Physiology of forage maize (*Zea mays* L.) in relation to its production and quality

Promotor : ir. M.L. 't Hart, oud-hoogleraar in de leer van de landbouwplantenteelt en het grasland

Co-referent: dr.ir. B. Deinum, wetenschappelijk hoofdmedewerker

P.C. STRUIK

PHYSIOLOGY OF FORAGE MAIZE (*ZEA MAYS* L.) IN RELATION TO ITS PRODUCTION AND QUALITY

Proefschrift
ter verkrijging van de graad van
doctor in de landbouwwetenschappen,
op gezag van de rector magnificus,
dr. C.C. Oosterlee,
hoogleraar in de veeteeltwetenschap,
in het openbaar te verdedigen
op vrijdag 16 september 1983
des namiddags te vier uur in de aula
van de Landbouwhogeschool te Wageningen.

ISN: 19216 4-03

ABSTRACT

Struik, P.C., 1983. Physiology of forage maize (*Zea mays* L.) in relation to its production and quality. Doctoral thesis, Wageningen, (IX) + 97 p., 7 tables, 12 figs, 329 refs, Eng. and Dutch summaries, plus 6 papers published in: Mededeling no. 64, Vakgroep Landbouwplantenteelt en Graslandkunde, Landbouwhogeschool, Wageningen (1982), 28 p., 7 tables, 9 figs, 41 refs, Eng. summary; Meded. Landbouwhogesch. Wageningen 83-3 (1983), 41 p., 12 tables, 16 figs, 93 refs, Eng. summary; Neth. J. agric. Sci. 30 (1982) 20 p., 9 tables, 4 figs, 36 refs, Eng. summary; Neth. J. agric. Sci. 31 (1983), 24 p., 6 tables, 11 figs, 12 refs, Eng. summary; Neth. J. agric. Sci. 30 (1982), 15 p., 3 tables, 6 figs, 27 refs, Eng. summary; Meded. Landbouwhogesch. Wageningen 83-2 (1983), 27 p., 9 tables, 4 figs, 60 refs, Eng. summary.

This thesis describes and discusses the quantitative effects of changes in temperature, light intensity and photoperiod on the development, dry-matter production, dry-matter distribution, digestibility and dry-matter content of forage maize. Cultivation techniques and hybrid choice are also discussed.
The productivity of maize in North-West Europe mainly depends on the rate of development during early seedling growth. Yet, development, productivity, maturation and digestibility are also strongly affected by climatic conditions during later stages of growth. Moreover, significant aftereffects of adverse conditions are often found. Some steps in the plant's development are especially sensitive, e.g. tassel initiation, silking and grain set.
Digestibility was found to be less variable than yield and dry-matter content. Climatic factors affected digestibility mainly through their effects on the proportion of (less digestible) structural material in the organic matter. Only prolonged high temperatures can induce large depressions in final cell-wall digestibility. Since the production of cell-wall components does not develop over time in the same way as the production of cell solubles, digestibility is not always affected in the same direction as yield. Differences between hybrids were predominantly caused by differences in cell-wall digestibility. Therefore selection for improved digestibility should be possible without affecting earliness or yield.
The suitability of the Dutch climate for growing forage maize is evaluated. Furthermore, the ideal weather and the ideal genotype for North-West Europe are described.

Free descriptors: development, yield, digestibility, cell wall, dry-matter content, dry matter distribution, temperature, light intensity, photoperiod, hybrid, cultural practice, ideotype.

Reference to the contents of Chapters 1 up to and including 6 should be made by citing the original publications.

Printed by PUDOC (CO), Wageningen, Netherlands.

Cover illustration: Pitao Cozobi, Collection Musée de l'Homme, Paris.

STELLINGEN

1. In Noordwest-Europa is de variatie in verteerbaarheid van snijmaïs bij normale teelttechniek gering maar niet onbetekenend.

Dit proefschrift.

2. De ontwikkeling, groei en omvang van de kolf zijn voor de opbrengst en kwaliteit van snijmaïs in Noordwest-Europa belangrijker dan de laatste jaren werd aangenomen.

Dit proefschrift.

3. Het aantal bladeren dat een maïsplant aanlegt is afhankelijk van klimaatsfactoren tijdens een zeer korte periode voor de aanleg van de pluim. Deze korte periode is daarom van wezenlijk belang voor de produktiviteit en de verteerbaarheid van snijmaïs.

Dit proefschrift.

4. Voor het ontstaan van verschil in celwandverteerbaarheid is strekkingsgroei van plantecellen noodzakelijk.

Dit proefschrift.

5. Bij het onderzoek naar de effecten van klimaatsfactoren op de verteerbaarheid van celwanden dient de chemische en fysische stabiliteit van de celwand in beschouwing te worden genomen.

Dit proefschrift.

6. Maïsgenotypen zijn slechts dan daglengteneutraal als daglengte geen invloed heeft op het tijdsinterval tussen mannelijke en vrouwelijke bloei.

Dit proefschrift.

7. De genotypische variatie van snijmaïs in droge-stofopname door herkauwers is veel groter en belangrijker dan zijn genotypische variatie in verteerbaarheid.

8. Ontmenging en onbedoelde selectie, optredend bij het hakselen, malen en bemonsteren van snijmaïs, vormen vaak de grootste bronnen van fouten in het onderzoek met dit gewas.

9. Het bewijs van Smith (1981) voor het feit dat bij maïs P_{fr} niet de actieve vorm van fytochroom kan zijn, is wankel.

Smith, Nature 293: 163-165 (1981).

10. Thiagarajah & Hunt (1982) nemen waar dat boven 24°C de snelheid waarmee de bladeren bij maïs worden aangelegd niet meer toeneemt bij een stijging van de temperatuur. De verklaring die zij voor dit verschijnsel geven, is onjuist.

Thiagarajah & Hunt, Can. J. Bot. 60 (9): 1647-1652 (1982).

11. Zelfs binnen één stolon geldt niet dat de eerst aangelegde aardappelknol bij de eindoogst automatisch de grootste zal zijn.

12. De indexering naar het prijspeil van de gezinsconsumptie van 1980 was reeds op het tijdstip van invoering achterhaald. De gezinsbestedingen zijn immers sinds 1980 sterk veranderd.

