

Morphological analysis of plant density effects on early leaf area growth in maize

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Abstract

In tillering Gramineae species, leaf-area growth at higher plant densities is limited because no higher-order tillers are formed. This paper analyses the mechanisms of density-related reduced leaf area per plant in non-tillering maize (*Zea mays* L.).

Maize crops with a wide range of plant densities were grown in the field for two years. Half of the plots were shaded (50% transmittance). Detailed measurements of leaf appearance, leaf size, and dry weights of leaves and other plant organs were made. Data were analysed using standard crop-ecological growth functions.

Leaf-appearance rates were lower at higher plant densities and under shade. These effects were not caused by the small differences in canopy temperature observed, but closely associated with reductions in the growth rate per individual plant. Leaf length was higher under shade than with full light; effects of plant density on leaf length were inconsistent over the two years, associated with inconsistent effects on leaf-elongation rate. Leaf-elongation duration was longer at higher plant densities in both experimental years.

The crop-ecological analysis showed that plant density affected leaf-area expansion of maize mainly through effects on leaf-appearance rates, and that these effects were closely related to density effects on plant-growth rate per leaf-appearance interval.

Keywords: *Zea mays*, plant density, photosynthetic photon flux density, temperature, leaf growth

Introduction

Current models describing leaf-area expansion of Gramineae species are empirical and species-specific. This is considered a major drawback. We are developing a more generic, morphological model that describes leaf-area expansion based on the dynamics of tillering (based on specific site usage), tiller characteristics (based on Haun Stage delay), leaf appearance and characteristics of individual leaves. The mechanistic model can only be built when new, accurate and detailed morphological information and insight in mechanisms are acquired. Therefore experiments were carried out for wheat and maize in which the effects of temperature, light intensity

and plant density on the morphological characteristics mentioned above were precisely quantified. For more details on the research and modelling approach see Bos (1999). In this paper, we report on density effects on leaf-area development in maize (*Zea mays* L.).

At higher plant densities, leaf area per plant is reduced in later phases of growth (Hay & Walker, 1989). As an example of a tillering Gramineae species, Bos & Vos (2000) analysed for wheat which morphological leaf components were affected by plant density and which mechanisms were involved. They found that the most significant effect of higher plant densities on leaf area per plant was the absence of later-formed tillers. The lack of tiller formation was related to low local assimilate availability, induced by low photosynthetic photon flux densities (PPFD) or low red/far-red ratios at the site of the incipient tiller. When a species does not form tillers, plant density can only affect the growth of leaves on the main stem. A study into the effects of environmental factors on the morphological development of such a plant type could lead to a better understanding of mechanisms involved in the effects of plant density on leaf-area development.

Modern maize (*Zea mays* L.) hybrids only rarely form tillers. Leaf-area development on one (main) stem fully determines the leaf-area development per plant, and effects of plant density must be related to effects on leaf-area growth of this main stem. Several authors (e.g. Williams *et al.*, 1965) found a decrease in leaf area per plant with an increase in plant density for maize. Grant & Hesketh (1992) assumed that leaf-area growth on a maize plant is a function of leaf dry weight and the increase in leaf dry weight. However, they tested this hypothesis on plants grown in a range of rather low plant densities (1.5–10.3 m⁻²), resulting in only small differences in leaf area per plant, even between the extreme plant densities. Such results cannot be used for our generic leaf-area growth model, because questions such as ‘How is leaf area reduced at higher plant densities (is the appearance of leaves reduced or are individual leaves smaller?)’ and ‘By what mechanisms is leaf area reduced?’ remain unanswered.

The objectives of the current paper are: (i) to determine which leaf-area variables in maize are affected by plant density, and (ii) to analyse which mechanisms could be involved. The effects of a wide range of plant densities and of 50% shade on leaf-area variables were tested in a field experiment repeated for two years.

