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Effect of light intensity after flowering on the productivity and quality of silage maize

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Summary

After flowering, different shading treatments were imposed on crops that varied in sowing date, genotype and plant density. It was found that ear yield was closely related to the amount of irradiance received during grain filling: it increased by approximately 10 kg ha^{-1} per MJ m^{-2} if density was not limiting. However, the intensity of carbohydrate redistribution from vegetative to reproductive plant parts differed greatly. Whole-crop yields were also affected by the distribution of irradiance over time.

The digestibility in vitro of the organic matter was affected most by shading during the last part of the growing season. Earlier shading reduced cell-wall production, thus limiting the detrimental effect of shading on whole-crop digestibility. Shading influenced digestibility through its effects on cell-wall content. Cell wall digestibility only differed slightly between shading treatments. For all crops, shading effects on whole-crop digestibility showed the same pattern, but not the same magnitude.

As well as affecting yield and quality, shading also affected suitability for ensiling, susceptibility to stalk rot (*Fusarium* spp.), leaf senescence and mineral uptake. A hypothesis is offered to explain the effect of shading on ear size, ear growth and longevity of leaves in terms of the prompt effects of shading on root activity.

Introduction

The Dutch climate shows some unfavourable characteristics for growing maize (*Zea mays* L.). Firstly, in spring soil temperatures are too low for a fast early development. Secondly, during the late part of the grain-filling period the intensity of light is normally too low, so that the carbohydrates, previously stored in vegetative plant parts, must be redistributed for grain filling to continue at an accep-

table rate. Although the second problem is connected with the first one, cultural practice emphasizes the disadvantages of the climatic conditions in September and October: maximum dry-matter yields are obtained by sowing fairly late hybrids at relatively high plant densities. It is questionable whether and to what extent redistribution itself affects production and quality (Bunting, 1975, 1976; Deinum & Knoppers, 1979), but it is clear that if the need for carbohydrate redistribution is avoided by choosing early genotypes or changing cultural practices in response to the unfavourable climate, the quality of the forage crop will improve, though unfortunately always at the expense of dry-matter yield. Maximum use of the possibilities of the growing season will give the highest yield, but it necessitates a more abundant, time consuming vegetative growth. In that case, later female flowering makes it necessary for the grains to be filled by means of redistribution.

This paper attempts to quantify the effect of irradiance during the grain-filling period on dry-matter production and quality. The consequences of periods of shading on crops that differed in intensity of redistribution due to differences in sowing time, genotype or plant density, were investigated in three trials.

Materials and methods

In 1977, 1978 and 1979 shading experiments were done on a light, moist sandy soil with abundant fertilization (both organic and inorganic) and with optimum weed and disease control. In 1977 and 1978, trials were laid out as a split-plot design with shading as sub-plot treatment and with five replicates. The 1979 trial was laid out as a completely randomized block design with four replicates.

Treatments

Light intensity was reduced during two distinct periods after silking, by hanging tents of black plastic gauze of 8 m × 4,5 m above and around the crop. These tents reduced light intensity to about 40 %. The following shading treatments were applied:

Code	Treatment A (mid-August to mid-September)	Treatment S (mid-September to final harvest)
A_uS_u	untreated	untreated
A_uS_s	untreated	shaded
A_sS_u	shaded	untreated
A_sS_s	shaded	shaded

These treatments were applied to crops grown in different years and under different cultural practice. In 1977, the hybrid LG 11 was sown on two dates: 28 April (normal; code St_1) and 25 May (late; code St_2). In 1978, two extreme hybrids were used: Ula (H_1) with a FAO index of 190 and Axia (H_2) with a FAO in-

dex of 500. In 1979, LG 11 was again grown in three plant densities: approximately 5 (D_1), 10 (D_2) and 15 (D_3) plants/m^2.

Cultural details and methods of measuring crop development

In 1977 and 1979, sowing densities were 20.0 and 16.7 seeds/m^2, respectively. In both years, the crops were thinned to 10 plants/m^2 or to the desired plant density shortly after emergence. In 1978, sowing density was 10.7 seeds/m^2 for Ula and 9.3 seeds/m^2 for Axia. The rows were always 75 cm apart and the plots were 6 m × 10 m (8 rows of 10 m); wide borders separated the plots from each other.

In 1978, early development of the late hybrid Axia was accelerated by means of a plastic mulch applied for 33 days (i.e. from sowing until 8-leaf stage). To check the effect of the plastic mulch, one extra plot of Ula was treated with plastic mulch and one extra plot of Axia was grown without plastic mulch.

If necessary, drought was prevented by sprinkling.

Growth and development were measured weekly by estimating plant height, number of leaves (young, full-grown and dead leaves) and the physiological stage of reproductive organs of four plants per plot. Leaf area was estimated shortly after flowering with an area meter (1978) or by the length × maximum width × 0.75 method (1979) (Montgomery, 1911). Maximum diameter in the middle of the second above-ground stem internode was measured with a marking gauge as an estimation of stem thickness. The degree of *Fusarium* present was estimated by pushing 10 plants in each plot. The number of broken (i.e. severely infected) plants was used to indicate the seriousness of the disease.

Yield determinations

The second, fourth and sixth rows in each plot were used for subsequent samplings. The seventh row was used for estimating *Fusarium* infection at final sampling. Plots were sampled at the start of the A and S periods and in October. At each sampling date, a row 6 m long (4.5 m^2) was harvested by cutting off the plants at soil level.

The number of plants in each sample was counted. The samples were then temporarily stored in a cold chamber and separated into relevant fractions: in 1977 into ears and stover (stem, leaves, husks, shanks and tassel) and in 1978 and 1979 into upper ears, lower ears, husks + shanks and stems (stems, leaves and tassels). This separation was necessary to provide additional information and for adequate subsampling. After estimation of fresh weight, the ears were chopped in a vegetable cutter, subsampled and dried to a constant weight in forced ventilated ovens at a maximum temperature of 70 °C. The vegetative parts of the plant were chopped with a stationary tractor-mounted 1-row chopper (Fahr MH 70). This chopper blew the material directly through an exhaust onto a conveyor belt which transported it into a concrete mixer. Subsamples were taken after mixing and were subsequently treated like ear samples.