13. Geweldloze burgerlijke ongehoorzaamheid leidt niet tot uitholling maar eerder tot verrijking van de democratie, omdat deze vorm van verzet tegen meerderheidsbeslissingen aanleiding geeft tot weging van stemmen naast louter telling ervan.

14. De huidige teruggang van het ledental van veel protestantse kerken is voor een aanzienlijk deel te wijten aan het gebrek aan eigentijdse goede kinder- en jeugdbijbels in vorige generaties.

15. Het is beter rood te staan dan zwart te bezitten.

Proefschrift van P.C. Struik
Physiology of forage maize (*Zea mays* L.) in relation to its production and quality
Wageningen, 16 september 1983

WOORD VOORAF

Dit proefschrift beschrijft en bespreekt de resultaten van onderzoek, dat is uitgevoerd bij de Vakgroep Landbouwplantenteelt en Graslandkunde. Velen hebben daadwerkelijk en moreel bijgedragen tot de totstandkoming van dit proefschrift. Mijn erkentelijkheid hiervoor beperkt zich niet tot de personen en instellingen die ik hieronder met name wil noemen.

Het is voor mij een grote eer te mogen promoveren bij professor ir. M.L. 't Hart. Ik ben hem zeer erkentelijk voor de stimulerende wijze waarop hij het onderzoek en het op schrift stellen ervan begeleidde. Zijn veelzijdige landbouwkundige kennis en groot kritisch vermogen bleken telkens onmisbaar.

Dr.ir. B. Deinum, mijn co-referent, is steeds zeer nauw bij dit project betrokken geweest. Hij verrichtte het vooronderzoek, formuleerde het voorstel voor het promotie-onderzoek en was mijn dagelijkse begeleider en stimulator. Zijn kennis van het gewas, de analysetechnieken en de dier- en plantenfysiologische achtergronden vormden een voortdurende toetssteen en bron van inspiratie.

Prof.ir. L.J.P. Kupers was als adviseur bij het onderzoek betrokken. Zijn grondige kennis van de plantenteelt en de gewasfysiologie leverden vaak nuttige adviezen en ideeën. Tevens ben ik prof. Kupers dankbaar voor de ruimte die hij in de beginperiode van mijn nieuwe functie bood, waardoor dit proefschrift versneld kon worden afgerond.

De discussie met vele anderen binnen en buiten de Landbouwhogeschool hebben aanzienlijk bijgedragen tot de totstandkoming van dit proefschrift. Hierbij denk ik o.a. aan ir. J.P.M. Bink, prof.dr. J. Bruinsma, prof.ir. J.G.P. Dirven, dr.ir. O. Dolstra, prof.dr.ir. A.J.H. van Es, dr.ir. Y. van der Honing, ir. H.A. te Velde en prof.dr.ir. S.J. Wellensiek.

Mevr. L.M. van Ravenswaaij-Bouw is 2½ jaar nauw betrokken geweest bij het onderzoek. Met grote precisie en veel geduld heeft zij talloze bepalingen verricht en gegevens verwerkt, dit alles met een bewonderenswaardige evenwichtigheid. Haar aanstelling werd mogelijk gemaakt door financiële steun van het Nederlands Graan Centrum. Deze stichting ben ik daarvoor zeer erkentelijk.

De aanleg en bewerking van de veldproeven was in de bekwame handen van de heer L.A. Mol en zijn medewerkers. Met name de beschaduwingsproeven vergden veel aandacht. De fytotron-proeven werden uitstekend verzorgd door de heer J.C.M. van der Pal.

Ook aan de heer J.A. Möhring en medewerkers is veel dank verschuldigd,

daar zij bij fytotron-proeven en bij de daglengte-proeven in het veld de technische installaties en hulpapparatuur aanlegden, verzorgden en draaiende hielden.

Biologische en chemische analyses van de samenstelling van het plantmateriaal vormden een wezenlijk onderdeel van deze studie. De tienduizenden analyses werden uitgevoerd door mevr. W. van Heusden, mevr. C. de Wit-Krechting en mevr. I.A.M. Reurink-van Ettinger, terwijl mevr. J.G.M. Miechels-de Beijer en mevr. L.M. van Ravenswaaij-Bouw indien nodig bijstand verleenden. Het analysewerk gebeurde niet alleen uiterst vakkundig, maar ook met een gezonde, kritische opstelling ten aanzien van het verkregen resultaat.

In het kader van hun doctoraalstudie of als stagiair hebben de volgende studenten voor langere tijd aan de proeven of de verwerking daarvan meegewerkt: Helmy Asfour, Lubbert van den Brink, Barbara Frischknecht, Harrie de Graaf, Pablo Härri, Roel Hoekstra, Gert Jan Hoornenborg, Aalt van de Pol, Trees de Vent, Bert Wassink en Jan de Wilt. Daarnaast werkte een groot aantal studenten, stagiairs en vakantiehulpen voor kortere tijd mee. Tevens heeft de heer J. Knoppers als assistent van dr.ir. B. Deinum een belangrijk aandeel in het werk gehad in de beginfase van het onderzoek.

Verschillende firma's en instellingen hebben zaad beschikbaar gesteld ten behoeve van dit onderzoek. Van hen wil ik met name noemen het Station d'Amélioration des Plantes fourragères (INRA, Lusignan, Frankrijk), het Koninklijk Kweekbedrijf en Zaadhandel D.J. van der Have B.V. te Kapelle en het Kweekbedrijf Zelder B.V. te Ottersum.

Ir. H.A. te Velde (RIVRO) ben ik dankbaar voor de gegevens, die verwerkt zijn in de inleiding van dit proefschrift.

De heer J.C. Rigg corrigeerde op kundige wijze de Engelse tekst van hoofdstuk 5. Mevr. J. Burrough-Boenisch redigeerde niet alleen bekwaam de overige tekst, maar trok ook veel tijd uit voor de bespreking ervan. Daardoor heb ik veel van haar kunnen leren.

