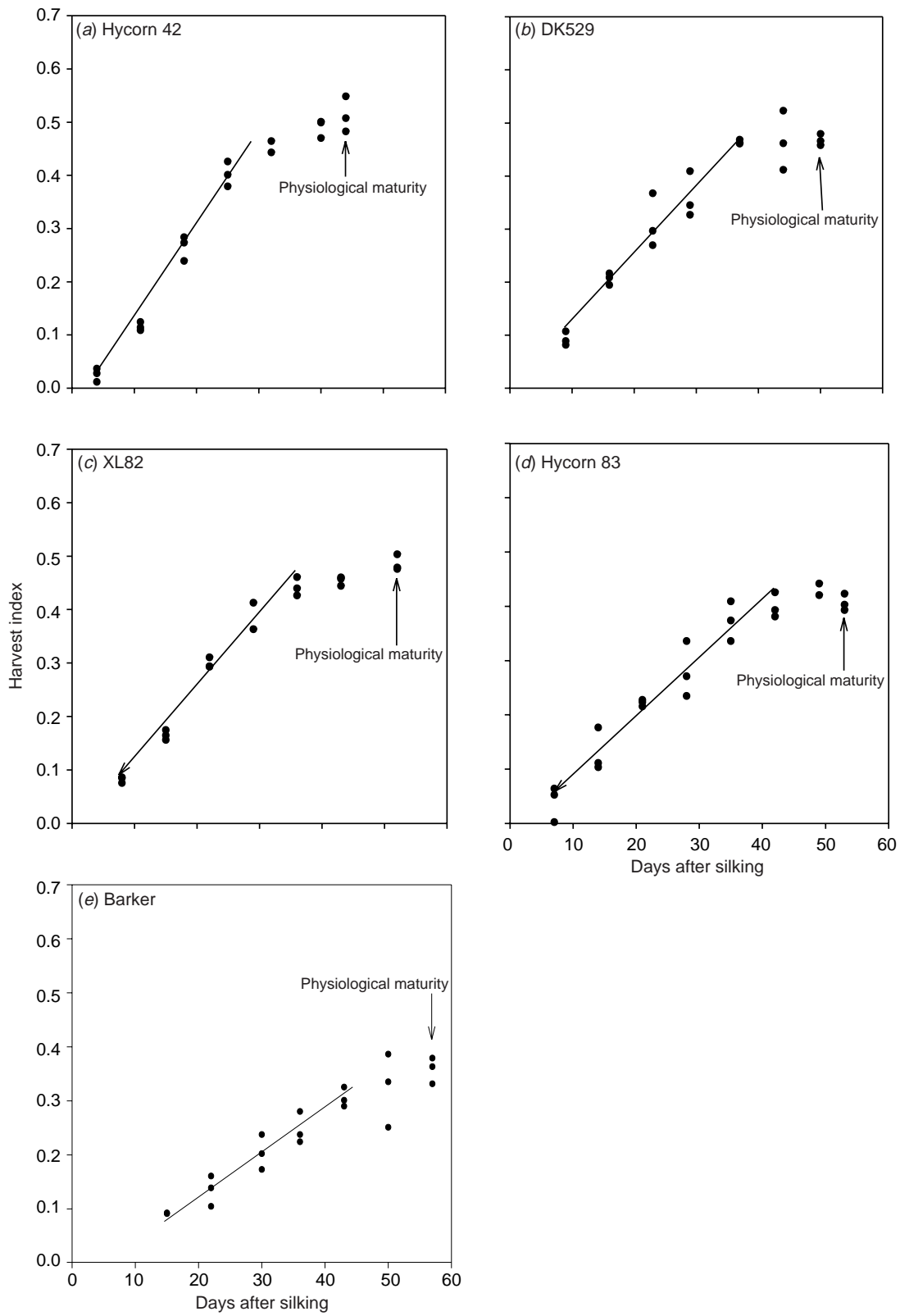


Fig. 7. Relationship between harvest index (individual replicate data) and time (days) after silking.

Table 4. The delay from silking to the start of linear increase in harvest index (Delay) (degree-days, using base, optimum, and maximum temperatures of 0, 34, and 40°C (Birch 1996a) and rate of increase in harvest index (δ HI) determined by piecewise regression

Cultivar	Delay (degree days)	s.e. of Delay	δ HI	s.e. of δ HI	r^2
Hycorn 42	86	41	0.016	0.002	0.88
DK529	90	66	0.014	0.002	0.92
XL82	108	20	0.014	0.001	0.94
Hycorn 83	135	49	0.012	0.001	0.91
Barker	166	44	0.011	0.001	0.79