Materials and methods

Field experiment 1993 (F93)

Maize seeds (hybrid ‘Luna’) were sown by hand in a square plant arrangement (equidistant grid) in a heavy clay soil in Wageningen (52°N, 6°E) on 25 and 26 May 1993; plants emerged on 6 June. Treatments included all combinations of four densities and two shading levels in two blocks. Densities were: widely spaced or approximately 0 plants m⁻² (code: D0), 7.7 plants m⁻² (code: D7.7), 31 plants m⁻² (code: D31), and 123 plants m⁻² (code: D123). The two shading levels were: not shaded

(code: S0) and shaded (S1). D0 plots were sown in a plant density of 4.5 m^{-2} , and this density decreased in time by periodic harvesting. In early growth stages plots were irrigated and abundantly fertilised. Twelve days after emergence (DAE) (appearance Leaf 5) shading treatments were started by placing white nets above the S1 plots. Transmission of the nets was 50% in the wavelength range 400–800 nm, with no effects of the nets on the red/far-red ratio. Nets were lifted during growth to assure a distance of 30 cm between the top of the crop canopy and the net. Individual plots were $5.40 \times 4.32 \text{ m}$ and the inner $3.24 \times 2.16 \text{ m}$ was regarded as net plot. Every full-grown 5th leaf on a plant was marked to facilitate leaf identification.

Field experiment 1994 (F94)

Seeds were sown in a heavy clay soil in Wageningen on 20 May 1994; plants emerged on 31 May. Experimental layout was as in the F93 experiment. Fifteen DAE (appearance Leaf 4) shading treatments were started.

Measurements and calculations

Harvesting procedure. Plots were sampled 16, 30, 43 and 56 DAE (F93) or 24, 35 and 55 DAE (F94) by harvesting above-ground parts of eight plants. Due to severe lodging, the D123S0 plots in both blocks in the F94 experiment were discarded in Harvests 2 and 3. Plant material was dissected into individual leaf blades ('leaves'). The remaining plant was divided into three fractions: sheaths, stems and tassels. Leaves were counted acropetally. If more than 50% of a leaf was yellow or the leaf was broken off from the plant, it was considered dead and discarded. Full-grown leaves were cut off at their ligule, growing leaves were cut off at the uppermost visible ligule on the plant. In this way, a leaf was supposed to have appeared when its tip reached above the uppermost visible ligule. Dissected material was oven-dried at 70°C to constant weight.

Temperature and light measurements. Daily values of maximum and minimum air temperatures and global radiation were recorded within 1 km from the experimental sites. Figure 1 shows that the first 25 DAE were colder and darker in F94 than in F93 and that between 25 DAE up to 55 DAE temperature and PPFD were lower in the F93 than in the F94 experiment. Crop temperatures at -1, 0 and 40 cm above soil level were recorded every two hours in all plots in one block in the F93 experiment from 19 DAE onwards.

Leaf appearance. The base temperature for leaf appearance was calculated as a linear function of growing degree days (gdd). Growing degree days were calculated with two methods: in Method 1 daily average air temperatures were used; in Method 2 the suggestion of Grant (1989) and Yin *et al.* (1996) that diurnally fluctuating temperatures should be used, was taken into account for calculation of gdd. To do so, from the daily maximum and minimum measured air temperatures, hourly values were calculated with equations given by Goudriaan & Van Laar (1994). Leaf-appearance rate (LAR) was calculated with linear regression as the slope of the number of appeared leaves (a leaf is here defined to be appeared when its tip is visible) vs. gdd.

Leaf-appearance rate (LAR) was fitted as a function of plant density using a hyperbolic spacing formula (De Wit, 1960):

$$LAR = \frac{LAR_0}{\frac{\beta}{LAR_0} D + 1} \quad (1)$$

where LAR_0 ($^{\circ}C^{-1} d^{-1}$) is the fitted LAR for plant density (D) = 0 m^{-2} and β ($^{\circ}C^{-1} d^{-1} m^2$) the fitted slope of the curve for $D = 0 m^{-2}$.