Dhr. G.C. Beekhof verzorgde op nauwkeurige wijze de tekeningen, terwijl het manuscript zorgvuldig uitgetikt werd door mevr. T. van Roosendaal-van Hal. De redactie en de drukker van het Netherlands Journal of agricultural Science ben ik erkentelijk voor de vlotte wijze waarop met name hoofdstuk 4 voor opname in dit proefschrift beschikbaar kwam. Dit proefschrift werd op snelle en bekwame wijze gedrukt door Centrale Offsetdrukkerij PUDOC te Wageningen.

Tenslotte wil ik mijn ouders danken voor de kansen, die zij mij boden. Mijn vrouw en zoon ben ik veel verschuldigd voor het geduld dat zij getoond hebben en voor hun morele maar ook daadwerkelijke steun bij het volbrengen van dit werk.

CURRICULUM VITAE

Paul Christiaan Struik werd geboren op 27 november 1954 te Nieuw Vennep (gemeente Haarlemmermeer). Vanaf 1967 bezocht hij het Christelijk Lyceum Dr. W.A. Visser 't Hooft te Leiden. In 1973 behaalde hij het diploma Gymnasium β. In september van datzelfde jaar werd begonnen met de studie aan de Landbouwhogeschool te Wageningen. In september 1978 studeerde hij met lof af in de richting landbouwplantenteelt. Doctoraalvakken waren de leer van het grasland, de landbouwplantenteelt, de fysiologie der planten en de erfelijkheidsleer. Van oktober 1978 tot oktober 1981 was hij werkzaam als promotie-assistent bij de Vakgroep Landbouwplantenteelt en Graslandkunde van de Landbouwhogeschool. In deze periode werd het onderzoek verricht dat geleid heeft tot dit proefschrift. Sinds 1 januari 1982 is de auteur als wetenschappelijk ambtenaar werkzaam bij dezelfde vakgroep. Hij verricht daar onderzoek naar de fysiologische aspecten van de knolsortering bij eetaardappelen.
Hij is gehuwd en heeft een zoon.

CONTENTS

GENERAL INTRODUCTION

1. BOTANY OF *ZEA MAYS* L.

It is difficult to discuss the ecophysiology of forage maize without having a clear picture of the development and the habitus of the plant. Therefore, in the following section these will be described and at the same time, the botanical terms used in this thesis will be defined.

Maize is a tall, vigorously growing annual of the Gramineae (or Poaceae) family.

A fully grown plant bears at least eight leaves on the main stalk (Duncan, 1975). Hybrids grown in The Netherlands generally produce 13-17 leaves on average. At lower latitudes, a maize plant normally has many more leaves (up to 48). The leaves are sessile, with rigid sheaths surrounding the stem internode. The sheath and lamina meet at a definite collar on which a small, thin ligule develops. The first leaf of the seedling is spatulate; subsequent leaves are long, sword-shaped or linear-lanceolate, acuminate-pointed, and have prominent midribs. The leaf blades (usually called 'leaves') are mostly curving. Both leaf angle and inclination are variable. Some genotypes even show erect, stiff upper leaves. The upper surface of the blades is pubescent, while the lower surface is glabrous.

The surface area of the successive leaves increases exponentially up to the leaves from the middle of the stalk, which can exceed 1000 cm^2. Further up the stalk the area of the individual leaves drops sharply.

The alternate leaves are usually arranged in two opposite orthostiches, although pronounced torsion may occur. However, genotypes with a decussate leaf arrangement have also been reported (Blanco, 1976).

During early vegetative growth the shoot apex elongates and tassel-branch primordia instead of leaf primordia are initiated. At this stage the number of leaves is fixed.

The shoot may finally reach a height of 7 m, depending of the number of leaves (and thus number of stem internodes) and factors determining the length of each individual phytomere. The usual height of the stem in temperate regions is 200 - 300 cm.

Unlike most other grasses, the stalks of the maize plant are filled

with parenchymatous tissue called 'pith'. This tissue, in which some vascular strands are embedded, adds strength to the stalk (Zuber et al., 1980) and enlarges the capacity to store non-structural carbohydrates. The tissue enclosing the pith is very fibrous and is called 'rind'.

In addition to the radicle, the seminal roots and the nodal roots, maize may also produce aerial or 'brace' roots. Aerial roots appear on the lower stem nodes at the end of the vegetative growth. If these aerial roots reach the soil, they develop into normally functioning roots. Plants bearing these roots are better protected against root lodging.

Maize also differs from most other grasses in having unisexual inflorescences, although the species is monoecious. The male and female inflorescences are borne apart. The staminate inflorescence is a panicle, called 'tassel'. The tassel terminates the main shoot. The tassel branches carry spikelets, occurring in pairs: one member is pedicellate and the other is subsessile. Each spikelet contains two flowers and each staminate flower contains three anthers. The glumes of the spikelets are robust; the lemmas and the paleas of the staminate flowers are also well developed. Since each anther produces about 2500 pollen grains and since the tassel of a normal plant grown under temperate conditions produces about 400 spikelets, a maize plant produces approximately 6,000,000 pollen grains. Kiesselbach (1949) estimated that an average-sized plant grown under American conditions even produces 25,000,000 pollen grains.

During early stem development a shoot is initiated in the axil of each present leaf. Such axillary shoots in the mid-section of the stem normally develop into an ear shoot. Ear shoots are composed of a very short stalk (called 'shank') bearing a number of leaves, the sheaths of which are well developed, but whose laminae are mostly rudimentary. These leaves are called 'husks': they envelop and protect the pistillate flowers. The ear shoots are terminated by an ear.

Ears consist of a robust rachis ('cob'), bearing 4 - 30 rows of almost sessile spikelets. There is always an even number of rows, because spikelets are arranged in pairs, as in the tassel. Although two flowers are produced in each female spikelet, only the upper one usually develops into a functional flower. The pistils of these flowers have very long styles covered with stigmatic branches. The style, including stigmatic branches, is called a 'silk' and the process of extrusion of these silks out of the husk envelope is called 'silking'. The two glumes of the female spikelet enclose the ovary, but the silk extends beyond them and can reach an enormous length if it is not

pollinated . The glumes are too small to enclose the caryopsis when it has reached its maximum volume; the two lemmas and the two paleas of each female spikelet are even shorter than the glumes (Miller, 1919). Mature caryopses are thus not individually enclosed.

