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The effects of short and long shading, applied during different stages of growth, on the development, productivity and quality of forage maize (*Zea mays* L.)

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Summary

In two field experiments, shading was applied to normal stands of forage maize. The shading treatments differed in duration and date of initiation.

Short shading during vegetative development affected leaf area, plant height, stem thickness and reproductive development. Final effects on dry-matter yield and quality, however, were small. Short shading during silking drastically reduced ear size and final ear yield. Although the deleterious effect on ear yield was partly compensated for by the higher stover yield, productivity was low after the shading tents were removed. Digestibility was also greatly reduced because the production of total dry matter was hampered more than the production of partly indigestible cell walls. Short shading soon after silking curtailed cell-wall formation more than dry-matter production and as a result, crop digestibility was not adversely affected. The reduction in dry-matter production, however, remained large, especially in the ear, because there was extensive abortion of kernels. Shading after grain set stimulated the depletion of short carbohydrates in the stover and slowed down the decrease in the cell-wall content of the whole crop.

Crops shaded for long periods yielded more than expected on the basis of the short treatments. The long shading treatments lasted until final sampling. Therefore, the earlier a long treatment was initiated, the greater the reduction in yield. The same was true for whole-crop digestibility, except in the earliest shading treatment in which poor vegetative development accompanied poor ear development.

Shading affected digestibility mainly by affecting the cell-wall content.

Introduction

Long periods of low light intensity are common in northwest Europe. Such periods affect the development, physiology, production pattern and quality of forage

maize. In a previous report (Struik & Deinum, 1982) the effects of reduced amounts of radiation during the post-silking period were described. One of the striking results reported in that paper was that shading had a major effect on cell-wall formation. Shading during certain periods of intense production of structural material might reduce cell-wall production more than dry-matter production, thereby improving crop quality. It was also observed in these earlier experiments that maize may adapt to adverse climatic conditions, because during long periods of low light intensity maize produced more than had been expected on the basis of short shading treatments. Shading during and around flowering is known to limit reproductive development dramatically (e.g. Early et al., 1967, 1974), thus inducing a different pattern of dry-matter distribution.

To study these effects of shading more closely, two trials were set up in which long and short periods of shading were applied to standard crops of forage maize during different stages of early and late development.

Materials and methods

In 1980 en 1981 the hybrid LG 11 was sown on a light, sandy soil with optimum fertilization, weed and disease control. LG 11 is in current use in the Netherlands and is known to be tolerant to density (and thus shading). The sowing date was 24 April in both years. Seed density was high enough to ensure a final plant density of 10 m^{-2}. If necessary, the crop was thinned shortly after emergence. In the 1981 experiment drought was prevented by sprinkling.

The trials were laid out as completely randomized block designs with four replicates. In the 1981 experiment the continuously unshaded and continuously shaded treatments had two plots in each block to enable these treatments to be sampled on each sampling date.

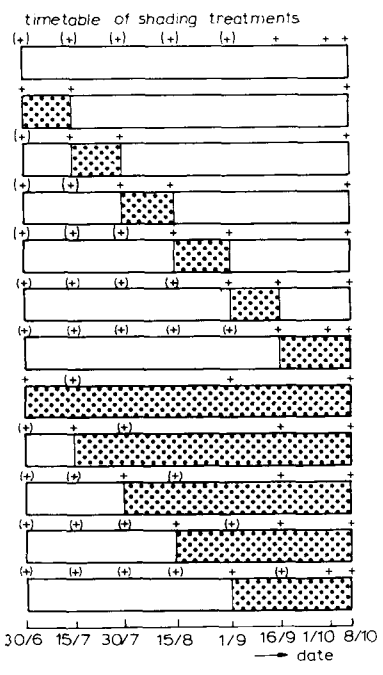
Treatments

Light intensity was reduced to 40 % of natural light intensity as described by Struik & Deinum (1982). The timing, duration and code of each shading treatment are schematically recorded in Fig. 1, together with the sampling dates, the main physiological processes occurring in the control crop in that period and the average natural light intensity during the period involved, as recorded at Wageningen.

The 1980 experiment (henceforth called Experiment 1) contained five short treatments each about two weeks long, and five longer treatments. Each long treatment terminated at final harvest, and therefore the later the treatment was initiated, the shorter its duration. Treatment S_2 was of intermediate duration. It will be considered as the final long treatment; the treatment also proved to be useful because it enabled the probable effect of short treatments initiated during the final development of the crop to be estimated.

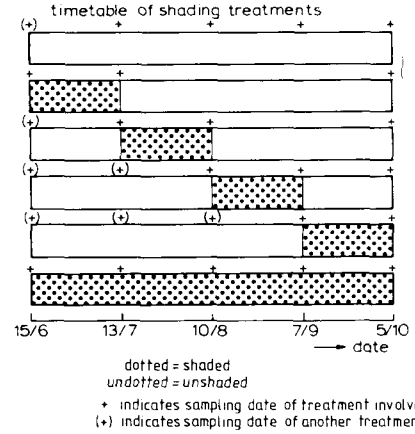
The 1981 experiment (henceforth called Experiment 2) contained four shading treatments, each lasting four weeks, and one continuously shaded treatment.

The controls (i.e. unshaded treatments) of both experiments are regarded as shading treatments initiated on the date of final harvest.



1980

duration (days)	code	physiological characterization	av. natural light intensity during treatment (J cm^{-2} day^{-1})
0	control	-	1254
15	J_1 s	leaf appearance ; stem elongation	1195
15	J_2 s	stem elongation ; tassel emergence	1595
16	J_3 s	anthesis; silking ; fertilization	1479
17	A s	grain set + start of grain filling	1261
15	S_1 s	grain filling	1207
22	S_2	grain filling and maturation	924
100	J_1 l	from late vegetative period until harvest	1254
85	J_2 l	from tassel emergence until harvest	1264
70	J_3 l	flowering, grain set and grain filling	1193
54	A l	grain set and grain filling	1109
37	S_1 l	grain-filling period	1039



1981

duration (days)	code	physiological characterization	av. natural light intensity during treatment (J cm^{-2} day^{-1})
0	control	-	1225
28	J_1 s	vegetative growth; development of inflorescences	1304
28	J_2 s	flowering and grain set	1407
28	A s	grain set and early grain-filling period	1323
28	S s	late grain-filling period	865
112	J_1 l	vegetative growth until final harvest	1225

\+ indicates sampling date of treatment involved.
(+) indicates sampling date of another treatment projected to the treatment in question.

Fig. 1. Timetable of the treatments in 1980 and 1981.

Crop measurements and yield estimates
Vegetative development was analysed as described by Struik & Deinum (1982). Estimates of flowering and desynchronization were done as described by Struik (1983a). Ear length and number of 'active' (i.e. dry-matter accumulating) kernels were recorded at final sampling. 10 top ears were analysed per plot. Each short treatment was sampled at the start of the treatment, at the end of the treatment and at final harvest. Each long treatment (excluding treatment J_1l in Experiment 2) was sampled at the start of the treatment, at final sampling and once in between. Treatment J_1l (the long shading treatment, initiated in June) in Experiment 2 was sampled on each date that a new short treatment was initiated, and at final harvest. Pretreatment samplings were used for estimating the production of the control crop. In addition, control crops were sampled on 16/9, 1/10 and 8/10 in Experiment 1 and on 13/7 (4 plots), 10/8 (4 plots), 7/9 (4 plots) and 5/10 (8 plots) in Experiment 2. Thus control samplings always involved two plots per block except for the final two sampling dates in Experiment 1. The estimate of yield made when a short shading treatment was terminated also gives an estimate of the yield of the ongoing long treatment that had been initiated on the same date.