Individual leaf-area variables. Length and maximum width were measured on all appeared leaves. On one plant per plot, length, maximum width and width of full-grown leaves were measured at six or seven equidistant places covering the whole leaf length. With numerical rectangular integration, leaf area was calculated from leaf length and the leaf widths. After this, the leaf-shape factor k was calculated:

$$k = \frac{Leaf\ area}{Leaf\ length * Maximum\ leaf\ width} \quad (2)$$

For analysis of maximum leaf width and full-grown leaf length, data were used from leaves that were recently full-grown.

Leaf-elongation rate (LER) and leaf-elongation duration (LED) were not directly determined but were calculated for Leaf 7. Leaf 7 was chosen because it elongated in the period during which observations were done. The calculation is as follows:

- i) the number of appeared leaves was plotted against the number of full-grown leaves (two example treatments shown in Figure 2). Linear regression was used to estimate the number of appeared leaves at the time Leaf 7 was full-grown;
- ii) the LED of Leaf 7 can now be calculated in units of ‘appeared leaves between emergence and cessation of elongation of Leaf 7’ (Figure 2);
- iii) using the estimated LAR, LED can be expressed in gdd ($^{\circ}C d$);
- iv) average LER ($cm^{\circ}C^{-1} d^{-1}$) was calculated by dividing full-grown leaf length (cm) by LED.

Dry weight. Above-ground dry-matter production per plant (W (g)) in time (t (d)) was fitted with the expolinear equation (Goudriaan & Van Laar, 1994):

$$W = \frac{c_m}{r_m} \ln(1 + e^{r_m(t-t_b)}) \quad (3)$$

where c_m is the maximum growth rate for $t \rightarrow \infty$ ($g d^{-1}$), r_m the initial relative growth rate ($g g^{-1} d^{-1}$) and t_b the moment at which the linear phase effectively starts (d). While shading treatments commenced some time after emergence, Equation 3 was rewritten to obtain Equation 4 and one common W value (W_{sh}) was estimated at the day when the shading treatments started (t_{sh}) for the two shading treatments per plant density per year.

$$W = W_{sh} \frac{\ln(1 + e^{r_m(t-t_b)})}{\ln(1 + e^{r_m(t_{sh}-t_b)})} \quad (4)$$

Variable W was log transformed and W_{sh} , r_m and t_b were estimated with nonlinear regression. The coefficient c_m was calculated with Equation 5:

$$c_m = \frac{W_{sh} r_m}{\ln(1 + e^{r_m(t_{sh}-t_b)})} \quad (5)$$

To examine whether plant growth rates (expressed in $g^{\circ}C^{-1} d^{-1}$) could explain effects of plant density on LAR, plant growth rate was calculated for the period LAR was determined:

$$\text{Plant growth rate } (g^{\circ}C^{-1} d^{-1}) = \frac{(W(g) \text{ at } gdd = 210^{\circ}C d) - (W(g) \text{ at } gdd = 90^{\circ}C d)}{(210-90)^{\circ}C d} \quad (6)$$

Results and discussion

Temperatures in the crop

Between 19 and 56 DAE in the F93 experiment, mean daily temperatures in the crop were lower in shaded treatments and at higher plant densities. The maximum difference in temperature was observed between D0S0 and D123S1 plots. The average temperatures during the measuring period in the D0S0 plot were 2.7 (at -1 cm), 2.8 (at 0 cm) or 0.5 (at 40 cm height) $^{\circ}C$ higher than in the D123S1 plot.

Dry-matter accumulation

Fitted values for r_m (Equation 4) were not significantly ($P < 0.05$) different between plant densities. Therefore, the analysis was redone with one common estimate for r_m for the four plant density treatments per shading level per year and one common estimate for W_{sh} for the two shading treatments per plant density per year. Parameter t_b was estimated for every individual treatment. Table 1 shows the estimates of W_{sh} , c_m (recalculated using Equation 4), r_m and t_b . Parameter r_m was higher in F94 than in F93, probably related to the higher temperatures in F94 from 25 DAE onwards (Figure 1). Shading decreased r_m and especially c_m . These effects are probably related to a reduced photosynthesis for shaded plants (Lawlor, 1987). At higher plant densities, t_b was lower, indicating that competition between plants for resources started earlier at higher plant densities. Also c_m (expressed per plant) was lower at higher plant densities, indicating that at later stages there was competition for resources between plants (Goudriaan & Van Laar, 1994).