At first all the flowers of the tassel and of the ears on the main stem show primordia of both stamina and pistils (Bonnett, 1966). Phytohormones and environmental factors (e.g. temperature, photoperiod) regulate the sex expression of each flower.

Self-pollination is possible but wind and protandry stimulate cross pollination. The fertilized ovary develops into a caryopsis called 'kernel' or 'grain'.

An axillary bud is present in the axils of all husks; this may develop into a secondary ear (also called 'axillary ear' or 'shank ear'). As these ears are enveloped by husks with their own buds, a stem internode may bear many ears. Since each stem internode (except perhaps the 3 - 7 internodes immediately below the tassel) are potentially capable of producing ear shoots, the number of ears per plant is almost indeterminate.

Normally only one or two internodes bear one ear shoot. Under Dutch conditions, approximately 400 florets of the top ear will extrude silks. Thus 15,000 pollen grains are available for each silk.

The axillary buds of the lower leaves may develop into tillers rather than into ear shoots. The tendency to tiller is small in modern hybrids: tillering only occurs when plant density is low. Tillers usually bear a hermaphrodytic top inflorescence on which round kernels are set on tassel branches, not protected by husks.

The shape of the kernels on the ear shoot and the characteristics of the endosperm are very variable and form the basis of a classification into different commercial types: dent, flint, flour, waxy, pop and sweet ('sugary') corn. Numerous other endosperm mutants, such as opaque, amylose-extender, brittle, dull, soft starch, and shrunken, have no or only very limited commercial value. A special type of kernel mutant is pod corn in which the glumes are not vestigial but enclose the kernel like chaff does in other cereals. Commercial forage-maize hybrids, grown in The Netherlands are all flint, dent, or flint/dent types.

The kernel mainly consists of endosperm, the major component of which is starch (amylose and amylopectin). A specific characteristic of the mature maize kernel is the presence of a closing layer between the basal endosperm and the vascular region of the pedicel (Kiesselbach & Walker, 1952). This

plate of tissue several cells thick develops early in the kernel development but at the end of the grain-filling period is compressed and then appears as a black layer. This 'black-layer formation' serves as an indicator of physiological maturity in maize (Daynard & Duncan, 1969). Under Dutch conditions of growing silage maize, black layers only become visible in tip kernels in which the accumulation of dry matter has been started but has only lasted for a short while. Once compressed, the black layer prevents the passage of chemical compounds. In this way the plant adjusts its number of dry-matter accumulating kernels to the prevailing conditions. The process of adjustment is referred to as 'kernel abortion'.

2. ORIGIN AND DEVELOPMENT OF MAIZE AS A MAJOR CROP

The C_4-plant maize has been known throughout North, Central and South-America since prehistoric times. Ancient Indian civilizations, like those of the Incas, the Aztecs and the Mayas, were founded on maize. The dependence on maize for staple food was so complete that the plant played an important role in the religions of these peoples. The presence of special godheads for maize, e.g. Pitao Cozobi (see cover), illustrates this.

Maize is a crop made by man. Galinat (1971) stated that the modern maize ear has a Darwinian fitness approaching zero. Maize only survived thanks to the domestic propagation by the Indians. All its closest relatives became extinct. Modern scientists are still trying to trace the origin of *Zea mays* L. and do not even agree about the taxonomy of the tribe of the Maydeae (or Tripsaceae), of the very small genus *Zea* and of the subspecies of maize.

Today maize is one of the main crops of the world; it has a very wide ecological range. Like many other cultivated plants, e.g. peanut, potato and tobacco, the plant was spread over the world after the 'discovery' of America by Columbus. Today the main maize-growing regions are: the U.S. Corn Belt (centred in Iowa and Illinois), the Danube Basin, the Po Valley, the plains of northern China, north-eastern Argentina, south-eastern Brazil and southern Africa. The northern limits of the range of grain maize run through southern Canada, central Europe, southern U.S.S.R. and China. These limits are shifting northwards, because breeders are succeeding in developing productive hybrids that mature with ever lower accumulated temperature totals.

The traditional maize areas in Europe are characterized by a mean temperature of 17°C or more during the period from 1 May to 30 September.

At present, grain maize is also grown in areas with a seasonal mean temperature of approximately 15.5°C (Bunting, 1980).

Several times during this century the area of grain maize in The Netherlands has reached a substantial size (Becker, 1976), mainly during periods of economic crisis, wars, or when grain prices have been extremely high.

The mean seasonal temperature in The Netherlands (approx. 14.5°C), however, is still much too low for grain maize to be grown profitably in normal times, in spite of subsidies from the Common Market.

In early days maize was not used as a forage crop, but the European colonists in America soon discovered that the stover was a useful roughage for their livestock. The temperature requirements of forage maize are lower than those of grain maize because the forage crop is harvested before grain maturity. Forage maize can be grown in areas with a mean seasonal temperature of 13.5°C and above. Considerable areas of forage maize are even found in Scandinavia.

In The Netherlands a revolutionary development of the area of forage maize started in the early 1970s (Fig. 1; source: C.B.S.), initially mainly on the sandy soils of the southern and the eastern part of the country, but later also more to the north and even on the Frisian Islands.