Chemical analyses

After drying, samples of the replicates were bulked per plant part and per treat-

ment and ground in hammer mills. Samples were analysed for true digestibility in vitro of the organic matter, using the method described by Van Soest et al. (1966). These values were standardized and converted to apparent digestibility of organic matter by means of a series of standard-maize samples with known digestibility in vivo (sheep). Cell-wall constituents were estimated according to Van Soest's (1977) method. Cell-wall digestibility was calculated from true digestibility, cell-wall content and ash content. Analysis for water-soluble carbohydrates was done with ferricyanide on an automatic analysing device, and expressed in glucose units.

Results and discussion

Weather

Table 1 shows climatic data for 1977, 1978 and 1979. In all three years, temperatures were below normal in May, June, July, August and September, but were above average in October. In all years precipitation was low, especially in September and October. Total solar irradiance was somewhat below normal in 1977 and 1978. Damaging night frosts at the end of the growing season only occurred in 1979.

Influence of shading tents on climatic factors

Tents reduced light intensity to about 40 % of normal irradiance. This percentage was not constant, as the sun's altitude influenced the reduction to some extent.

As well as light intensity, many other climatic factors were affected by shading: day length, mean air temperature, temperature of plant organs, differences between air temperature and plant-tissue temperature, diurnal temperature cycles

Table 1. Climatic data for 1977, 1978 and 1979 at Wageningen, compared with the means over 30 years (1931-1960) at De Bilt, Netherlands.

	Average temperature (°C)				Rainfall (mm)				Solar irradiance (MJ/m²)			
	1977	1978	1979	mean	1977	1978	1979	mean	1977	1978	1979	mean
May	11.9	12.4	11.7	12.4	55.2	33.1*	75.7	52	543	473	516	518
June	14.6	15.1	15.0	15.5	64.3	61.6	148.4	57	425	507	493	531
July	16.7	15.3	15.8	17.0	68.0	56.7	31.4	78	484	480	461	478
August	16.2	15.1	15.3	16.8	134.4	31.0	84.8	89	388	417	409	415
September	13.5	13.3	13.2	14.3	6.1*	68.8	17.8	71	292	251	332	304
October	11.2	10.6	10.8	10.0	36.9	36.6	36.6	72	184	162	194	177
Average/ total	14.0	13.6	13.6	14.3	364.9	287.8	394.7	419	2315	2289	2405	2423

* Drought was prevented by sprinkling.

(e.g. the occurrence of night frosts!), relative humidity of the air, water supply (pF value of the soil), light quality (e.g. ratio direct: diffuse light), light extinction, wind speed, and perhaps also the CO_2 gradient within the crop (cf. Gerakis & Papakosta-Tasopoulou, 1979). The following relevant plant processes may change in intensity as a result of shading: photosynthesis, transpiration, respiration, nitrate reduction and protein synthesis, mineral uptake and root growth, transport, translocation, grain filling, senescence (both in vegetative and reproductive plant parts) and hormonal production. In addition, resistance to *Fusarium* spp. may decrease. Of course, all these processes will interact. So, shading altered the entire climate and this change in climate induced a complex reaction in the crop.

Crop development

Since shading treatments started some time after flowering, there were no effects on vegetative development and flowering. For a description of the different crops, see Table 2.

In 1977, 50 % emergence occurred about 14 days later in the late sowing than in the early sowing. However, the dates on which 50 % female flowering was achieved were only 11 days apart, indicating that the later sown crop developed

Table 2. Crop descriptions.

	1977		1978		1979		
	St_1	St_2	H_1	H_2	D_1	D_2	D_3
Sowing date	28/4	25/5	20/4	20/4	25/4	25/4	25/4
Density (plants/m^2)	10.03	10.13	8.03	9.21	5.30	10.50	15.43
Number of leaves	15.3	15.2	13.5	17.5	13.8	13.8	13.8
Height of plant (cm)	261	265	205	246	202	214	214
Maximum leaf area (m^2/m^2)*	–	–	2.20	4.70	1.91	3.52	4.84
Estimated date of 50% ♀ flowering	8/8	19/8	28/7	4/8	2/8	3/8	5/8
Stem diameter (cm)	–	–	–	–	2.71	2.21	2.00
Pre-treatment data							
Start of treatment A	15/8	22/8	14/8	14/8	20/8	20/8	20/8
Dry-matter yield at start of treatment A (Mg ha^{-1})	9.79	8.21	7.82	10.45	6.36	8.00	8.48
Digestibility at start of treatment A (%)	73.5	71.9	74.6	73.7	74.0	72.5	70.8
Start of treatment S	12/9	12/9	4/9	4/9	17/9	17/9	17/9
Data from untreated stands at final sampling							
Date of final sampling	26/10	26/10	10/10	11/10	15/10	15/10	15/10
Final ear yield (Mg ha^{-1})	7.66	6.00	6.95	6.93	6.50	7.20	7.38
Final stover yield (Mg ha^{-1})	7.78	8.97	4.99	8.42	4.55	5.60	7.50
Final whole-crop yield (Mg ha^{-1})	15.44	14.97	11.93	15.35	11.04	12.80	14.87
Whole-crop dry-matter content (%)	30.3	24.5	34.2	29.0	32.0	30.4	28.5
Fusarium infection (%)	30	8	38	rare	20	45	40
Digestibility at final sampling (%)	71.5	69.7	72.8	71.1	75.7	74.8	73.5
Cell-wall yield (Mg ha^{-1})	7.12	7.48	4.97	7.69	4.31	5.15	6.29

* Of the main shoot only.

more rapidly, possibly because of the higher temperatures during vegetative development. From the unshaded plots, it can be seen that late sowing resulted in a non-significant reduction of 0.48 Mg ha^{-1} in the final yield, which was only 18 kg ha^{-1}per day the sowing was delayed. This was much lower than normal (Becker, 1976; Struik, 1982), because of the low temperatures during April and May and the late date of final sampling. The differences were even smaller for shaded crops. Digestibility was lower in the later sown crop, because cell-wall production was higher and ended later.