Metselaar (1999) carried out extensive sensitivity and uncertainty analyses of maize models including formulae for dry-matter production and leaf-area expansion and showed that the approach used above is robust. However, uncertainty of parameters relating to leaf-area index is above average and these parameters are very sensitive to conditions.

Leaf area per plant

Leaf area per plant was clearly lower at higher plant densities: e.g. for the F93 exper-

Table 1. W_{sh} (estimated per density*year combination), r_m (estimated per shading*year combination) and t_b (estimated per individual treatment) in Equation 4 (exponential growth equation), and calculated c_m (Equation 5; expressed per plant and per area) for different plant densities and shading levels in the F93 ($R^2_{adj} = 99.3\%$) and F94 ($R^2_{adj} = 99.8\%$) experiments. Standard errors are indicated between brackets.

	W_{sh} (g)	r_m (g g ⁻¹ d ⁻¹)	t_b (d)	c_m (g pl ⁻¹ d ⁻¹)	c_m (g m ⁻² d ⁻¹)
<i>F93:</i>					
D0S0	0.24 (0.02)	0.170 (0.008)	36 (2)	2.6	–
D7.7S0	0.26 (0.02)	0.170 (0.008)	34 (2)	1.9	15
D31S0	0.26 (0.02)	0.170 (0.008)	30 (2)	0.94	29
D123S0	0.26 (0.02)	0.170 (0.008)	20 (1)	0.20	25
D0S1	0.24 (0.02)	0.161 (0.009)	35 (2)	1.4	–
D7.7S1	0.26 (0.02)	0.161 (0.009)	32 (2)	1.2	8.9
D31S1	0.26 (0.02)	0.161 (0.009)	27 (2)	0.48	15
D123S1	0.26 (0.02)	0.161 (0.009)	21 (2)	0.19	23
<i>F94:</i>					
D0S0	0.032 (0.003)	0.285 (0.008)	37 (1)	4.7	–
D7.7S0	0.028 (0.003)	0.285 (0.008)	36 (1)	2.8	22
D31S0	0.034 (0.003)	0.285 (0.008)	31 (1)	0.96	29
D123S0	–	–	–	–	–
D0S1	0.032 (0.003)	0.246 (0.007)	40 (1)	3.4	–
D7.7S1	0.028 (0.003)	0.246 (0.007)	38 (1)	1.9	14
D31S1	0.034 (0.003)	0.246 (0.007)	32 (1)	0.58	18
D123S1	0.032 (0.004)	0.246 (0.007)	27 (1)	0.16	19

iment 30 days after emergence leaf area per plant of treatment D0S0 was 1.7 times as high as treatment D123S0 and even 3.2 times as high 56 days after emergence (data not shown).

Leaf-appearance rate (LAR)

When daily average air temperatures (Method 1) were used to calculate the number of appeared leaves as a linear function of growing degree days (gdd) for unshaded free standing plants (D0S0 treatments in F93 and F94), a very low base temperature of -8°C fitted the data best ($R^2_{adj} = 95.6\%$). This is a very unrealistic value. Using estimated hourly temperature values (Method 2), a base temperature of 11.1°C fitted the data best ($R^2_{adj} = 99.3\%$). Although this value is higher than commonly found in maize literature, the hourly method with a base temperature of 11.1°C was used to calculate gdd (Figure 1), because more variance was accounted for by the use of hourly instead of daily values while a realistic base temperature was obtained (Ellis *et al.*, 1992).

The LAR per treatment was plotted against plant density in Figure 3. The data are fitted to Equation 1. Figure 3 shows that LAR was lower at higher plant densities and for shaded plots compared to unshaded plots over the entire range of plant densities.