The final sampling in 1980 had to be advanced by one week because of bad weather. In Fig. 1 the dates on which treatments were sampled are marked by a + sign. (+) marks a sampling of another treatment that was projected to the treatment in question. The methods of sampling, separation into fractions and subsampling used in these trials have been described in earlier papers (Struik & Deinum, 1982; Struik, 1983a).

Chemical analyses
Subsamples were analysed for digestibility in vitro of the organic matter (expressed as apparent digestibility), cell-wall content and cell-wall digestibility. Subsamples of Experiment 1 were also analysed for concentrations of N, PO_4, Ca and non-structural carbohydrates. The methods used have been described in a previous paper (Struik, 1983b).

Results and discussion

Climatic conditions

The weather in 1980 was not favourable for growing maize. During May, temperatures were below normal and precipitation was insufficient. The first part of July was cold, extremely wet and overcast (cf. Fig. 1).

1981 was a very good year for growing maize, mainly because of the favourable conditions in May, when temperatures were high and rainfall was sufficient. In 1981, however, there were long overcast periods in the second half of June (see Fig. 1). Thus in both years shading treatment J_1s was probably more effective than normal.

Vegetative development

Rate of leaf appearance and number of leaves. Leaf appearance was slowed down by shading in both years. This effect of light on the rate of early vegetative development has also been reported by Gmelig Meyling (1973). Shading probably lowers the temperature of the growing point, which is the main factor in determining the rate of leaf appearance.

The final number of leaves was unaffected by shading. Averages were 14.2 leaves/plant in 1980 and 14.9 leaves/plant in 1981.

Leaf area and leaf-area duration. Maximum leaf area was measured shortly after midsilk. At that time, only a limited number of treatments was in progress: the results from these treatments are presented in Table 1. Only the size of the upper leaves was affected. Shading during intensive leaf synthesis reduced leaf area by reducing leaf length and leaf width. Leaves grown in high light intensities usually contain more and larger cells than those grown in low light (Dale, 1982). However, final leaf expansion was hardly affected by shading during period J_2, suggesting that the effect was mainly obtained by a reduction in the number of cells.

Shading also affected the longevity of the leaves. Table 2 illustrates this phenomenon with the number of green leaves at final sampling as a criterion of longevity. However, it must be remembered that the fact that a leaf is green does not necessarily mean it is active.

The effects of the shading treatments depended on when they were initiated and on their duration.

1) Short shading initiated before flowering stimulated the longevity of the leaves. Long shading had a similar effect, but only if shading was initiated long before flowering.

2) Shading initiated at flowering hastened leaf senescence, especially when the shading was prolonged.

3) Short shading initiated during grain set had a small positive effect on the leaf lon-

Table 1. Mean leaf area per plant (in dm^2) shortly after silking for all treatments initiated before silking.[1]

Treatment code	Experiment 1	Experiment 2
J_1S	35.7^{ab}	32.6^{a}
J_2S	38.1^{b}	38.5^{b}
$J_3S = J_3I$	37.6^{ab}	
J_1I	33.6^{a}	32.7^{a}
J_2I	36.9^{ab}	
Control	38.3^{b}	39.6^{b}

[1] Means without a letter in common are significantly different at $P < 0.05$ according to Tukey's studentized range test.

Table 2. Number of green leaves per plant at final sampling (A leaf was classified as green if less than 50 % of its area was yellow or dead).

Experiment 1		Experiment 2	
treatment code	number of green leaves	treatment code	number of green leaves
J_1s	6.6	J_1s	8.1
J_2s	6.4	J_2s	5.9
J_3s	5.1	As	6.5
As	5.9	Ss	1.3
S_1s	4.3		
J_1l	6.6	J_1l	6.4
J_2l	4.1		
J_3l	3.5		
Al	1.7		
S_1l	0.7		
S_2	2.3		
Control	5.2	Control	6.1

gevity. Long shading initiated at this stage greatly reduced the longevity of leaves. 4) Shading during grain filling greatly accelerated leaf senescence, especially when shading was prolonged and when shading was initiated at a late stage of grain filling.

Leaves formed under the low light conditions of early shading may be able to tolerate low light intensities during autumn: this would account for the positive effect of early shading. Another possible explanation is the fact that in shading treatments initiated early in the crop's development, the relative sink size of the ear is better adapted to the poor light conditions during ear filling. (The latter hypothesis might also explain the small, positive effect of the As treatments.)

Shading initiated at flowering affected leaf senescence because the ear sink was greatly reduced by such treatments. When a strong ear sink was absent, the leaves soon turned purplish red and leaf senescence started earlier (cf. Allison & Weinmann, 1970). The occurrence of the red colour and the earlier onset of leaf senescence were also observed when the effect on the *final* number of green leaves was only small (e.g. J_3s). The effects were most pronounced for treatment J_2l of Experiment 1.

Shading during grain set also reduced the sink strength of the ear but to a smaller extent than shading during flowering. As stated earlier, a small reduction in the sink size might affect the longevity of the leaves but only when shading is not long. For treatment Al the source was limited so much that even the considerable reduction of the sink could not prevent senescence being accelerated as in treatments that had been initiated later. When initiated at later stages of grain development, both short and long shading affected leaf senescence dramatically: the effects of shading appeared more rapidly if shading was applied later, although the repercussions of the treatment still depended on its duration. The existence of an ear sink whose size and

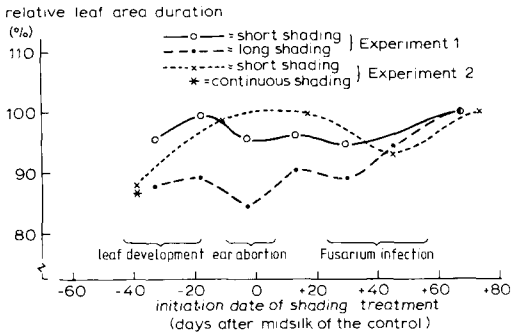


Fig. 2. Effect of date of initiation of short and long shading treatments on the relative duration of leaf area. Leaf-area duration of the controls = 100 %.

strength can no longer be substantially reduced by shading apparently causes the plant to die prematurely if the source is limited.

The effects of shade on leaf senescence after grain set were strongly connected with the severity of *Fusarium* infection (cf. Struik & Deinum, 1982). It is not clear whether the *Fusarium* infection is the actual cause of the premature senescence or just a concomitant side-effect of shading.

Leaf-area duration illustrates the combined effects of shading on leaf size and on leaf senescence. Leaf-area duration after silking was calculated from the weekly data on the number of green leaves, and the areas of the leaves shortly after silking. The resulting patterns, shown in Fig. 2, are essentially similar if the duration of the treatments is taken into account. The three factors that affect leaf-area duration are clearly discernable in the pattern for Experiment 1.

Plant height and stem diameter. Table 3 illustrates that early shading reduced plant height considerably. The later a shading treatment was initiated, the taller the final plant height. Prolonged shading initiated just before flowering even tended to stimulate the longitudinal growth of the stem. Differences between short and long treatments initiated on the same date were significant but inconsistent. Probably both di-

Table 3. Effect of shading treatments on plant height and stem diameter (means ± standard error of the mean).