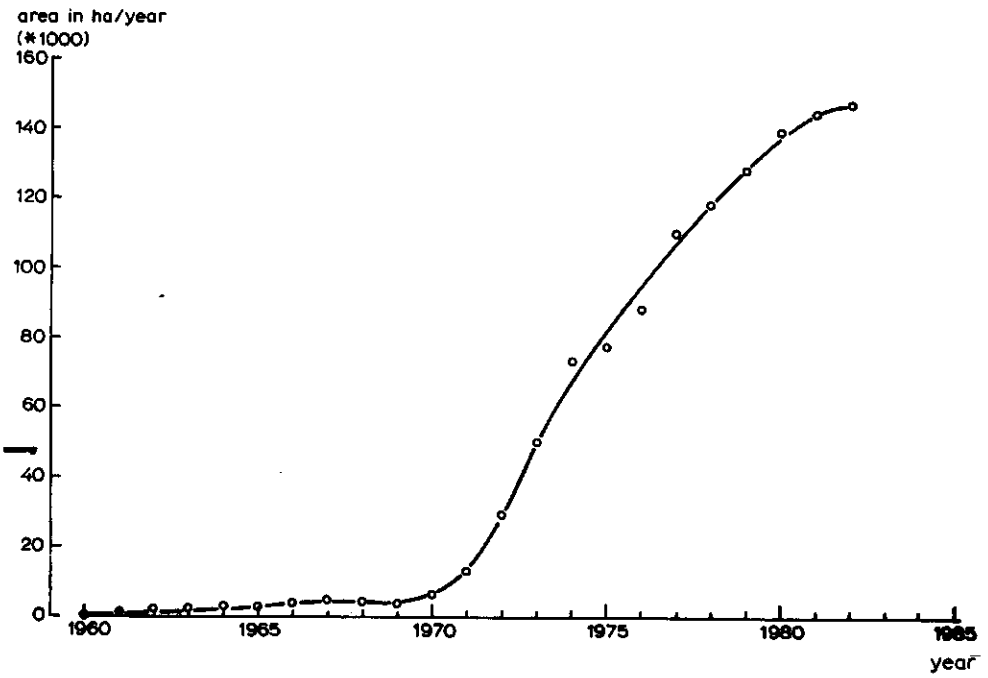


Fig. 1. Development over time of the area of forage maize in The Netherlands.

By 1982, forage maize was the second arable crop (in terms of area) in The Netherlands. The same dramatic development was found in neighbouring countries (Table 1).

Table 1. Area of forage maize in northern Europe (x 1000 ha), excluding corn-cob mix.

year	1965	1970	1975	1980	1982
country					
Netherlands	3	6	77	139	147
Belgium	5	18	66	90	92
W. Germany	100	190	430	700	775
France	360	400	870	1140	1280

There are many reasons for the rapid increase in the forage-maize area. Some of these are:

characteristics of the maize crop

- maize yields are high, partly because well-adapted hybrids are available
- maize is a good-quality roughage (high energy content, tasty, very digestible), suitable for meat and milk production and for the rearing of young cattle
- the composition is favourable for ensiling: a high proportion of fermentable carbohydrates and a low buffering capacity
- maize can tolerate very high gifts of slurry and manure, which are produced in enormous quantities on pig, chicken and dairy farms

cultural factors

- weed control has become easy as a result of the use of chemicals; the chemical control of certain weeds, however, is getting more troublesome
- there are no severe diseases or pests that reduce the forage yield to a great extent; continuous cropping of forage maize is still possible without severe yield depressions
- the soil conditions (e.g. pH) demanded by forage maize are not as exacting as those required by other forage crops (e.g. fodder beet)
- the maize crop shows a low water deficit compared with other forage crops grown in The Netherlands; therefore maize can give stable yields on soils with low water-bearing capacity

socio-economical factors

- cultivation, harvest, ensiling and feeding are completely and efficiently mechanizable; cultivation, harvest and ensiling are mainly done by contractors
- production costs per feeding unit are low
- because of low labour input, maize can easily be grown on fields a long distance from the farmstead
- the trend from mixed farming towards cattle farms with a large number of animals per hectare
- forage maize is not only a forage crop but also a commercial one
- the know-how necessary for growing forage maize quickly became available

The cultivation of maize for corn-cob mix (CCM) and high-moisture grain (feeds mainly used for rearing pigs in North-West Europe) has also become increasingly popular during recent years, mainly in France, Belgium and W. Germany. To date this development has not been of great importance in The Netherlands. This lack of interest not only reflects adverse climatic conditions but is also because the Dutch compound-feed industry is highly developed.

3. AIM OF THE PRESENT STUDY

Forage maize is grown to feed the livestock that is reared for meat and milk production and is used especially during winter. The value of a maize crop is therefore not only determined by factors affecting dry-matter yield, but also by factors affecting dry-matter distribution, ageing, preservation and the efficiency of the conversion to valuable animal product.

Fig. 2 indicates the factors involved in the agronomic value of a forage-maize crop. The present study was focussed on the factors written in italics.

The average increase in dry-matter yield in the variety trials carried out by the Government Institute for Research on Varieties of Cultivated Plants (RIVRO) in the period 1954-1981 was approximately 160 $kg.ha^{-1}.year^{-1}$ (te Velde, 1983). This increase is proportionally larger than the corresponding increase in most other crops (Scheijgrond, 1978) but agrees with the findings of Schuster et al. (1977) on forage maize in W. Germany. These large increases in forage-maize yields must partly be attributed to improved cultivation techniques and partly to the introduction of new varieties. Fig. 3 shows that

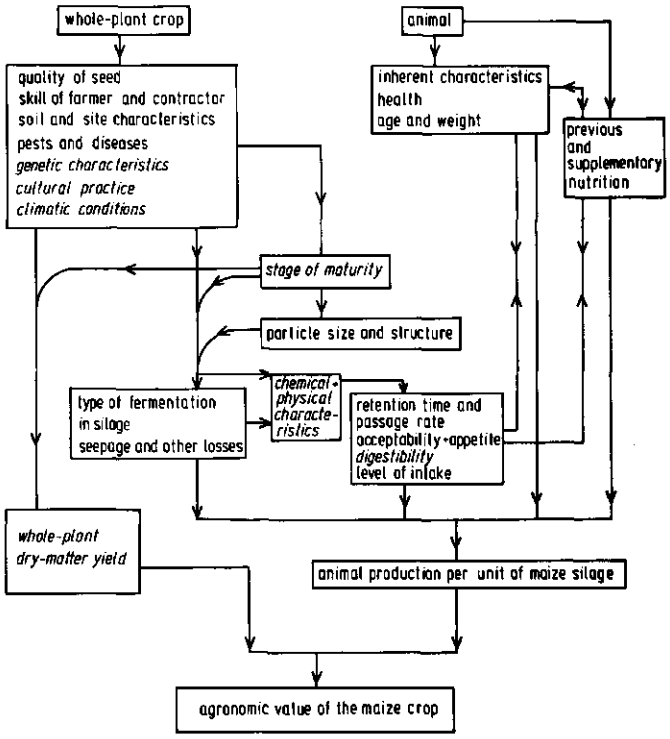


Fig. 2. Factors affecting the agronomic value of a forage-maize crop. The factors within one frame are interdependent or interact. The factors in italics were part of the present study.

the yield increase of forage maize resulting from plant breeding during the last three decades has been approximately 1.0% (i.e. approx. 125 $kg.ha^{-1}.year^{-1}$). The increase in average yield of the varieties used by growers in the period 1954-1981 (average weighted according to the area of the different hybrids), however, was only 69 $kg.ha^{-1}.year^{-1}$ (i.e. 0.54%.$year^{-1}$; te Velde, 1983; te Velde, personal communication).