Temperatures in the crop were lower for shaded treatments and at higher plant densities. Crop temperature differences between plots were up to 2.8°C , which will reduce LAR for this hybrid by 20% (Bos *et al.*, 2000). Differences in LAR were much larger and temperature can therefore only partly explain the effects of plant

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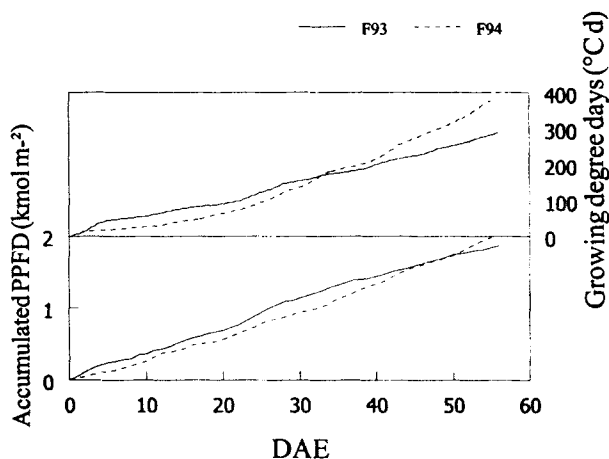


Figure 1. Accumulated photosynthetic photon flux density (PPFD) and growing degree days (base temperature 11.1°C based on hourly values) after crop emergence. Solid lines: F93 experiment; dashed lines: F94 experiment.

density on LAR. Plots were irrigated during the experiments and therefore no water shortage occurred. In an environment without irrigation, soil moisture reserves would be depleted much faster at high plant densities than at low plant densities, resulting in an even more drastic difference in crop temperature and perhaps also an even stronger effect of plant density on LAR.

Figure 4 shows a very close relationship between plant-growth rate and LAR independent of year, plant density or shading level. While the effects of growth rate on LAR were independent of shading level, it seems likely that the amount of assimilates determines LAR in the wide range of plant densities studied here. Effects of other factors such as red/far-red ratio cannot be ruled out, but are probably less important (discussions in various chapters of Bos, 1999).

Leaf length, LER and LED

Shading significantly increased the length of full-grown leaves that appeared after

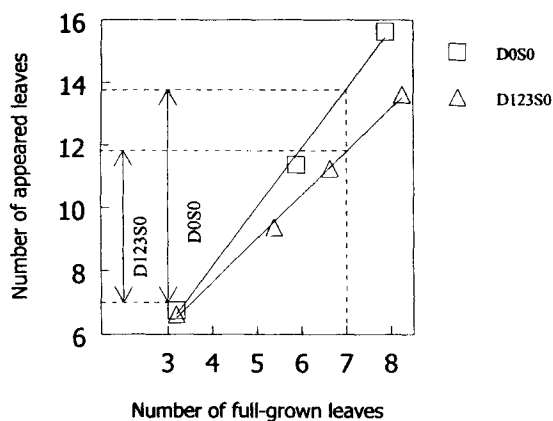


Figure 2. Illustration of the calculation of the number of appeared leaves during elongation of Leaf 7. Lines are fitted linear regressions and the length of the arrows represents the number of appeared leaves during elongation of Leaf 7 for treatments D0S0 and D123S0 in the F93 experiment.

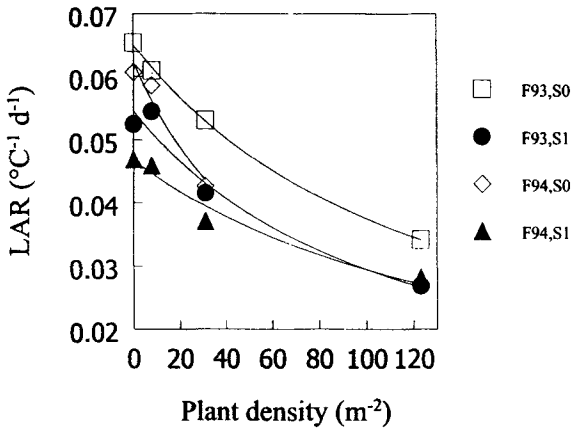


Figure 3. Effect of plant density on LAR for the two field experiments and shading levels. Lines are fitted curves using Equation 1.

the shading treatments commenced in both experimental years (data not shown). The effect of plant density on full-grown leaf length differed between the experimental years: in F93 full-grown leaves in both unshaded and shaded treatments were longer at higher plant densities at leaf positions higher than 5 (shown for unshaded treatments in Figure 5a), while in F94 there was no significant effect of plant density on full-grown leaf length, neither for unshaded nor for shaded treatments (shown for unshaded treatments in Figure 5b).