Experiment 1			Experiment 2	
code	plant height (cm)	stem diameter (cm)	code	plant height (cm)
J_1s	189 ± 4.8	2.11 ± 0.06	J_1s	189 ± 6.1
J_2s	197 ± 3.7	2.26 ± 0.08	J_2s	241 ± 4.9
J_3s	206 ± 4.2	2.23 ± 0.09		
J_1l	178 ± 3.1	2.03 ± 0.04	J_1l	210 ± 4.1
J_2l	198 ± 3.6	2.35 ± 0.05		
J_3l	220 ± 2.7	2.23 ± 0.05		
Control	215 ± 1.4	2.33 ± 0.03	Control	235 ± 2.2

vision and elongation of stem cells were sensitive to shading. The number of cells along the longitudinal axis may have declined as a result of shading: in that case, the duration and date of initiation of the shading would have played a role. Short shading treatments probably reduced cell number less than long shading; early shading probably resulted in fewer cells being formed than late shading.

But shading normally stimulates cell elongation in stems (etiolation!). This stimulation would have been more effective if more cells were in the process of elongating during the shading treatments. A combination of the effects of shading on number and size of the cells could explain the observed effects on plant height. The pattern of radial cell growth (see stem diameter, Table 3) was similar to the pattern of longitudinal growth, except that J_3s and J_3l had lower values than expected.

Data on stem development may be relevant to digestibility, since the number and the size of the stem cells affect the plant's ability to form cell walls of poor digestibility (cf. section 'Quality').

Reproductive development

Anthesis, silking, anthesis-to-silking interval and lower-ear development. The flowering dates for treatments initiated before flowering are listed in Table 4. Treatments J_3s and J_3l of Experiment 1 can be regarded as the same treatment for all observations mentioned in this table, except for the number of lower ears. These treatments received the same amount of radiation until the end of flowering. Be-

Table 4. Flowering dates, desynchronization, degree of total sterility, and development of lower ears for all treatments initiated before flowering.

	Anthesis (♂) date (days after sowing)	Silking (♀) date (days after sowing)	Desynchronization (♀-♂; days)	Percentage of sterile tassels	Percentage of sterile top ears	Number of lower ears per plant
1980						
J_1s	103	101	—2	5	0	1.1
J_2s	103	101	—2	2	5	0.9
J_3s	101	99	—2	0	9	1.3
J_1l	106	103	—3	12-13	12-13	0.6
J_2l	105	104	—1	4	15	0.3
J_3l	101	99	—2	0	9	1.0
Control	102	99	—3	0	0	1.2
1981						
J_1s	97	96	—1	5	3	1.1
J_2s	94	95	+1	0	42	1.0
J_1l	99	98	—1	4	5-6	0.2
Control	94	91	—3	0	0	1.0

cause the shading of J_3s was stopped before the end of lower-ear development, the effects of treatments J_3s and J_3l on the number of lower ears differed.

Shading before flowering retarded both anthesis and silking, especially when shading was prolonged. Silking, however, was delayed more than pollen shed, especially in Experiment 2. This resulted in the female inflorescence having a smaller lead (see desynchronization values in Table 4). Desynchronization was always small, therefore pollination was not hampered by this shading effect. Shading, however, not only retarded but also reduced flowering by inducing complete or partial sterility in tassels and ears. Only the proportions of complete sterile tassels and ears are given in Table 4, but the fecundity of the fertile inflorescences in treatments with a high percentage of sterile inflorescences was also low. Sterility in the tassel was mainly induced by early shading an increased concomitantly with the duration of shading. Sterility in the ear, however, was mainly induced by shading during silking. If long shading was initiated long before flowering, however, the crop adapted sufficiently to maintain its ability to silk (cf. J_1l, Experiment 2), though silking was not prolific. For treatments J_1s and J_1l in Experiment 1 the relation between the proportion of flowering plants and time was not sigmoid but double sigmoid. This indicates that early shading divided the crop into two separate populations. Development of lower ears (i.e. all ears below the top ear that protrude from the axils of the leaves) was inhibited by early, long shading and – to some extent – by short shading that ended before silking.

The lower ears can only develop if conditions permit several ears to develop per plant at about the same (fast or slow) rate, or if conditions are adverse for the development of the top ear but are less unfavourable for the lower ears.

Ear size. Fig. 3 illustrates the success of development of the top ear. Ear length and the number of active kernels at final sampling are plotted against the date on which shading was initiated. All three curves of Fig. 3a clearly show that shading had a pronounced effect on the size of the top ear when it was applied during silking. In the long treatments, the effects of shading were just as large if the shading was initiated before silking. Short shading that had been terminated before silking had little effect on ear length. The effects of long and short shading after silking on ear length decreased, concomitantly with the progress of the ear development.

The effects of shading on the number of active kernels were similar to the effects on ear length (Fig. 3b). However, since shading induced kernels to abort after grain set, the effects remained considerable during early grain fill.

The results from treatment J_1s in Experiment 1 were atypical. The low number of active kernels resulted from a reduction in pollination. Pollen was scarce during the silking period of the tip kernels of J_1s plants. The partial or complete sterility of many tassels in this treatment might have been responsible for this. The pollinated basal kernels, however, were larger than normal. In addition, the rachides of the top ears of this treatment were also thicker than normal.

The length of the top ear is a more accurate and more objective characteristic than the number of active kernels. The number of active kernels, however, is more significant, since it is more closely related to the actual sink strength of the ear.

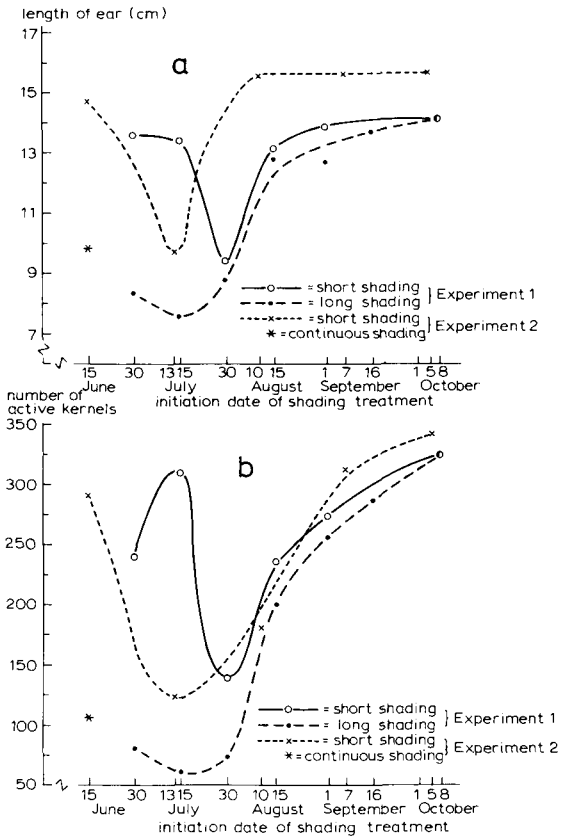


Fig. 3. Effect of date of initiation of shading (a) on length of the top ear and (b) on number of active kernels on the top ear.