Radiation use efficiency

RUE values found here are in the upper end of the range measured by Muchow and Davis (1988) and compare favourably with other recent reports for maize (Kiniry *et al.* 1989; Major *et al.* 1991; Tollenaar and Aguilera 1992; Watiki *et al.* 1993; Muchow 1994; Andrade 1995). Kiniry *et al.* (1989) reported RUE of 3.5 g/MJ, but they used 45% of incident radiation as PAR. Had they used 50%, their RUE would have been 3.15, which is close to, and thus supports, our mean value (3.00 g/MJ). Muchow (1994) also reported similar RUE for the pre- and post-silking growth (until just prior to PM), provided N supply was adequate, but RUE was lower if N supply was limited. Declining RUE close to physiological maturity is consistent with mobilisation of N from leaves to grain, resulting in lower leaf productivity (Sinclair and de Wit 1975). The small differences we found in RUE among cultivars other than De Kalb 529 mean that our average RUE (3.0 g/MJ) can be used until 240 degree-days before physiological maturity. This contrasts with the reduction in RUE in AUSIM-Maize (33%) and CORNF (20%) (Stapper and Arkin 1980), and applied for less than half of the post-silking period (25%) in the Muchow–Sinclair model. Except for CERES-Maize, these models use similar values of RUE (3.2–3.4 g/MJ) before silking. The Muchow–Sinclair model does not include root growth, whereas CERES-Maize uses RUE of 5 g/MJ, but has unrestricted partitioning of excess photosynthate to roots.

Since root DM was not assessed in this study, RUE has been underestimated, and an adjustment will be needed for models that partition some DM to roots. Despite small differences in RUE for above-ground DM in maize, it is apparent that RUE declines as the crop ages, when account is taken of DM allocated to roots. Linear adjustments to RUE seem reasonable from the data of Fairey and Daynard (1978) and Tollenaar (1989). In the absence of better data, average factors of RUE to adjust for root growth are proposed, and based on the references above are 1.4 (emergence to tassel initiation), 1.25 (tassel initiation to silking), and 1.13 (for 2 weeks after silking). The proportion of daily DM production allocated to roots by these factors would be 28%, 20%, and 10%, and do not differ greatly from those in AUSIM-Maize.

Dry matter partitioning

Leaf dry weight

The concept used in developing a new approach to allocating DM to leaves is that the plant produces leaf area and accumulates carbon, which is allocated to leaves, stems, roots, and ears according to stage of growth. The relationship found (Eqn 5) relies only on leaf number at a particular time and total leaf number. Use of these variables for calculation of percentage of DM allocated to leaves (Eqn 5) accommodates differences in maturity of individual cultivars, as differences in allocation of DM to leaf are mediated by total leaf number.

Specific leaf area (SLA, cm²/g), or its reciprocal, specific leaf weight (SLW, g/cm²), may be able to be further developed for use as intermediate variables, if, for instance, the effect of plant population were being examined, and a method of allocating total canopy leaf area to individual plants was needed. However, in the present study, SLA declined linearly with thermal time accumulation from emergence to silking, after which no further change occurred (data not presented). Also, since SLA does not describe the process of distribution of DM by the plant, Eqn 5, which does, should be preferred as a predictive tool. The present study does not provide a method of adjusting leaf area on individual plants when plant populations differ from those used here. An adjustment, perhaps including the use of SLA related to thermal time from emergence or a process of assimilate remobilisation in response to low radiation intensities in the lower part of the canopy, as an intermediate variable, is needed.

Stem dry weight

The increase in stem dry weight for 2 weeks after silking found in this study coincides with the period of increase in root DM after silking reported by Fairey and Daynard (1978) and accounts for the remaining assimilates after allocation to the developing grain and the roots. The development of a robust relationships for %DML until silking (Eqn 5), and for ear growth before and after silking (Eqn 6), means that stem growth can be predicted by difference. Withdrawal of assimilate from stem during grain filling reduced stem weight to

80–90% of the stem weight at silking, a reduction similar to that found by Lorens *et al.* (1987) for irrigated maize. A variable for assimilate that can be remobilised from the stem, rather than a minimum to which stem weight can fall, is needed. It appears that the size of the remobilisable pool is at least equal to the stem growth that occurs after silking, but may also include up to 20% of stem dry weight at silking. However, more detailed data than collected here are necessary to develop the appropriate equations.

Prediction of grain yield by use of components of yield

We were not able to improve on the approach to prediction of grain number per plant proposed by Edmeades and Daynard (1979) (Eqn 2), which relies on average daily photosynthesis over a short period after silking. However, calibrating the asymptote in Eqn 2 (i.e. potential number of grains per plant, PGPP) produced substantial range in GPP. All PGPP values were within the expected range of 400–1000 grains/plant (Eberhart 1979) and, except for Barker, were higher than the 680 grains per plant used in AUSIM-Maize. The sensitivity of predictions of grain yield and individual grain weight by AUSIM-Maize to changes in the value of PGPP was low to very high for individual experiments (Birch 1996a). Hence, better estimates of PGPP are needed. An approach that uses both average daily radiation and thermal conditions has been found useful in sunflowers (Cantagallo *et al.* 1997), and may be applicable to maize. Although we do not have sufficiently detailed data to explore this possibility for maize, it should be assessed, as current methods of estimating GPP are unsatisfactory. Alternatively, the approach of relating GPP to intercepted PAR per plant soon after anthesis, presented by Kiniry and Knievel (1995), should be further developed. Our data cover a narrow range in GPP and intercepted radiation per plant, so it was not possible to develop a regression between these variables. However, they agree quite well with the regression developed by Kiniry and Knievel (1995) for 7 cultivars of maize grown at Temple, Texas. Kiniry and Knievel (1995) found that their regression did not fit all cultivars or all locations at which it was tested. Hence, they concluded that the potential GPP needs defining for cultivars grown at low populations under non-stressed conditions. Consequently, it appears that, whichever approach is used, genotype constants for GPP are needed.