The calculated LER and LED of Leaf 7 relative to the value for spaced unshaded plants (treatment D0S0) are shown in Table 2. For both years, length and LED of Leaf 7 of shaded plants were longer. In the F93 experiment, at higher plant densities LED was longer and LER was unaffected resulting in longer leaves. In the F94 experiment, at higher plant densities LED was longer but LER was slower, resulting in no or a small effect of plant density on full-grown leaf length.

In all experiments, LED was longer at higher plant densities and for shaded treatments. For wheat, a good relationship existed between LED and leaf-appearance in-

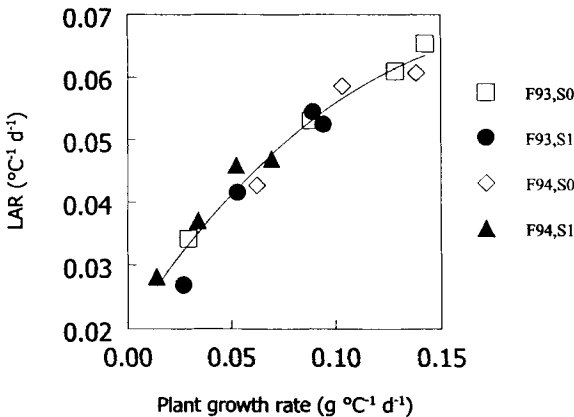


Figure 4. Relation between LAR and plant growth rate, calculated with Equation 6. A second order polynomial equation was fitted.

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Table 2. Full-grown length, LED and LER of Leaf 7 relative to spaced, unshaded plants (D0S0 treatment). Average temperature and growth rate during elongation of Leaf 7 are given.

	Relative length	Relative LED	Relative LER	Average temperature (°C)	Plant growth rate (g appeared leaf ⁻¹)
<i>F93:</i>					
D0S0	1 (= 48.6 cm)	1 (= 104 °C d)	1 (= 0.47 cm °C ⁻¹ d ⁻¹)	16.2	1.99
D7.7S0	0.99	1.11	0.89	16.3	1.97
D31S0	1.14	1.16	0.99	16.4	1.66
D123S0	1.45	1.35	1.07	16.2	0.907
D0S1	1.08	1.19	0.91	16.4	1.90
D7.7S1	1.33	1.22	1.09	16.4	1.69
D31S1	1.54	1.31	1.17	16.2	1.44
D123S1	1.64	1.79	0.91	16.4	1.08
<i>F94:</i>					
D0S0	1 (= 60.1 cm)	1 (= 114 °C d)	1 (= 0.53 cm °C ⁻¹ d ⁻¹)	19.2	1.98
D7.7S0	0.90	0.97	0.93	19.2	1.60
D31S0	0.93	1.16	0.80	19.1	1.48
D123S0	–	–	–	–	–
D0S1	1.23	1.04	1.19	19.0	1.49
D7.7S1	1.11	1.09	1.01	19.1	1.31
D31S1	1.17	1.23	0.95	19.5	0.971
D123S1	1.13	1.33	0.85	19.8	0.496

terval (Bos & Neuteboom, 1998). Such a relation also existed between LED and leaf-appearance interval of Leaf 7 (Figure 6). In tillering Gramineae species such as barley (Tesařová *et al.*, 1992), tall fescue (Skinner & Nelson, 1995) and wheat (Bos & Neuteboom, 1998), the growth of successive leaves is related in such a way that on average a constant number of visible leaves (between 1 and 2) is elongating per tiller. For maize, LED of Leaf 7 is four to seven times higher than the leaf appear-