Dry-matter production

Production of controls and of continuously shaded treatments

Since the controls and the J_1l treatments serve as references in these trials, their production patterns in both experiments are presented in Fig. 4. The productivity of J_1l during the entire experimental period was 35.4 % of the control in Experiment 1 and 35.0 % of the control in Experiment 2, i.e. productivity was reduced more than illuminance. Because of the responses of photosynthesis, respiration, dry-matter distribution and leaf development (and thus light *interception*) to such drastic reductions in light this is not unrealistic. In both years there was a characteristic decline in stover yield and husk + shank yield during the later part of the grain-filling period. Natural light conditions in the Netherlands during September are so poor that the growth rates of the ear are much higher than growth rates of the whole crop. This necessitates the redistribution of water-soluble carbohydrates and other com-

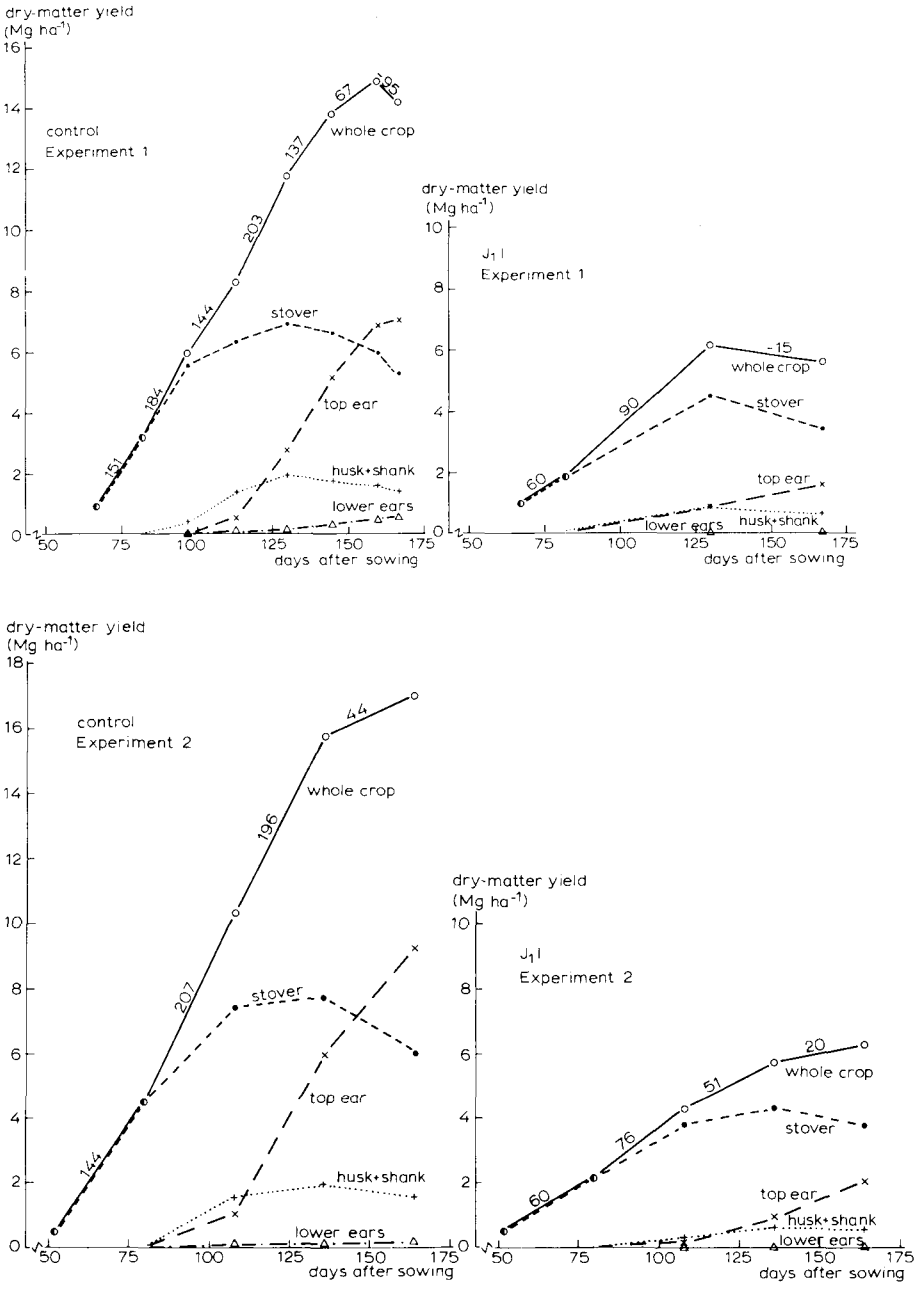


Fig. 4. Production pattern of unshaded and continuously shaded crops in both experiments. (— ○ — = whole crop; - - - ● - - - = stover; . . . + . . . = husk + shank; — × — = top ear; . — △ . — = lower ears; numbers indicate production rates in kg ha^{-1} day^{-1} for the periods involved).

pounds from vegetative parts to the growing grains. The intensity of the redistribution depends on the sink size of the ear and on the productivity of the leaves.

Final dry-matter yields

Fig. 5 illustrates the relation between the final dry-matter yields of stover, husk + shank, top ear + lower ears and of the whole crop and the date of initiation of the shading treatment.

Stover yields were comparatively little affected by shading. A very significant yield increase, however, was obtained when shading was initiated just prior to silking, especially for short treatments. The absence of an ear sink in these treatments resulted in a marked accumulation of water-soluble carbohydrates in the stover instead of in the redistribution mentioned earlier. The effects were similar to those resulting from the prevention of pollination (e.g. reported by Bunting, 1975; Deinum & Knoppers, 1979). The productivity of such grainless crops probably depends on the storage capacity of the stems, cobs, husks and shanks.

Stover yield was greatly reduced when long shading was initiated during vegetative development. The earlier the prolonged shading was initiated, the larger the reduction in stover yield. Shading during grain filling caused small (non-significant) reductions in stover yield because redistribution was more intense (cf. Struik & Deinum, 1982). The yields of husks and shanks declined if long shading was initiated at an early date. In contrast, short shading treatments J_1s tended to stimulate the yield of this fraction in both years.

The effects of shading on the dry-matter yields of the ears were substantial and were very similar to the effects of shading on number of active kernels. Simple linear correlation coefficients of the relation between number of active kernels of the top ear and dry-matter yield of the ears were 0.968 for Experiment 1 ($P < 0.01$; $n = 12$) and 0.977 for Experiment 2 ($P < 0.01$; $n = 6$). In Experiment 1, J_1s deviated from the regression line. This deviation was very significant ($P < 0.001$) and resulted from the large size of the kernels and the thick cobs, mentioned earlier. The linear correlation coefficient calculated without this deviation was 0.995 ($P < 0.01$; $n = 11$).

The effects of shading on the yields of the various fractions resulted in large differences in whole-plant yield between treatments. These differences were similar to differences in ear yield, with the following exceptions:

— in all cases, shading during flowering affected whole-crop yield less than ear yield;

— for long shading treatments initiated well before anthesis, the effects on whole crop were even greater than the effects on ears.

Whole-crop yields depended both on the amounts of radiation and on the developmental stage of the crop when the light was reduced.