In 1978, emergence was not optimum for the hybrid Ula since Ula is very sensitive to cold. As this hybrid was also very early, the leaf area was low. Flowering dates of Ula and Axia were very different in spite of the development-accelerating effect of the plastic mulch. The very late hybrid Axia outyielded the extremely early Ula by about 3.4 Mg ha^{-1} in normal light conditions; the same difference was already found at the second sampling date (4 September). One extra plot of Axia without plastic mulching showed that the yield increase resulting from the mulch was about 2 Mg ha^{-1}, almost completely present in the uppermost ear. An extra plot of Ula with plastic mulching also showed a yield increase of 2.0 Mg ha^{-1}, of which 0.5 Mg ha^{-1} was in the vegetative parts and 1.5 Mg ha^{-1} in the ears. So the hybrid effect itself was only responsible for about 1.4 Mg ha^{-1}, although there were great differences in earliness and leaf area. The mean difference between Axia and Ula for all shading treatments was only 2.6 Mg ha^{-1} at all sampling dates.

At final sampling, the interaction hybrid × shading treatment was only significant for total yield. This interaction was probably caused by the difference in leaf area although no such interaction was found in the 1979 trial.

In 1979, rate of leaf appearance was lower at higher density, but rate of stem elongation was greater. Differences in final number of leaves and plant height, however, were small.

Dry-matter yields increased with density. This was true for all shading treatments. In neighbouring countries, higher plant densities are advocated (Belgium: 110 000 plants/ha, Behaeghe et al., 1981; United Kingdom: 110 000 plants/ha, National Institute of Agricultural Botany, 1979). In the Netherlands, a final plant density of 9-10 plants/m^2 is believed to be the optimum (Becker, 1976). For maximum dry-matter yields this is probably not true. The decrease in quality was relatively small compared with the yield increase, especially for unshaded crops. Lower digestibility and lower dry-matter content may therefore be reasons for growing at a density of less than 11 plants/m^2 only in climates with unfavourable weather during autumn.

Influence of shading on senescence and ripening

Light treatment caused different patterns in leaf senescence, partly connected with differences in disease infection. Patterns were similar in the three years; examples are given in Fig. 1 and Table 3, respectively. *Fusarium* infection was of minor importance for dry-matter yield and quality, but showed a connection with the carbohydrate content of the stover (Table 3). Differences in senescence

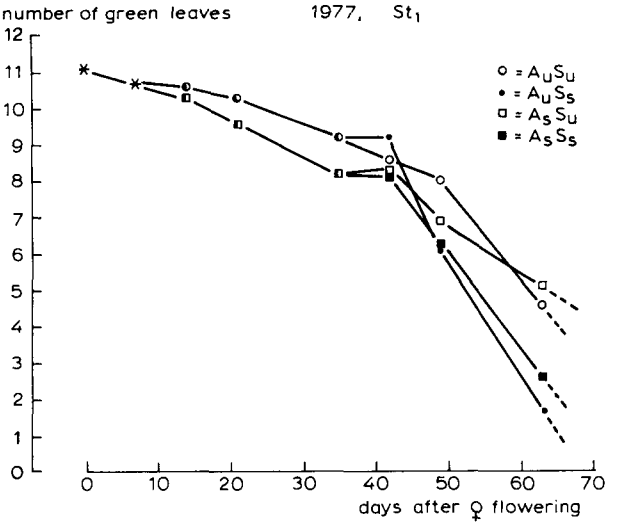

Fig. 1. Leaf-senescence pattern for four light treatments of early sowing in 1977.

were also visible in the ears. With continuous shading, the duration of grain filling increased from the tip to the base of the ear. Tip kernels shrivelled very soon, mid-kernels were half-filled and basal kernels showed almost normal habitus. In the control, hardly any kernel 'abortion' occurred. A_uS_s and A_sS_u were intermediate. This reaction in number of active kernels started very soon after the onset of shading and long before the amounts of carbohydrate in the stem could be limiting. 'Abortion' even occurred in crops that had increasing carbohydrate contents in their vegetative parts! Light treatment also caused different patterns in drying of stover, ear and whole crop (Table 3). The dry-matter content of stover was closely related to *Fusarium* infection (1977: $r^2 = 0.976$; $n = 8$).

Table 3. Proportion of plants that lodged when pushed, indicating infection by *Fusarium* spp.; content of water-soluble carbohydrates in stover; number of green leaves; ears as proportion of total fresh material; and dry-matter contents at final registration (1977 data).

	St_1				St_2			
	A_uS_u	A_uS_s	A_sS_u	A_sS_s	A_uS_u	A_uS_s	A_sS_u	A_sS_s
Fallen plants (%)	30	74	10	40	8	18	0	6
wsc content (%)	5.5	5.1	11.6	6.8	9.5	8.7	13.7	9.1
Number of green leaves	4.6	1.7	5.1	2.6	6.6	5.3	6.1	4.8
Ears, as portion of total fresh material (%)	29.3	28.3	17.9	16.9	23.3	21.6	13.0	12.3
Dry-matter content of stover (%)	21.6	25.1	20.3	22.6	19.1	20.5	18.6	19.8
Dry-matter content of ear (%)	51.4	48.9	43.2	42.1	42.0	38.1	35.6	32.3
Dry-matter content of whole crop (%)	30.3	31.8	24.4	25.9	24.5	24.3	20.9	21.3

However, the effects of shading on ear dry-matter content and on the proportion of ears in the fresh material were much greater and better correlated with dry-matter content in the whole crop. Shading A greatly reduced these ear parameters, while shading S caused a small additional decline. Effects were similar for all crops. The dry-matter contents of the whole crop at final sampling were not always significantly different for S_u and S_s treatments. If *Fusarium* infection was insignificant, the dry-matter contents of A_uS_s were slightly lower than those of A_uS_u, but when the S_s crops showed severe stalk rot, then the dry-matter contents of A_uS_u were lower than those of A_uS_s. There were large differences between the A_u crops and the A_s crops, but these differences also depended on the crop structure. The means over all years and cultural practices were 29.8, 30.2, 26.0 and 25.6 % for A_uS_u, A_uS_s, A_sS_u and A_sS_s respectively.