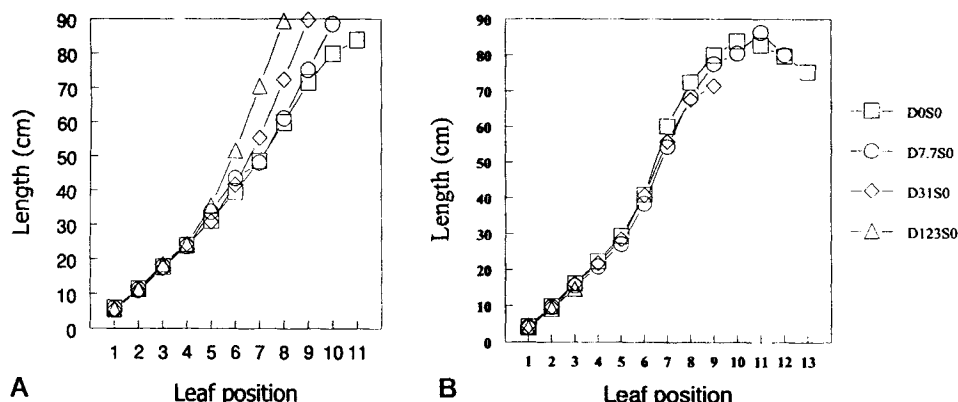


Figure 5. Full-grown leaf length of unshaded (S0) plants grown at different plant densities as a function of position on the plant in (a) the F93 experiment, and (b) the F94 experiment.

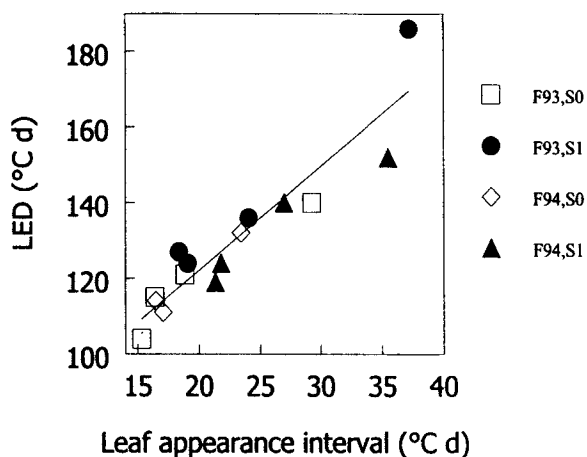


Figure 6. Relation between LED of Leaf 7 and leaf-appearance interval, fitted with linear regression. Data from different density treatments.

ance interval (Figure 6). This is in agreement with findings of Bos *et al.* (2000), who found that the number of growing leaves on a maize plant increases during development. Probably there is synchronisation between the growth of successive leaves, but this synchronisation is less simple than in barley, tall fescue or wheat.

Maximum leaf width

For both experimental years, shading significantly decreased the maximum width of leaves that appeared after the shading treatments were started. At higher plant densities, maximum leaf width was also significantly reduced, and already at a lower leaf position at higher plant densities (illustrated for F94 in Figure 7). This confirms earlier findings for wheat (Bos & Vos, 2000).

Possibly maximum leaf width is related to the plant growth rate per phyllochron.

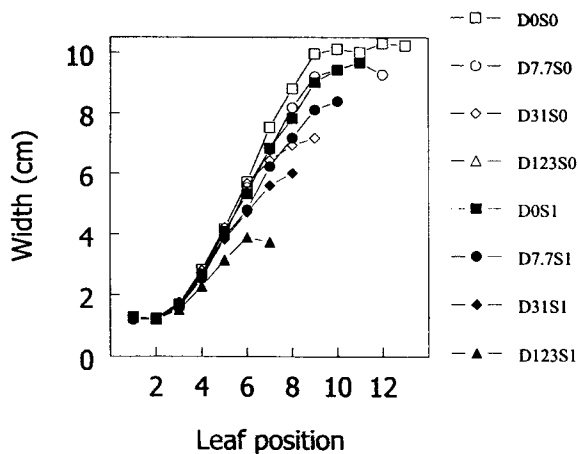


Figure 7. Maximum leaf width of plants grown at different plant densities and shading levels as a function of position on the plant in the F94 experiment.