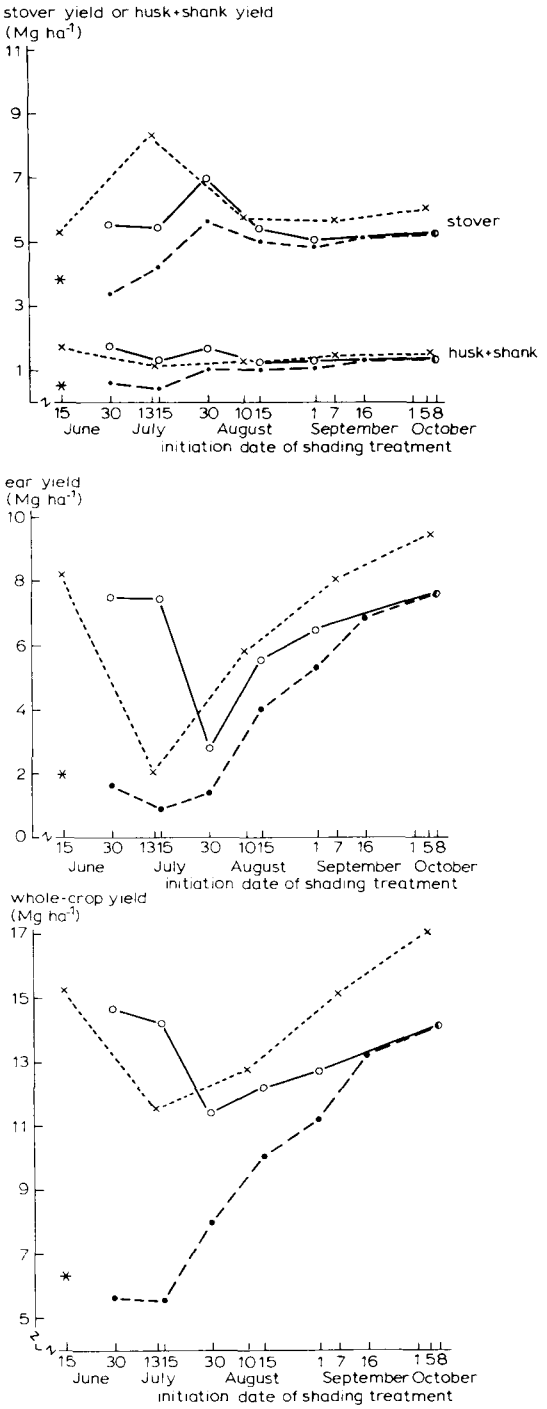


Fig. 5. Effects of shading on the yields of the various fractions and on whole-crop yield. (— ○ — = short shading, Experiment 1; – – ● – – = long shading, Experiment 1; - - - - × - - - - = short shading, Experiment 2; * = continuous shading, Experiment 2).

Production rates

Short shading treatments. Fig. 4 illustrated the production rates of the controls and of the J_1l treatments.

As expected, shading reduced production rate. (The method of calculating this reduction in rate of dry-matter production is given in Table 5, with J_1s and J_1l of Experiment 1 as an example.) One would expect this reduction to be dependent on the productivity of the control. In Experiment 2 this was certainly true (see Fig. 6). In Experiment 1, however, the effects of short shading also strongly depended on the physiological stage of the crop when the treatment was initiated. Short shading during early grain growth affected dry-matter production much more than was expected on the basis of the production rate of the control (Fig. 6). The discrepancy between the two experiments was probably caused by the difference in duration of the shading.

After the shading tents were removed, the crops in Experiment 1 that had re-

Table 5. Calculation of reduction in rate of dry-matter production for treatments J_1s and J_1l of Experiment 1.

Sampling date	Dry-matter yields (kg ha^{-1})		
	control	J_1s	J_1l
30 June	942	942	942
15 July	3204	1844	1844
1 September	11711	—	6165
8 October	14112	14676	5602

Reduction in rate of dry-matter production during short treatment (i.e. open circle in Fig. 6) (15 days):

$$\frac{(3204 - 942) - (1844 - 942)}{15} = 91 \text{ kg ha}^{-1} \text{ day}^{-1}$$

Reduction in rate of dry-matter production after short shading (i.e. closed circle in Fig. 6) (85 days):

$$\frac{(14112 - 3204) - (14676 - 1844)}{85} = -23 \text{ kg ha}^{-1} \text{ day}^{-1}$$

Reduction in rate of dry-matter production during long shading (○——○ in Fig. 7):
period 30 June to 15 July (15 days):

$$\frac{(3204 - 942) - (1844 - 942)}{15} = 91 \text{ kg ha}^{-1} \text{ day}^{-1}$$

period 15 July to 1 September (48 days):

$$\frac{(11711 - 3204) - (6165 - 1844)}{48} = 87 \text{ kg ha}^{-1} \text{ day}^{-1}$$

period 1 September to 8 October (37 days):

$$\frac{(14112 - 11711) - (5602 - 6165)}{37} = 80 \text{ kg ha}^{-1} \text{ day}^{-1}$$

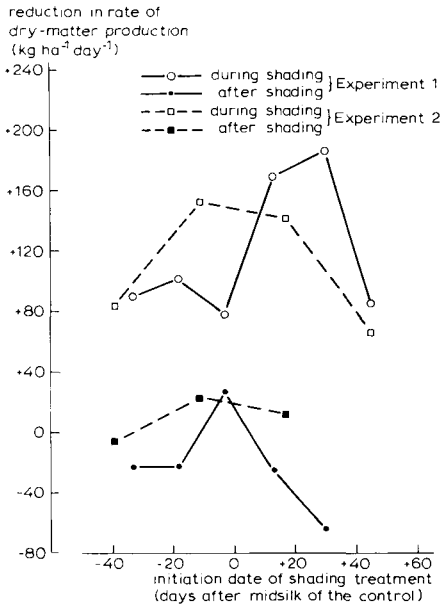


Fig. 6. Effect of date of initiation of short shading on the reduction in rate of dry-matter production during and after the treatment (including S_2 treatment).

ceived the short treatments produced more than the control crop (i.e. the reduction in production rate was negative), with the exception of J_3s. Thus, in Experiment 1, the yield pattern shown in Fig. 5 was determined by the productivity during the shading period itself and during the post-shading period. Note that the more the initiation of the short treatment was delayed, the shorter the period after removal of the tents, and the less reliable the calculated reductions in production rates.

In Experiment 2, the reduction in productivity after shading was affected by the date of initiation of the treatment in the same way as the reduction in productivity during shading (Fig. 6).

Long shading treatments. The reduction in yield caused by prolonged shading was always less than expected on the basis of the cumulative effects of the short shadings. This was especially true for treatments initiated after silking (see Fig. 7). In Fig. 7 the reductions in productivity during different periods of the long shadings are plotted against time. For treatments initiated before silking (J_1l, J_2l and J_3l) the reduction in rate of dry-matter production eventually increased or remained constant. A small upward trend in the reduction of production rate was followed by a larger downturn during the final part of the growing season. The decrease was larger the later the shading was initiated. For treatments initiated during early grain filling (Al and S_1l) the initial reduction was extremely large but also declined sharply. A considerable decline was also found for treatment S_2.