So, a good ear development stimulated the drying of the crop, even if yields were similar (cf. A_uS_s and A_sS_u), resulting in less seepage during ensiling. On the other hand, the contents of readily fermentable carbohydrates were very low in the A_uS_s treatments, since almost all the non-structural carbohydrates were present in the ear as starch (as a result of redistribution) and these contents were very high in the A_sS_u treatments, where ear sink was weak. Ear parts are practically inert in good maize silages: starch does not play a part in fermentation and the ear parts are normally too dry to produce effluent. However, even when the dry-matter content of the whole crop is 30 %, seepage may occur if the stover is still too wet. So, the content of insoluble dry-matter such as cell walls, proteins etc. (on the basis of fresh weight) in vegetative parts is crucial. For example for A_uS_u, A_uS_s, A_sS_u and A_sS_s this content in 1977 (early sowing) was about 16 %, 19 %, 13.5 % and 16 %, respectively. Therefore A_sS_u was the most likely to seep and if seepage had occurred, the losses of digestible dry-matter would have been highest for that treatment. On the other hand, the intensity of the fermentation process would have been best and the pH would probably have been lowest for A_sS_u.

Influence of shading on dry-matter production

Ear. Ear yields were strongly affected by light treatments. In Fig. 2, ear yields are plotted against the cumulative irradiance. In all years the linear correlation coefficients were highly significant. Ear yields at first sampling or calculated ear yields at cumulative solar irradiance zero indicate the physiological age of the different crops at first treatment. St_2 was treated before the linear dry-matter accumulation in the ears had begun: the calculated intercept appeared to be negative. The regression coefficient was 7.85 kg ha^{-1}/MJ m^{-2} for D_1 and ranged from 9.33 to 10.87 kg ha^{-1}/MJ m^{-2} (i.e. 1 g per megajoule incoming irradiance) for all other stands. It is striking that in 1979 the ear yields (upper + lower ears) of the three densities did not differ significantly on any sampling date, except for the first date. Statistical analysis of the regression equations, however, showed that the regression coefficients (7.85, 9.50 and 9.66 kg ha^{-1}/MJ m^{-2} for D_1, D_2 and D_3, respectively) were significantly different ($P = 0.018$). Yields of top ears considered separately did show significant density effects at all sampling dates.

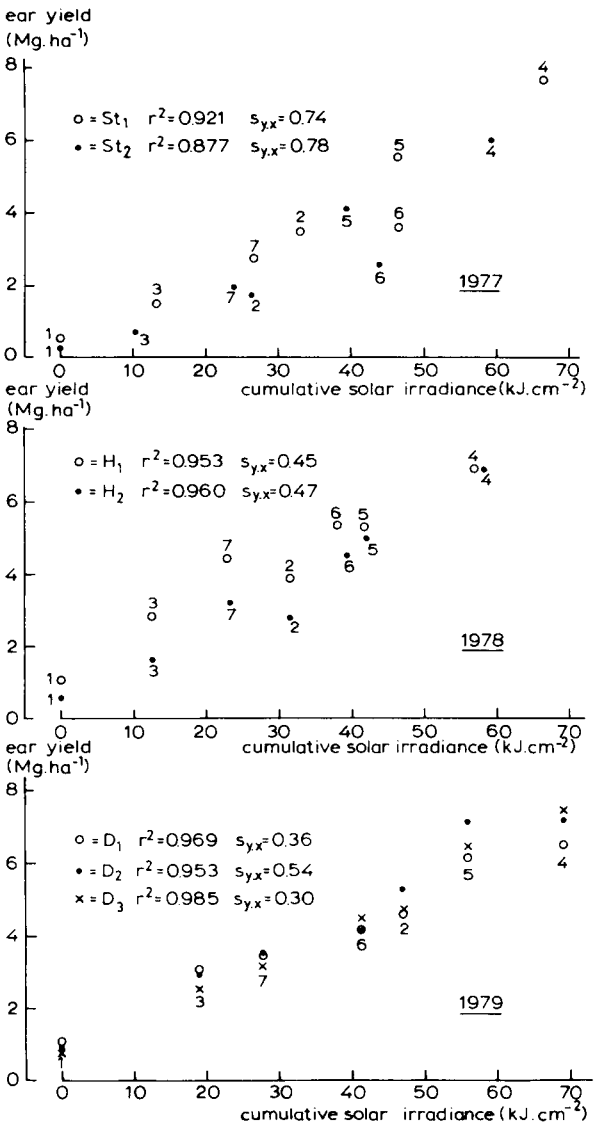

Fig. 2. Ear yields in relation to cumulative solar irradiance after start of A treatment.
1 = pre-treatment sampling, thus sampling at solar irradiance 0.
2 = A_u: second sampling; unshaded during A.
3 = A_s: second sampling; shaded during A.
4 = A_uS_u, 5 = A_uS_s, 6 = A_sS_u, 7 = A_sS_s: final samplings; treatments as indicated in 'Materials and methods'.

In this case, regression coefficients also showed greater differences (P = 0.001).

Crop reactions to variations in light intensity were more marked in the lower ears than in top ears, because lower ears flower later and are not as competitive. The consequences of these marked effects on total ear yields, however, were very small, except for the lowest density in 1979, where lower ear yields were 19 %, 17 %, 11 % and 8 % of total ear yields for A_uS_u, A_uS_s, A_sS_u and A_sS_s, respectively.

Table 4. Stover yields (stems + leaves + tassels + husks + shanks) at final sampling dates (Mg ha^{-1}).