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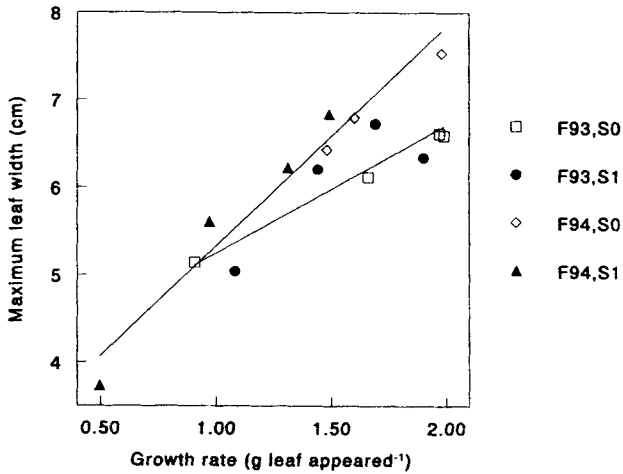


Figure 8. Relation between maximum leaf width of Leaf 7 and plant-growth rate (expressed in g per phyllochron) during elongation of Leaf 7. Linear regressions are shown per experiment (F93 and F94).

This measure adjusts for the effect of plant density on LAR and indicates the dry matter produced during one leaf-appearance interval. At appearance of Leaf 7, dry-matter production per plant and number of appeared leaves per plant were not yet affected by plant density. The plant-growth rate per appeared leaf at appearance of Leaf 7 can therefore not explain the differences in maximum leaf width between plant densities. If the growth rate per appeared leaf is calculated for the period that Leaf 7 is elongating, a good positive relationship was found between maximum leaf width and the growth rate per appeared leaf (Figure 8). Apparently, if leaf width is determined by growth rate per appeared leaf, maximum leaf width is not set at appearance of the leaf but during elongation.

Leaf-shape factor (k)

The leaf-shape factor k (Equation 1) decreased from 0.82 for Leaf 1 to 0.69 for Leaf 3 and was between 0.67 and 0.71 up to Leaf 8. Shading nor plant density had a significant effect on the value of k . Sanderson *et al.* (1981) found very small effects of plant density on k . Apparently area per leaf position is determined by the maximum width and length, in a manner which is rather independent of plant density or shading.

Leaf lifespan

There was no significant effect of plant density or shading on the number of dead leaves per plant as a function of DAE within the duration of the experiment (data not shown). At lower densities, old leaves died mainly due to wind, putrefaction (leaves laying on the ground) or penetration of their sheath by crown roots. At high plant densities old leaves mainly died by yellowing.

Conclusions

Plant density affected the leaf-area expansion in maize mainly through effects on LAR.

The effects on LAR were well related to effects on the plant-growth rate per leaf-appearance interval.

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Appendix. Abbreviations.

c_m	Maximum growth rate for $t \rightarrow \infty$ (Equation 5)
D	Plant density
DAE	Days after emergence
F	Field experiment
gdd	Growing degree days
LAR	Leaf-appearance rate
LAR_0	LAR at $D = 0 \text{ m}^{-2}$ (Equation 1)
LED	Leaf-elongation duration
LER	Leaf-elongation rate
PPFD	Photosynthetic photon flux density
r_m	Initial relative growth rate (Equation 4)
R^2_{adj}	Percentage of variance accounted for
S	Shading treatment (S0: unshaded; S1: 50 % shaded)
t	Time
t_b	Time when the linear growth rate effectively starts (Equation 4)
t_{sh}	Time when the shading treatments started
W	Dry weight above-ground parts per plant
W_{sh}	W at t_{sh}
β	Slope of Equation 1 at $D = 0 \text{ m}^{-2}$