The pattern illustrated in Fig. 7 indicates that when prolonged shading starts after silking, the main effect is achieved during the first part of the treatment. This

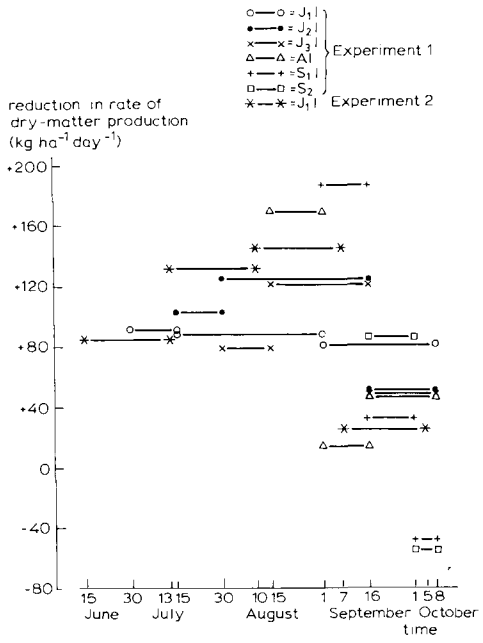


Fig. 7. Development over time of the reduction in rate of dry-matter production caused by long shading treatments initiated at different stages of growth.

shock effect is more severe if shading is applied later and does not occur if shading is applied before silking. After the shock, however, the production capacity of a shaded crop is much higher (or the yield losses are much lower) than circumstances would suggest. This phenomenon cannot solely be explained in terms of the development over time of the rate of dry-matter production of the control.

Dry-matter content

Data on the final dry-matter content of the whole crop are listed in Table 6. Shading influenced the dry-matter content by the following mechanisms.

— The drying of the stover and of the husk + shank fraction was stimulated by shading when shading enhanced *Fusarium* infection. *Fusarium* mainly occurred when the concentration of sugar in the stover was low.

— The dry-matter content in vegetative parts was also high when ears failed to develop. In these cases high levels of water-soluble carbohydrates were responsible for the high dry-matter content. The concentrations of sugar-free dry matter in the vegetative parts were mainly determined by the *Fusarium* infection.

— Ear dry-down was inhibited by shading when it induced ear abortion or reduced the number of active kernels.

— As well as decelerating the drying of the ear, shading concomitantly reduced the proportion of ear in the fresh matter.

These data clearly illustrate how important successful ear development and grain fill are to ensure high dry-matter content and thus the crop's suitability for ensiling

Table 6. Dry-matter content of the whole crop from each treatment at final sampling.[1]

Experiment 1		Experiment 2	
treatment code	dry-matter content (%)	treatment code	dry-matter content (%)
J_1s	33.0^{de}	J_1s	33.3^{cd}
J_2s	31.7^{cde}	J_2s	30.6^{bc}
J_3s	28.0^{abc}	As	29.3^{b}
As	31.1^{cde}	Ss	35.7^{d}
S_1s	34.4^{e}		
J_1l	25.0^{ab}	J_1l	25.4^{a}
J_2l	23.6^{a}		
J_3l	26.4^{ab}		
Al	29.4^{bcd}		
S_1l	35.8^{e}		
S_2	34.7^{e}		
Control	31.6^{cde}	Control	33.8^{d}

[1] Numbers without a letter in common are significantly different according to Tukey's studentized range test ($P < 0.05$).

and for ensuring a high intake of dry matter by the ruminant. They also indicate that shading determined the chemical composition of the non-structural carbohydrates by affecting ear development. The ratio of starch to total non-structural carbohydrates varied greatly. The composition of the non-structural carbohydrates may affect the processes in the silage, the digestibility and the feed efficiency (Wilkinson, 1976; Phipps, 1980).

The data on dry-matter content of the post-silking treatments agree with data obtained earlier (Struik & Deinum, 1982).

Quality

Development of quality parameters of the controls and of the J_1l treatments. Fig. 8 presents the development over time of the proportion of ear in the organic matter, the cell-wall yield, the proportion of cell wall in the organic matter, the cell-wall digestibility and the apparent digestibility of the organic matter.

Ear proportion might affect whole-crop digestibility, because ears are more digestible than vegetative parts. In the unshaded crops the proportion of ear increased rapidly from 0 % to about 55 % in approximately 80 days.

Cell-wall production was intense during the period from 70 to 125 days after sowing, but ceased thereafter. Therefore the cell-wall content increased prior to silking and was at its maximum at silking. Grain filling was accompanied by a decline in the cell-wall content of the crop. The cell-wall content is extremely important for whole-crop digestibility. The cell wall is the only organelle of the plant that cannot be digested completely by ruminants. In addition to the content of the cell walls, the extent to which the cell walls can be digested in the rumen affects the digestibility of