	1977		1978		1979			Mean
	St_1	St_2	H_1	H_2	D_1	D_2	D_3	
A_uS_u	7.78	8.97	4.99	8.42	4.55	5.60	7.50	6.83
A_uS_s	7.14	8.08	4.53	8.21	4.47	6.33	6.95	6.53
A_sS_u	7.76	8.99	4.72	7.85	4.03	5.68	7.99	6.72
A_sS_s	7.28	8.53	5.17	7.45	3.82	5.13	6.62	6.29
Mean	7.49	8.64	4.85	7.98	4.22	5.69	7.27	

Mean $A_uS_{u,s}$ 6.68; mean $A_sS_{u,s}$ 6.50; mean $A_{u,s}S_u$ 6.77; mean $A_{u,s}S_s$ 6.41

Almost all shading treatments fitted the regression lines. Apparently, low irradiance during the A period reduced the sink strength of the kernels, but did not affect the grain filling during the S period, except in 1977. In that year, A_sS_u gave much lower ear yields than expected, given the received irradiance at both sowing dates. Probably the S period lasted so long that the storage capacity in the ears with many aborted kernels became limiting.

Stover. Yields of stover (i.e. stem + leaf parts + tassel + husks + shanks) increased during the A period for unshaded crops, except for the very early H_1 in 1978, but decreased for the shaded crops except for St_2A_s (1977) and D_3A_s (1979), where a small increase was still possible, because of the lateness of these crops. After the A period, all stover yields declined. Rates of decline during the S period showed clear differences, ranging from about 0 to about 100 kg dry matter ha^{-1} day^{-1}, and were always greater if crops were unshaded during the A period and were also higher when shaded during the S period itself. However, in 1979 night-frost damage disturbed this ranking order, since the shading tents prevented damage in S_s treatments. Table 4 presents stover yields at final sampling. Effects of sowing time, hybrid and density were highly significant. Light-treatment effects on stover yields were significant at the end of the A period in all years. In 1977, shading effects on stover yield at final sampling were not significant, but the pattern was consistent and logical. In 1978 and 1979, yields of husks + shanks were very significantly negatively affected by S shading, but the effects on yields of stem + leaves + tassels were only significant (at $P < 0.10$) in 1979.

Whole plant. Whole-plant yields at final sampling are recorded in Table 5. Table 6 shows the linear correlation coefficients, the standard deviations from regression, and the regression coefficients of the relations between cumulative solar irradiance and total dry-matter yield. In all seven cases the r^2 for whole-plant yields was lower than the r^2 for ear yields. The distribution of the irradiance over time was also relevant, especially in crops where there was a strong decline in the efficiency of the green area at the end of the growing season. In these crops (St_1,

Table 5. Whole-crop dry-matter yields at final sampling dates (Mg ha^{-1}).

	1977		1978		1979			Mean
	St_1	St_2	H_1	H_2	D_1	D_2	D_3	
A_uS_u	15.44	14.97	11.93	15.35	11.04	12.80	14.87	13.77
A_uS_s	12.65	12.21	9.81	13.23	10.61	13.42	13.41	12.19
A_sS_u	11.36	11.55	10.09	12.33	8.20	9.76	12.44	10.82
A_sS_s	10.03	10.50	9.46	10.63	7.32	8.70	9.77	9.49
Mean	12.37	12.31	10.32	12.89	9.29	11.17	12.62	

Mean $A_uS_{u,s}$ 12.98; mean $A_sS_{u,s}$ 10.15; mean $A_{u,s}S_u$ 12.30; mean $A_{u,s}S_s$ 10.84.

H_2, D_2), A_s treatments were more detrimental than S_s treatments.

Moreover, the same stands produced hardly any dry-matter during shading, while other stands (St_2, H_1, D_1, D_3) were able to produce dry matter if shaded. Although the r^2 values in Table 6 do not differ significantly, these physiologically younger (St_2, D_3) or open (H_1, D_1) stands showed the highest r^2 values. Ignoring the frost damage in 1979, both types of reaction are illustrated schematically in Fig. 3.

The regression coefficients do not vary strongly. They were not even significantly different in 1979 although they correlated closely with the plant density ($r^2 = 1.000$; $n = 3$).

Influence of shading on quality of the organic matter

Sowing date, genotype, year and plant density all affected the apparent digestibility of the whole crop (D_{crop}), as has already been demonstrated in Table 2. In control stands, considerable production of cell walls – both in vegetative parts and in ears – took place during the A period, while the quality of the partly indigestible cell walls continued to decrease after flowering. However, ear development ensured that cell-wall production ended.

Table 6. r^2, $s_{y.x}$ and b for the linear relations between cumulative solar irradiance and total dry-matter yield ($n = 7$).

		r^2	$s_{y.x}$ (Mg ha^{-1})	b (kg ha^{-1}/MJ m^{-2})
1977	St_1	0.688*	1.30	7.85
	St_2	0.860**	0.90	9.99
1978	H_1	0.852**	0.54	6.27
	H_2	0.753**	1.00	8.21
1979	D_1	0.864**	0.72	7.13
	D_2	0.742**	1.28	8.45
	D_3	0.908**	0.79	9.68

* $P < 0.05$
** $P < 0.01$
} one-sided.

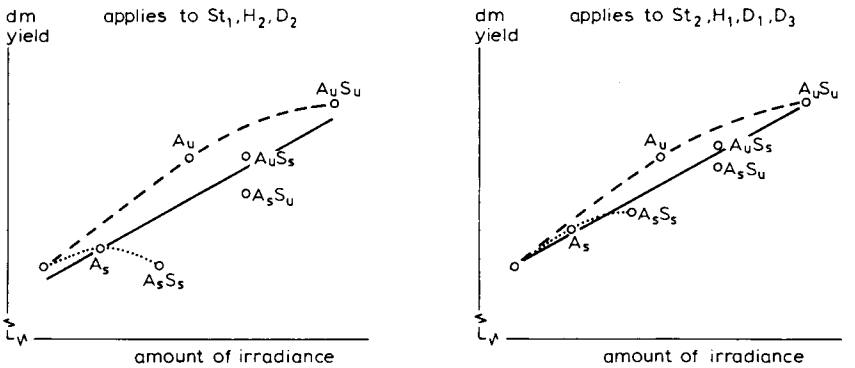

Fig. 3. Relation between dry-matter yield and amount of irradiance received (schematic). (—— = regression line, --- = control; . . . . = continuously shaded crops).