Final GPP was comparable with those in other trials at Gaton (Birch 1989; Carberry and Abrecht 1991; Karanja and Birch 1994) in Hycorn 42, XL82, and Hycorn 83, despite high maximum temperatures (35–42°C) during tasselling and silking, which can reduce pollen viability and seed set. The experiment was irrigated frequently to ensure that water supply was sufficient to maintain pollen viability and minimise the incidence of desynchronisation of pollen shedding and silk receptiveness. The strategy was successful, as reductions in grain set associated with high temperatures (Runge

1968; Johnson and Herrero 1981; Schoper *et al.* 1986) did not occur. There are several reports that maximum and mean temperatures <38°C can reduce grain set in maize, e.g. maximum and mean temperatures of 30 and 27°C in controlled environments (Struik *et al.* 1986), day/night temperatures of 38/32°C (average 35°C) (Schoper *et al.* 1986), and >32°C [Berbecel and Eftimescu (1973), cited by Shaw (1988)]. Thus, the maximum temperature threshold for heat stress (38°C) in AUSIM-Maize is probably too high.

Daily grain growth rate (mg/grain.day) could only be examined in relative terms, and differences among cultivars were detected. The highest rate of grain growth can exceed 10 mg/grain.day (Ritchie *et al.* 1986; Tollenaar and Bruulsema 1988) and the lowest may be below 6.0 mg/grain.day (Jones and Simmons 1983). At best, our observed figures may be used to calculate potential grain growth rates for the varieties we used against that in AUSIM-Maize for XL82 (9 mg/grain.day).

Use of linear increase in harvest index to predict grain yield

The Muchow–Sinclair model predicts grain yield from a linear increase in harvest index, to a maximum of 0.50 (increasing at 0.0135/day) (unless terminated earlier in the model by accumulated thermal time or water deficit). The linear increase in harvest index commences 67 degree-days ($T_b = 8^\circ\text{C}$) after silking and is reduced if daily mean temperature is below 19°C. Temperature was always higher in the present study. The use of either threshold thermal time (1150 degree-days, $T_b = 0^\circ\text{C}$) or maximum harvest index of 0.5 from the Muchow–Sinclair model would have predicted the end of effective grain filling 1–15 days later, or 2–10 days earlier than observed PM, respectively. Although not directly comparable, the wide differences between predicted end of grain filling and observed PM indicate that the method of predicting grain yield in the Muchow–Sinclair model is not applicable across cultivars. We found differences in the rate of increase in harvest index (δHI) (Table 3) and in final harvest index, being lower in the tropically adapted hybrids (Hycorn 83 and Barker) than in the other cultivars. These were consistent with earlier reports of lower harvest indices in tropical hybrids (Aluko and Fischer 1987), and in a waxy maize cultivar, GH5019wx (Karanja 1993; Karanja and Birch 1994). Thus, methods of altering δHI , and limiting final harvest index in cultivars that do not reach 0.50, are necessary. The present study does not allow development of such procedures, so as an interim measure, δHI and final harvest index would have to be supplied as genotype parameters.

Conclusions

This study provided several simple and robust relationships to describe DM production and partitioning, but further improvements could be made by using an explicit reserve pool of remobilisable assimilate in the stem for use during

grain filling. Also, there was little variation in RUE and radiation extinction coefficient among cultivars, nor did RUE, assessed from above-ground DM, vary much through the life of the crop, until close to physiological maturity.

Allocation of DM to leaves during canopy production was related to the number of leaf tips that were present and total leaf number. Ear weight was related to thermal time from 150 degree-days before silking until the start of linear grain growth. However, a more biologically sound method of calculation of ear weight should be sought, based on allocation of daily photosynthate production, rather than a measure of plant age (thermal time). Daily increase in stem dry weight from emergence to silking and after silking can be calculated by difference after allocating daily photosynthesis to the leaf, ear, and root (root only until 2 weeks after silking) growth. A minimum of 80% of stem dry weight at silking must be imposed, as the lower limit to which stem weight can be reduced by translocation to the grain. This, however, is an interim measure pending the modelling of a reserve pool of remobilisable assimilate in the stems.

The use of a components of yield approach to prediction of grain yield requires further investigation, to provide reliable data on potential grain number per plant and potential grain growth rate. The rates of increase in harvest index and final harvest index differ among cultivars, and for wide application, genotype constants for these are needed. Alternatively, a method of generalising them needs to be developed.

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