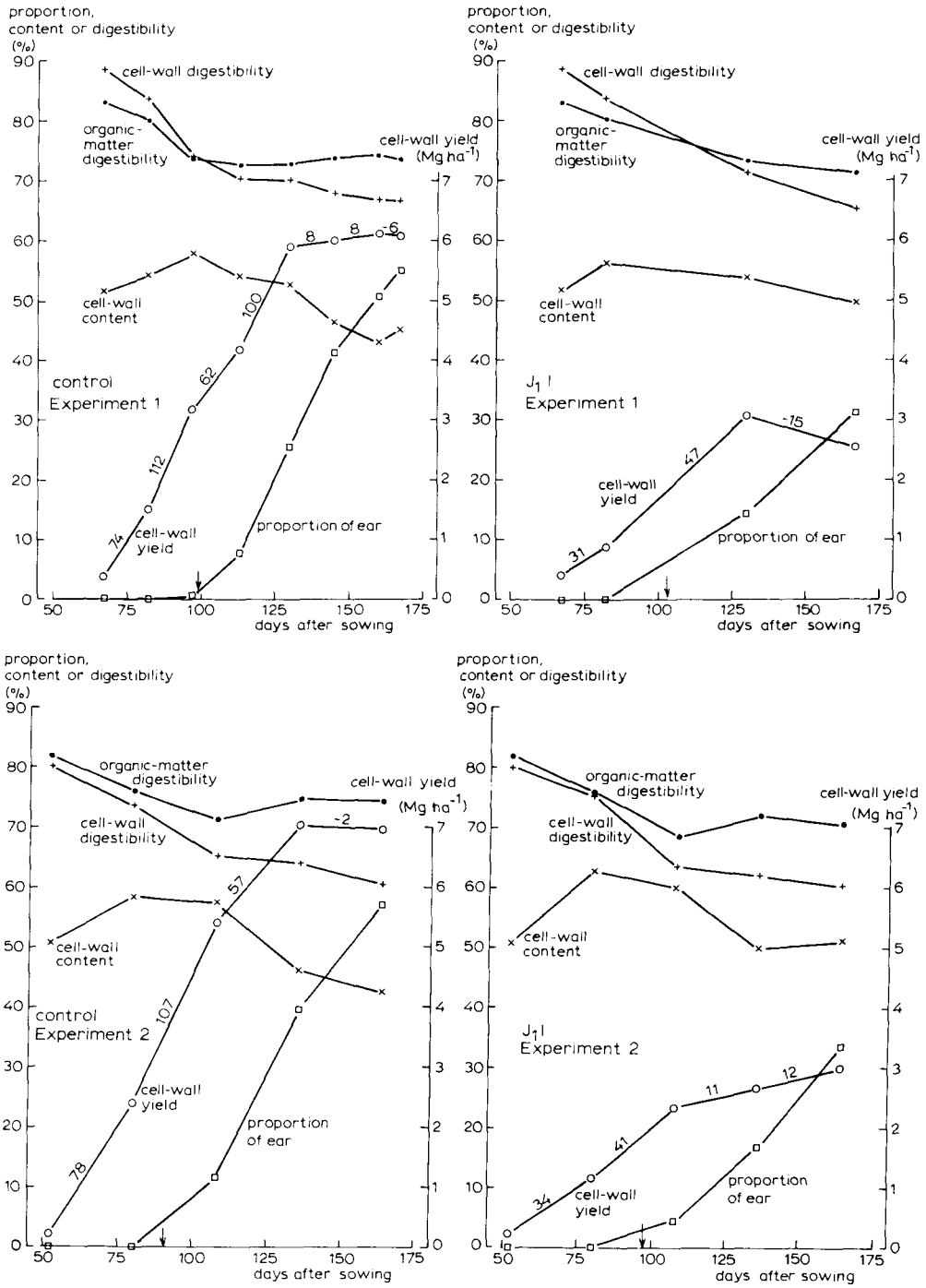


Fig. 8. Development over time of certain quality parameters in the control and J_1l treatments of both experiments. Numbers indicate rates of cell-wall production in kg ha^{-1} day^{-1}. Arrows indicate 50 % silking.

the crop. The digestibility of the cell walls in the whole crop declined steadily during crop growth but this decline was most pronounced before silking.

Digestibility in vitro only depends on the cell-wall content and on the digestibility of the cell walls and therefore the digestibility of the organic matter declined rapidly during the pre-silking period. After silking the decline sometimes reverses and becomes a small increase, as cell-wall content falls and the decline in the digestibility of the cell walls is decelerated. If climatic conditions limit the decline in cell-wall content (as was the case for J_1l, Experiment 1) the decline in digestibility of the organic matter may continue. Cell-wall digestibility was little affected by continuous shading. Patterns were similar in both years. Differences in cell-wall digestibility between years were caused by differences between in vitro runs. These differences disappear after standardization.

Effects of shading treatment on in vitro digestibility. The effects of shading on whole-crop digestibility are illustrated in Fig. 9. The differences observed mainly developed during the final part of the growing season. At intermediate samplings, differences never exceeded 3 units.

Digestibility was poor when ear development was poor. Ear proportion correlated significantly with whole-crop digestibility. In Experiment 1 the linear correlation coefficient was 0.856 ($P < 0.01$) and in Experiment 2 it was 0.826 ($P < 0.05$). The digestibility of the treatments initiated before grain set was particularly well predicted by the linear regression equation. The good digestibility of treatments J_1l, for example, arose because low stover yields accompanied low ear yields, whereas in treatments J_2l, J_3s, J_3l (Experiment 1) and J_2s (Experiment 2) similar ear yields were accompanied by much higher stover yields.

The digestibility of the treatments initiated after grain set did not fit the regression equation very well. The effects of long shading treatments were mostly greatly overestimated and those of short treatments were sometimes underestimated. An explanation will be offered below.

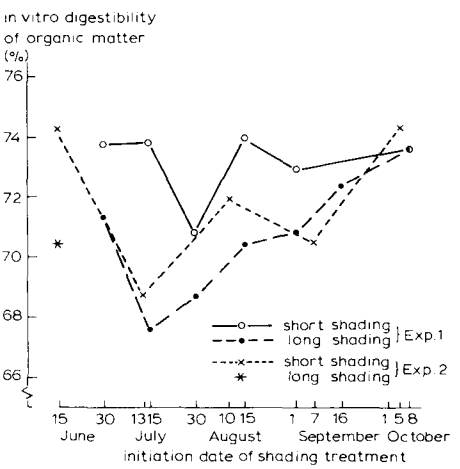


Fig. 9. Effect of date of initiation of long and short shading treatments on the digestibility in vitro of organic matter at final sampling.

Relation between cell-wall formation and crop quality. The way newly synthesized sugars are used varies during the growing season. In Fig. 8 it has already been shown that the synthesis of cell-wall constituents ceases before that of dry matter. Reducing productivity during the final part of the growing season only reduces the yield of the completely digestible cell solubles (predominantly starch and short carbohydrates): shading at the end of the growing season will thus affect quality more than earlier shading.

In contrast, cell-wall production is intense from mid July until September. During this period about 40 % of the dry matter produced consists of cell-wall constituents. During the first half of August this proportion may even exceed 50 %. Reducing the light intensity during this period will reduce the amounts of cell-wall constituents more than final dry-matter yields if shading affects the cell-wall production of the whole plant to the same extent as dry-matter production.

However, in both years continuous shading reduced cell-wall formation much less than dry-matter production (see Fig. 8). The short shading treatments of both experiments showed that this was only true for the pre-silking period. But during the final period of cell-wall formation (i.e. during treatments As in 1980 and in 1981) production of cell-wall constituents was reduced twice as much as dry-matter production.

In Fig. 10a the effects of shading treatments on final cell-wall yield are illustrated. The reduction in the cell-wall yield caused by long shading was smaller the later shading was initiated, up until the end of the period of cell-wall formation. The cell-wall yield of J_3l was remarkably high because of the large amount of cell wall in the stover: this was in turn connected with the increased plant height (Table 3). Short shading in Experiment 1 affected the cell-wall yield of the whole crop most when applied during and just after grain setting. In Fig. 10b the amounts of cell wall in the fractions are plotted against the dates on which the short treatments were initiated. The final amounts of cell wall in the stover of short treatments of Experiment 1 were always 450 kg ha^{-1} less than the control, except in treatment J_3s. In that treatment some additional cell-wall constituents were produced after the shading tents were removed, resulting in exactly the same amount of cell-wall constituents as for the control. The high level of non-structural carbohydrates that resulted from the failure of ear development enabled this 'luxuriant' cell-wall formation to occur.

This additional cell-wall production was also observed for the husk + shank fraction, though less clearly, because early short shading also stimulated cell-wall production in this fraction (cf. Fig. 5).

The amounts of cell wall in the ears reflected the success of ear development. Early short shading, however, resulted in a comparatively high cell-wall content in the ear because of a low shelling percentage. As mentioned earlier, J_1s had thick cobs.

The pattern was similar in Experiment 2. However, the longer duration of the treatments, the smaller number of treatments and the faster development made the pattern less pronounced. However, in this trial the cell-wall yield of As was also comparatively low.