The most relevant process in relation to changes in digestibility after grain set is the dilution of the then present cell-wall material with new products of photosynthesis. The newly synthesized sugars are completely digestible and may be stored in grains (as starch) or in vegetative parts (as short carbohydrates). The final crop quality is determined by:

- content, amount and quality of cell walls present at grain set.
- increase in cell-wall yield after grain set.
- rate of decline in cell-wall digestibility after grain set.
- yield increase of non-structural carbohydrates.

These properties varied according to sowing date, genotype and plant density. Moreover, the pattern varied from year to year. For example, in 1977, LG 11 showed an abundant vegetative development, resulting in a retarded ear development (and thus a delay in the dilution process), a high cell-wall production (more than 7 Mg ha^{-1} for both sowing times), and rather small ears; it received low amounts of irradiance during grain filling and was harvested late. In 1979, conditions for the same hybrid were quite different.

D_{crop} for all treatments at final sampling is reported in Table 7. As may be clear from the above-mentioned quality determinants, the effects of shading on D_{crop} depended on crop structure: the early sown crop reacted more severely than the later sown one, the early hybrid showed a more pronounced reaction than the late one and the densest crop showed a much greater effect of A shading than the other two.

Shading effects can partly be explained by non-structural carbohydrate production during the treatment (see also Fig. 1). In addition, cell-wall production almost stopped with low light intensity: shading A caused a final reduction in the cell-wall yield of vegetative parts of 440 - 660 kg ha^{-1} for St_1, St_2, H_2, D_1 and D_2; the reduction of cell-wall yield in ear parts was 540 - 970 kg ha^{-1}. As a result, digestibility was only slightly reduced by shading A, although ear yield was greatly reduced. The effect of shading S on digestibility was practically confined

Table 7. Apparent digestibility of the whole crop at final sampling in % of the organic matter (calculated from data on the different fractions).

	1977		1978		1979			Mean
	St_1	St_2	H_1	H_2	D_1	D_2	D_3	
A_uS_u	71.5	69.7	72.8	71.1	75.7	74.8	73.5	72.7
A_uS_s	68.6	68.9	69.7	69.4	73.8	73.3	71.9	70.8
A_sS_u	70.0	69.2	72.4	71.1	74.5	74.1	71.9	71.9
A_sS_s	67.5	68.0	69.1	68.4	73.5	72.8	70.1	69.9
Mean	69.4	69.0	71.0	70.0	74.4	73.8	71.9	

Mean $A_uS_{u,s}$ 71.8; mean $A_sS_{u,s}$ 70.9; mean $A_{u,s}S_u$ 72.3; mean $A_{u,s}S_s$ 70.4

to a reduction of cell-wall dilution and therefore greater, especially in 1978 when the A period was short. H_1 and D_3 reacted in different ways. H_1 only showed minor reductions in cell-wall yields. Also, dry-matter production was less affected by shading than it was in other stands, because Ula was an early and open crop. As cell-wall digestibility and dry-matter yield were low, these small reductions still had consequences of at least the same magnitude and direction as in the other crops. For D_3, the cell-wall yield of A_sS_u was intermediate between $A_uS_{u,s}$ and A_sS_s: some additional cell-wall production could occur in the stover during the S_u period for this treatment as compensation for 'neglected' earlier cell-wall formation, while for other light treatments the cell-wall yield decreased because of leaf senescence. This compensation caused a stronger decline in D_{crop} than was expected. Final reduction in cell-wall yield was 670 kg ha^{-1} for A_sS_u and 1510 kg ha^{-1} for A_sS_s.

The decline in cell-wall digestibility was unaffected by shading. The mean values of cell-wall digestibility for A_uS_u, A_uS_s, A_sS_u and A_sS_s were 65.0 %, 64.9 %, 65.4 % and 65.5 %, respectively. Cell-wall digestibility did show differences between crops of different density, genotype and year.

The apparent digestibility of the whole crop can be expressed by:

$$D_{crop} = (\text{ear content} \times D_{ear} + (100 - \text{ear content}) \times D_{stover})/100 \quad (1)$$

The ear content (organic-matter yield in ears as a percentage of organic-matter yield in the whole crop) showed a wide range in these trials (20.3 -63.1 %). Variation in ear digestibility (D_{ear}) was fairly small (range: 80.6 - 86.1 %). Ear digestibility was always lowest for A_uS_s. This treatment made a normal early ear development possible, but hampered late grain filling, thus causing a low shelling percentage. As the digestibility of the cob is much lower than of the kernels (Struik, 1982) a reduction in quality occurred. Among the other three light treatments, differences were small and inconsistent, as A_s treatment limited both cob and kernel development. Overall means were 83.6 %, 82.5 %, 84.5 % and 84.4 % for A_uS_u, A_uS_s, A_sS_u and A_sS_s, respectively. Quality differences in vegetative

Table 8. Apparent digestibility of the organic matter in the vegetative parts (%) at final sampling.

	St_1	St_2	H_1	H_2	D_1	D_2	D_3	Mean
A_uS_u	59.0	59.9	58.4	61.1	61.8	60.5	61.7	60.3
A_uS_s	56.6	60.9	56.2	61.2	61.9	59.4	61.0	59.6
A_sS_u	62.8	64.5	59.5	63.3	63.4	65.4	63.4	63.2
A_sS_s	60.6	63.6	57.5	61.7	62.6	62.5	61.6	61.4
Mean	59.8	62.2	57.9	61.8	62.4	62.0	61.9	

Mean $A_uS_{u,s}$ 60.0; mean $A_sS_{u,s}$ 62.3; $A_{u,s}S_u$ 61.8; mean $A_{u,s}S_s$ 60.5.

parts were greater (range 56.2 - 65.4). Stover digestibility for all treatments is given in Table 8. Cell-wall production in vegetative parts, physiological age, relative source size (and thus measure of storage or redistribution), year and genotype all affected the quality of the vegetative parts. Since cell-wall production was reduced in the A_s period and redistribution was unnecessary because of poor ear development, stover digestibility was always highest in the A_sS_u treatment.