In the same period several other relevant agronomic properties of the collection of hybrids listed on the descriptive variety list produced by the RIVRO have improved slowly (Fig. 4). Differences in proportion of ear between the hybrids listed, however, declined. Fig. 4 clearly shows that the breeders'

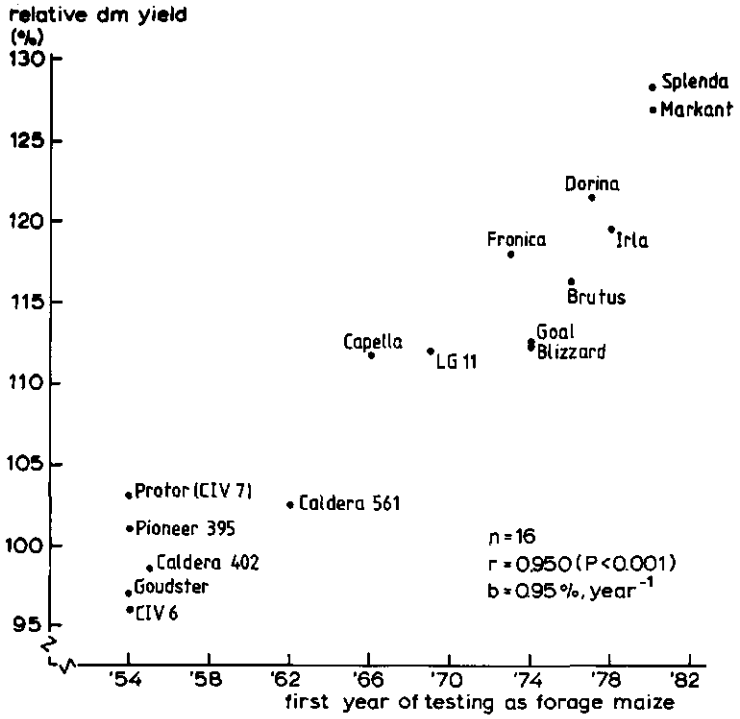
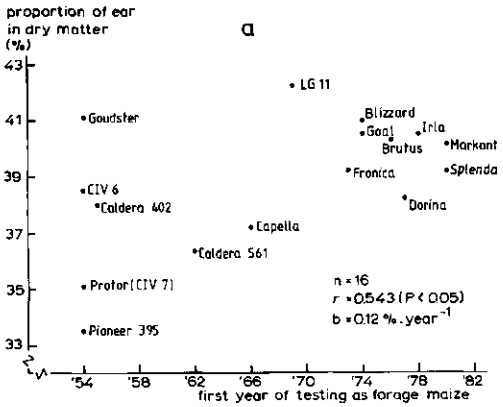


Fig. 3. Relative dry-matter yield of forage-maize hybrids, that have been or are being grown by farmers on a large scale, in relation to the first year of testing as forage maize by the Government Institute for Research on Varieties of Cultivated plants (RIVRO). Pioneer 377A has been excluded since it was only recommended for growing as fresh forage. Data kindly provided by Ir. H.A. te Velde (RIVRO). The method of analysing the data has been described by te Velde (1983). This method enables hybrids to be compared even though they were tested in different years, at different locations and under different cultivation techniques.

interest was mainly focussed on improving dry-matter yield.

A comparison with data recorded in the descriptive variety lists of the last two decades (RIVRO, 1963 up to and including 1983), however, shows that both dry-matter content of the whole crop and proportion of ear in the dry matter increased steadily as a result of improved cultivation techniques. One of the most drastic changes in cultural practice was a reduction in the plant density from 14 to 10 plants/m^2.

In addition to the quality characteristics mentioned in Fig. 4, RIVRO also paid some attention to feeding value. Comparisons of feeding value were based on crude-fibre and ash content. Maize quality hardly varies between hybrids according to these chemical analyses: close relationships were therefore found



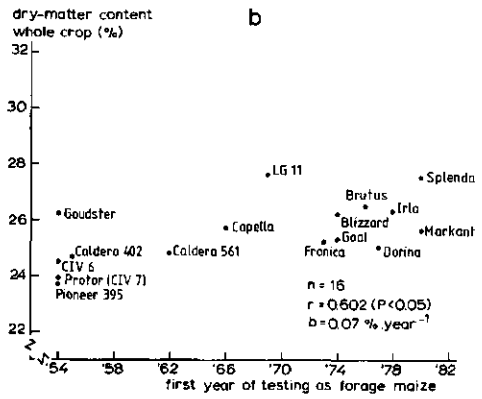


Fig. 4. Dry-matter content of the whole crop (a) and proportion of ear in the dry matter (b) in relation to the first year of testing as forage maize for the same hybrids as in Fig. 3. Data kindly provided by Ir. H.A. te Velde (RIVRO). Method as mentioned under Fig. 3. Note that the absolute values in this figure are low compared to the data in recent variety lists.

between relative dry-matter yield and relative starch-equivalent yield or relative VEM yield, calculated from crude-fibre and ash content (e.g. Ebskamp, 1981).

Deinum & Bakker (1981), however, showed that significant genetic differences in digestibility between hybrids from the collections submitted for agronomic testing did exist if digestibility was estimated by the in vitro disappearance of organic matter. Recent research indicates that the narrow-sence heritability of forage-maize digestibility may be high (Beerepoot, 1981; Deinum & Struik, 1982) and that the existence of genetic differences in

apparent digestibility found by means of in vitro digestion of fresh material can be confirmed by in vivo digestion trials on ensiled products (Deinum & Struik, 1982). Therefore RIVRO decided to present new figures on relative feed-unit yields, based on in vitro digestibility data (RIVRO, 1983).