Because of these effects of shading on the amount of cell wall in the different

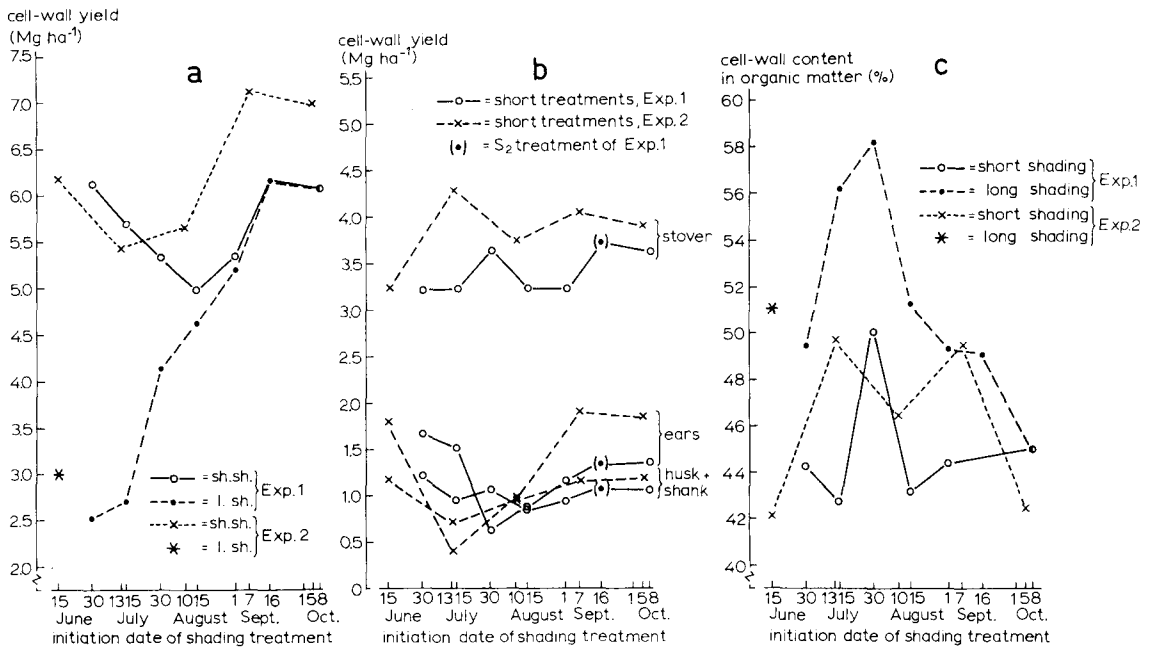


Fig. 10. The effects of shading (a) on the cell-wall yield of the whole crop, (b) on the cell-wall yield of the fractions (short shading only), and (c) on the content of cell walls in the organic matter at final sampling. In Fig. 10b the S_2 treatment has been added to show that the period during which cell-wall formation could be affected by shading had ended before final harvest.

plant fractions, the pattern of cell-wall yield differed from the pattern of the dry-matter yield of the whole crop, shown in Fig. 6. The consequences of this for the content of cell walls in the organic matter are shown in Fig. 10c. These cell-wall contents correlated significantly with organic-matter digestibility (Experiment 1: $r = -0.961$, $P < 0.01$; Experiment 2: $r = -0.935$, $P < 0.01$).

Cell-wall digestibility. The high linear correlation coefficients between cell-wall content and whole-crop digestibility suggest that the cell-wall digestibility was little affected by shading (cf. Fig. 8). Indeed, the cell-wall digestibility of the shaded crops hardly differed from the cell-wall digestibility of the control crops, except for J_2l of Experiment 1 and J_2s of Experiment 2. These treatments both induced an extremely high proportion of cell walls of the whole crop to be present in the stover. Because stover cell walls are less digestible than the cell walls in the ear shoot this resulted in a considerable decrease in the cell-wall digestibility of the whole crop. Other treatments e.g. J_3l and J_1l also showed high proportions of stover cell walls but in these cases these high proportions were compensated for by the better cell-wall digestibility of some of the plant fractions, for the cell-wall digestibility of the plant *fractions* was much more variable than the cell-wall digestibility of the *whole*

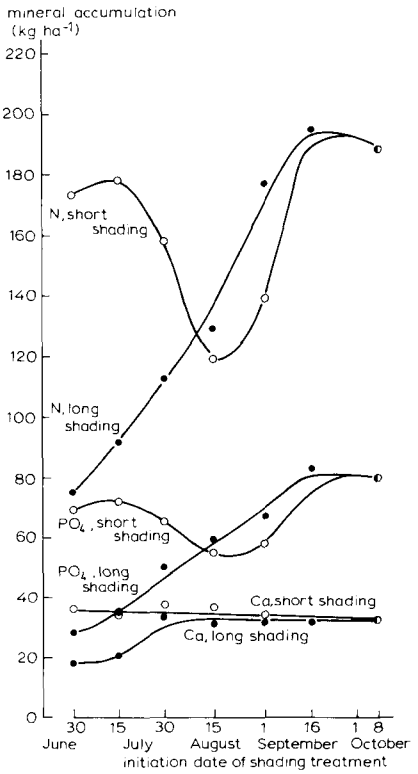


Fig. 11. Effects of shade on accumulation of Ca, N and PO_4.

crop. For example, poor ear development was often accompanied by a better digestibility of the cell walls of the whole ear shoot. However, it must be concluded that the effects of shading on cell-wall digestibility only played a minor role in determining differences in whole-crop digestibility. Thus, the effects of shading on cell-wall formation and on production rate were responsible for the variation in digestibility.

Mineral uptake

Fig. 11 shows how the accumulation of Ca, PO_4 and N in the above-ground parts of the plant at final sampling was affected by the date on which long or short shading was initiated in Experiment 1.

Calcium, the uptake of which is active (i.e. requires energy), is mainly present in vegetative parts. Ca accumulation was reduced by long shading if the shading was initiated during vegetative growth. Short shading before silking also reduced the uptake of Ca during the shading but uptake was probably faster after the shading tents were removed.

The accumulation of N and PO_4 was affected in the same way as cell-wall formation. Nitrogen and phosphorus uptake and cell-wall formation show the same development over time and also seemed to be very sensitive to shading during the same stage of crop development. After pollination has occurred, reproductive development might be favoured above all other plant processes.

However, for both N and PO_4 accumulation, the curves of the long shadings intersected the curves of the short shadings. In treatments Al, S_1l and S_2 high levels of these minerals were found in all plant fractions. These treatments also showed the most severe *Fusarium* infection. Long shading during grain filling may have reduced root activity to such an extent that selectivity in the uptake of ions that can be taken up passively was finally lost.

Mineral uptake thus illustrates that shading effects are not confined to the aboveground parts of the plant. Root growth and root activity were affected in the same manner as certain other plant processes (e.g. cell-wall formation). Part of the observed effects of shading might therefore be connected with mineral or protein depletion or shortage. Root functions other than water and mineral uptake may also have played a role (cf. Struik & Deinum, 1982).

Conclusion

The primary effect of reducing light intensity is to reduce photosynthesis. But the distribution of photosynthates over the plant is determined by the developmental stage of the plant, the growth rates of different tissues or organs, prevailing and previous weather conditions, and many other factors. In turn, this distribution affects the production capacity and the development of the crop in later periods. Light also influences growth directly by means of its photomorphogenetic effects on vegetative development. Moreover, maize has a short critical period in its development during which adverse factors such as low light intensity cause dramatic, irreversible damage to the reproductive organs.

The stage at which shading is applied and the duration of the shading thus affect productivity during and after shading, dry-matter distribution and quality. During shading, productivity is always reduced: after short shading, productivity may be higher, depending on the date of initiation and the duration of the short treatment. Long shading is accompanied by an adaptation to the adverse conditions, but also by an increased susceptibility to diseases and a decrease in reproductive capacity.

Shading affected quality mainly by its effects on cell-wall content. During vegetative growth, cell-wall production was affected less than dry-matter production. The opposite occurred during reproductive development. Since cell-wall formation continues until the early part of the grain-filling period, the cell-wall content was higher in shaded crops than in the control, except when short shading occurred during grain set. Later shading merely curtails the formation of cell solubles and therefore delays the favourable decline of the cell-wall content.

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