In these experiments, the different variables of Eq. 1 are not all mutually independent. In Table 9 their linear correlation coefficients are presented. The most conspicuous findings were the absence of a significant correlation between D_{stover} and D_{crop} (because of the ambivalent character of the influence of successful ear development) and the significance of the relation between ear content and D_{crop}, which was usually absent within years. Certain other significant relations also became less important if only the data from one year were pooled.

It is clear that the effects on crop quality are more complex than can be described by effects on proportion of plant parts or on the quality of plant parts. The D_{crop} can also be expressed by:

$$D_{crop} = (cwc\% \times D_{cwc} + (100 - cwc\%) \times D_{cc})/100 - b \qquad (2)$$

in which:

Table 9. Matrix of linear correlation coefficients of variables in Equation 1 (n = 28).

x ↓ y→	D_{ear}	100-ear content	D_{stover}	D_{crop}
Ear content	-0.306^{ns}	-1.000^{**}	-0.441^{*}	0.751^{**}
D_{ear}		0.306^{ns}	0.665^{**}	0.286^{ns}
100-ear content			0.441^{*}	-0.751^{**}
D_{stover}				0.230^{ns}

ns = not significant
* $P < 0.05$
** $P < 0.01$
} two-sided.

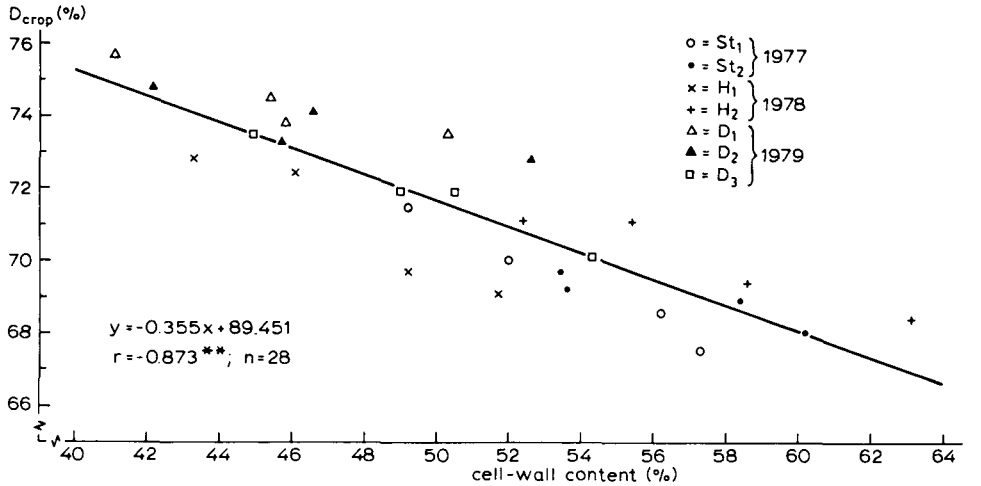

Fig. 4. The apparent digestibility of the whole-crop organic matter in relation to the cell-wall content of the whole crop (also as % of the organic matter) at final sampling.

cwc%	=	percentage of cell-wall constituents
D_{cwc}	=	true cell-wall digestibility
100 – cwc%	=	percentage of cellular contents
D_{cc}	=	true digestibility of cellular contents
b	=	difference between true digestibility and apparent digestibility. This difference includes undigested rumen microflora and endogenous excretion.

As stated earlier, cell-wall digestibility was hardly affected by shading treatment. The digestibility of the cell contents is always almost complete. The most variable components of Eq. 2 are thus cwc% and 100 – cwc%. Fig. 4 shows the relation between cwc% and D_{crop}. The cell-wall content of the whole crop is calculated from the cell-wall contents of the fractions. The correlation, although depressed by differences in cell-wall quality among the different crops, was high. The calculated regression coefficient was almost equal to the difference between D_{cc} and the mean D_{cwc}.

Résumé: ear yield, whole-crop yield and cell-wall yield of normal crops were mainly affected by shading during the A period. Because of its effect on ear development, shading A also determined the rate of crop drying. Digestibility, content of cell-wall constituents and of water-soluble carbohydrates, leaf area duration and *Fusarium* infection were mainly influenced by shading during the S period.

Neither cell-wall content nor digestibility correlated well with the amount of irradiance received after flowering, since cell-wall content was determined both by cell-wall production before and during the A period and by carbohydrate production during the A and S periods.

In subsequent papers more details will be presented about the effects of shad-

ing on the reduction of cell-wall production and its consequences for crop digestibility. The effects of temperature during the grain filling will also be discussed in future papers.

Implications

The effects of shading treatments were not confined to a reduction in photosynthesis. The most noticeable side-effects were:
– Ear size was severely affected, especially by shading during the A period, even at lower densities.
– Ear yields were closely related to amounts of irradiance, suggesting a direct connection between light and ear growth apart from photosynthesis.
– Cell-wall production after flowering, which normally occurs in stems, husks and ears, was more hampered by shading than was dry-matter production. Therefore, the differences in cell-wall content between unshaded and A_s treatments were smaller than expected (cf. Table 5 and Table 7).
– Longevity of leaves and disease resistance were affected by shading, especially during the S periods.

Shading has the following repercussions on the ears:
– Abortion of the younger tip and mid-kernels; actually this is an accelerated senescence of kernels, including a very early Black Layer Formation and early cessation of dry-matter accumulation. This abortion occurred too soon after the beginning of the shading to have been caused by exhaustion of carbohydrates. Abortion even occurred in crops that had increasing carbohydrate levels in their vegetative parts, and in crops with very low plant densities. So even if developing kernels are very weak sinks, it is unlikely that abortion is caused by carbohydrate shortage alone.
– The rate of dry-matter accumulation in the ear is modified without a noticeable time-lag, just as occurs after complete defoliation (Jenner, 1979; Major, 1980; Struik, unpublished data).