Fig. 5 shows that the widespread lack of interest in the quality differences of forage maize and the use of misleading feed-evaluation techniques have resulted in new introductions having slightly but continuously lower digestibility values, whereas other characteristics have steadily improved.

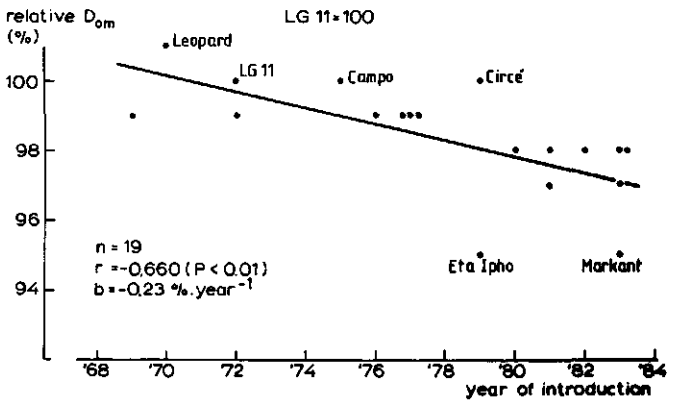


Fig. 5. Reduction of relative digestibility of the organic matter (D_{om}) resulting from the introduction of new varieties.

Yet it is possible to improve the digestibility of forage maize by breeding, without sacrifying much yield (Gallais et al., 1976; Deinum & Bakker, 1981), although Roth et al. (1970), Beerepoot (1981) and Gallais & Vincourt (1983) reported significant negative correlations between dry-matter yield and digestibility: these result from the negative correlation between yield and earliness (i.e. positive correlation between yield and cell-wall content).

If breeding programmes are to improve digestibility, special aspects of the morphology, anatomy and physiology of the maize plant must be known. Much information on the effects of physical factors influencing the quality of forages from the Gramineae family has already been collected (see e.g. reviews by Deinum, 1981; Wilson, 1982). Silage maize, however, needs special attention, because its physiology, production pattern and chemical composition

deviate from all other forages commonly used in North-West Europe, and are not fully understood.

This research aimed to gain insight into the ecophysiology of the plant, its development, its production, its distribution of dry matter and of chemical components, and the trend in whole-crop quality (dry-matter content, proportion of ear in the whole plant, digestibility). The possible inter-relations and interactions between these factors were also studied. These plant phenomena were investigated under controlled climatic conditions, with selected hybrids and certain cultural practices (cf. Fig. 2).

On the basis of data from the literature and the results described in Chapters 1 up to and including 6, the morphological and physiological characteristics of an ideal forage maize ('ideotype') for North-West Europe will be described and the suitability of the climate of this area for the production of forage maize of high quality will be evaluated.

These papers and descriptions should contribute to knowledge of the physiology, productivity and quality of forage maize in marginal and submarginal regions, to the understanding of cultural measures necessary to maximize the crop's potential and to developing selection criteria for breeding maize hybrids for forage production in North-West Europe. Moreover, they indicate that large-scale evaluation of the feeding value of maize silages for practical use can be replaced by a prediction based on climatic data and cultivation practice.

4. SOME NOTES ON ANALYTICAL PROCEDURES

4.1. *Dry-matter analysis and sampling problems*

This section describes the procedures used in field experiments. Phytotron experiments are not discussed because some steps were not necessary and there were fewer sampling problems because the plants were analysed quantitatively. The main source of variation in phytotron experiments therefore was plant-to-plant variability.

The complete procedure of processing and analysing maize in the field research was as follows:

1. harvest, i.e. cutting off and collecting the maize plants
2. transport and storage
3. separation into morphological fractions
4. determining fresh weight of the fractions

5. chopping
6. sampling
7. weighing the fresh samples
8. drying
9. weighing the dried samples
10. bulking
11. grinding
12. sampling and storing of the ground material
13. subsampling and chemical analysis of the ground material

Steps 4, 7 and 9 can be carried out without noticeable errors and therefore will not be discussed. All the other steps in the procedure are afflicted with an error, sometimes mainly systematic, sometimes mainly random. The relevance of these errors is presented in Table 2 and discussed below.

Step 1. Harvest

Plant-to-plant variability of maize is great (e.g. Deinum & Struik, 1980) especially in northern latitudes (Breeze & Milbourn, 1981), but it is similar to that in sugar beet and other non-tillering species. The variability, especially for ear characteristics generally increases with increasing plant densities (Glenn & Daynard, 1974; Edmeades & Daynard, 1979; Breeze & Milbourn, 1981). The frequency distribution of various plant parameters becomes bimodal instead of normal at high plant densities (Edmeades & Daynard, 1979; Daynard & Muldoon, 1983). Standard deviations increase as crop development progresses but coefficients of variation (CV) decline (Daynard & Muldoon, 1983). The decline in CV is also illustrated in Fig. 6 for dry-matter yield per plant (glasshouse experiment), plant height (field experiment) and dry-matter yield per plot (two field experiments). At the end of the growing season, 16-64 plants must be harvested to reduce the CV to 5%. My unpublished data suggest that the plant-to-plant variability in digestibility of the organic matter is very small in a uniform crop (CV = 1.55%, n = 10).

Because of the large plant-to-plant variability, a considerable amount of plant material must be collected in each plot on each sampling date. Therefore plots must be large. In addition, plots must be as homogeneous as possible and not be affected by surrounding plots or by vacant sites left from previous samplings (cf. Deinum & Struik, 1980). The latter requirement demands large borders (mostly 70-95% of the experimental area). The desired plot size therefore limits the number of plots that can be handled per

Table 2. Relevance of random and systematic errors and their sources.

	random error	systematic error			
		caused by process or conditions during process	selection by person	selection by machine	differential sedimentation caused by machine
Step in procedure					
harvest	++	+	±	-	-
transport + storage	-	+	-	-	-
separation into fractions	±	±	±	-	-
chopping	-	-	±	± or +	++
sampling	+	-	++	-	-
drying	-	±	-	-	-
bulking	-	±	-	-	-
grinding	-	±	±	+	++
resampling and storage	+	±	±	-	-
subsampling + analysis in chemistry lab.	++	±	±	±	-

- = irrelevant
+ = important
± = plays a minor role
++ = very important

experiment and makes demands on the facilities and man-power available. In the experiments reported in this thesis, plot size (excluding separation between blocks) ranged from 60-90 m^2. At least 4.5 m^2 was harvested per sampling date and per plot. The number of replicates ranged from 4-8.