Physiological implications
Hormones. Thus, the sink strength and sink size were limited before there was a shortage of carbohydrates. This limitation may be caused by plant hormones (e.g. auxins, cytokinins, gibberellins, abscisic acid), either being produced in the kernels themselves, or in other plant parts such as roots. The latter supposition is most likely. Roots play a leading part in the longevity and vitality of aboveground plant parts, since root tips produce cytokinins necessary for kernel development, sink activity and delay of senescence. For this production root *growth* is necessary (Vaadia & Itai, 1968; Boote, 1977). The roots themselves are weak sinks for carbohydrates after flowering (Noodén & Leopold, 1978) and they can only be provided with carbohydrates by the lower leaves (Lupton, 1966; Tripathy et al., 1972; Palmer et al., 1973; Fairey & Daynard, 1978). For several reasons lower leaves are in unfavourable position for photosynthesis, especially in shaded crops. After silking there is hardly any net increase in root

weight, although at least part of the normal degeneration is compensated for by renewal (Koedjikov, 1967; Mengel & Barber 1974; André et al., 1978). Renewal is hampered and degeneration is stimulated by shading (Pendleton & Weibel, 1965; Brouwer & De Wit, 1968; Hess, 1968; Boote, 1977; Crapo & Ketellapper, 1981). Root *activity* declines particularly strongly as a result of low irradiance, because of low carbohydrate levels in the roots (Crapo & Ketellapper, 1981; Massimino et al., 1981). Therefore, it is possible that certain prompt effects of shading are caused by a decrease in root activity and hence in cytokinin production. If shading occurs shortly after grain set, a new balance between root activity, leaf activity and ear activity may be achieved after a certain number of kernels have aborted, as partial sterility promotes the translocation of carbohydrates to the roots (Palmer et al., 1973). If shading treatment starts later or is applied to older crops, the effects will be more detrimental, because of a loss of compensating abilities of the crop.

N metabolism. Another possible explanation of kernel abortion due to shading may be the shortage of certain newly synthesized nitrogen compounds, because of a lack of nitrate reductase activity (Knipmeyer et al., 1962; Early et al., 1966; Early et al., 1967). Grain development requires special proteins. Since nitrate reduction and nitrogen metabolism are expensive in energy use, their assimilation may be hampered more than dry-matter production. As stated earlier, this explanation can also be used for cell-wall production; it is known that lignin production is also energy consuming (Penning de Vries, 1974). Both possibilities may be combined. Trewavas (1981a, b) postulated that although growth substances perform an essential function in plant organization, the controlling factor may be sensitivity to growth substances rather than a particular growth substance itself. The only way of varying this sensitivity is by changing the amount and/or characteristics of specific proteins that form the hormonal binding sites in the cells. Trewavas (1981a, b) and Bogers & Libbenga (1981) suggested that there might be a correlation between developmental stage and binder concentration. So protein and hormone synthesis may both be necessary for hormonal effect.

If the above-mentioned prompt reaction of root activity to shading is accepted, the fast reaction of kernel development and of ear growth could be explained. In analogy, hormonal activity might also explain the close relation between irradiance and ear yield. Finally, a part of the differences in leaf senescing pattern (especially in earlier stages) might be caused by differences in root activity (see Table 3 and Fig. 1), since root cytokinins are required for leaves to function and to inhibit senescence.

The above-developed hypothesis was tested by analysing the accumulation in the above-ground plant parts of certain minerals such as calcium and phosphorus that are difficult to take up. Estimating Ca uptake could be especially useful, since Ca is transported in the same way as cytokinin (Michael et al., 1970), Ca uptake requires energy and Ca is only slightly redistributed in the plant. How-

ever, mineral uptake decreases so fast after flowering that differences were only obtained for the A period.

Agricultural implications

In regions with low light intensity during grain filling, the ripening of forage maize is accompanied by a decline in crop quality. Yet, major falls in yield caused by a period with low irradiance do not automatically involve declines in digestibility, if this period occurs during a stage of crop growth in which cell-wall production is taking place. On the other hand, an overcast period shortly before harvesting will give a smaller yield loss, but will greatly depress digestibility and will stimulate *Fusarium* infection.

Suitability for ensiling is mainly determined by dry-matter content and content of readily fermentable carbohydrates. Shading shortly after flowering will cause a strong decline in the first parameter and will increase the latter. The opposite is true for shading after mid-September. Considerable losses during the ensiling process are most likely if shading occurs during the first part of the grain-filling period.

It is not possible to avoid the effects of an overcast autumn by simple modifications to cultural practice, although later sowing shows relatively smaller reductions in both dry-matter yield and crop quality. Later sowing, however, is not advisable, because in normal years yield and quality will decline considerably. Even the digestibility of a very early hybrid reacted sharply to shading is shading occurred in later stages of the growing season.

The effects of irradiance after grain set on digestibility will be minimized if
- little cell wall is present at grain set
- the quality of the cell wall is high and remains high
- cell-wall production after grain set is limited
- leaf activity is maintained for a long time.

Conclusions

1. Ear development is strongly hampered by shading during and shortly after grain set and ear growth is closely related to amounts of irradiance after grain set.
2. Final yields of vegetative plant parts are fairly independent of amounts of irradiance (except yields of husks + shanks), but the quality is affected by light reduction.
3. Whole-plant yields are determined by amounts of irradiance, but also to some extent by distribution of irradiance over time.
4. Whole-crop digestibility is only slightly reduced by shading during the first part of the grain-filling period, because cell-wall production is limited by shading during this phase. Shading after mid-September causes a more severe decline in crop quality, except in dense stands.
5. Infirmities of old age, such as the *Fusarium* disease, are promoted by shading during the final part of the growing season.
6. The above-mentioned effects are modified, but not altered by crop structure.

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