Stubble height must be very uniform. In the reported experiments, plants were cut off just above soil level, thus excluding variation in stubble height. Fallen leaves and small tillers were also collected.

Conditions during harvesting (e.g. rainfall, dew) influence absolute values of plant characteristics such as dry-matter content. The relative differences between treatments were hardly affected by these conditions since the harvest took little time and because plots were sampled replicate by replicate.

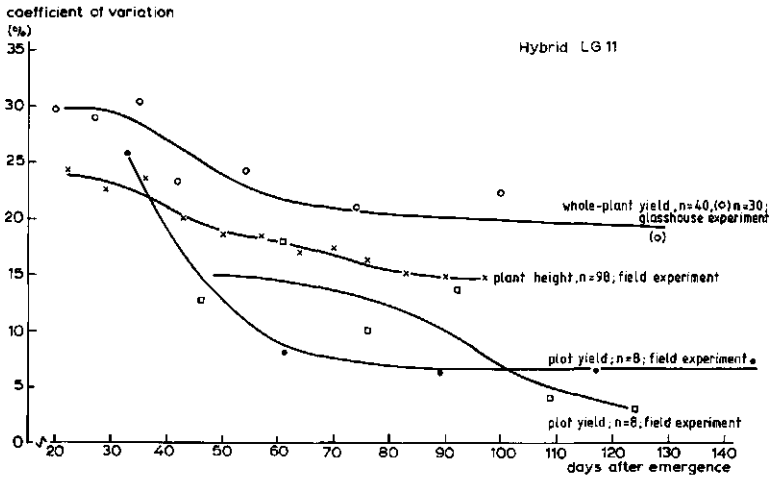


Fig. 6. Development over time of the coefficient of variation in different experiments. Per plot 4.5 m^2 was harvested (i.e. approx. 45 plants).

Step 2. Transport and storage

All field experiments were laid down within a radius of 7 km from the laboratory. Losses during transportation were therefore small.

In order to prevent losses of dry matter and of water, intact plant material was stored in a large cold chamber (temperature 2 - 3°C) during further processing. (Chopped material should even be stored in a deep freezer, since fermentation and rotting processes cause severe losses in this material within a very short time, even at temperatures just above freezing point.) Respiration losses and losses of water depend on the treatments applied in the experiment, as treatments affect the mass fractions of readily respirable and fermentable assimilates and of water: therefore the duration of storage was kept minimal. In addition, whenever possible ear samples were treated after stover and husk + shank samples, since ear samples lose water and dry matter at the slowest rate.

Step 3. Separation into fractions

Separation into plant fractions (mostly stover, top ear, lower ears, husk + shank) can be carried out without large errors if the criteria for separation are strict. Separation was therefore a very minor source of variation in dry-matter yield or quality of the fractions, except perhaps for the lower-ear fraction.

Step 5. Chopping

Chopping is necessary for proper sampling.

Ear samples were chopped in a strong vegetable cutter (0.7 kW) into particles of 0.5 - 1.0 cm. This cutter homogenizes the material in a horizontal direction, but vertically, differential sedimentation occurs. In addition, in early stages of ear development, material with a very low dry-matter content may accumulate in the head of the machine that protects the knives. In very late stages of ear development kernels can remain unchopped or even be swung out of the cutter. By chopping for a long time and covering the bowl, these problems might be minimized.

The capacity of this vegetable cutter is too small for large samples. To overcome this problem, sample size must be reduced by randomly selecting complete ears.

Stover and *husk + shank samples* were chopped with a tractor-mounted, stationary, 1-row chopper (FAHR MH 70; see Fig. 7). Samples of plants

harvested before silking, cannot be chopped with this chopper, since very wet material sticks in the machine. The rate of input, the power and the sharpness of the knives determine the particle size. Optimum particle size for the stover is 0.5 - 0.8 cm. Particles must be as spherical as possible. Dead leaves, however, remain uncut; pith is cut into small, spherical particles, which are very light, whereas the rind is chopped into thin, filamentous, oblong pieces. If the material is too wet, small amounts of the green leaves might lodge somewhere in the machine on their way from the knives to the end of the cyclone. Usually this effect is not very relevant. Husk + shank samples are not chopped well, especially when the material is very dry. The effect of chopping is then restricted to loosening the husks and chopping the (moister) shank.

Step 6. Sampling

The maize plant is composed of various differentiated structures, organs and tissues, each with its own dry-matter content, nutritive value, resistance to chopping and other physical or chemical characteristics (see e.g. Struik, 1982). Chopped maize is therefore a conglomeration of particles varying in shape, specific gravity and composition. This variation within the plant places constraints on proper sampling. The bias introduced by the sampler is particularly large. These constraints can be reduced considerably by separating the plant into the four fractions mentioned earlier, and then chopping and sampling them separately. However, when discussing step 5 it was already noted that the chopping process itself selects, fractionates and causes differences in shape, size and specific gravity and thus even relatively uniform material is differentially sedimented. This effect of chopping is most pronounced for stover samples but also occurs when ears are chopped. Careful mixing of the material is therefore crucial. In these experiments, ear samples were mixed by the vegetable cutter itself (see above). To eliminate the adverse effects of the cutter, the wet material in the head of the machine must be redistributed and samples must consist of a complete segment of the contents of the bowl. If samples are taken this way, no problems should arise. However, samples of stover and husk + shank must be mixed after chopping. In the procedure used in the present trials this was done by using a concrete mixer. The chopped material was transported from the cyclone on the chopper into the concrete mixer by a conveyor belt modified for this purpose (see Fig. 7). Samples must be taken from the stream of material while the mixer is being emptied, to avoid discrimination by handpicking.

Sample size is a compromise between drying capacity and accuracy. Large samples reduce random errors but increase systematic errors during drying and reduce drying capacity. If mixing is done properly, the ideal sample size is approx. 500 - 750 g fresh weight.

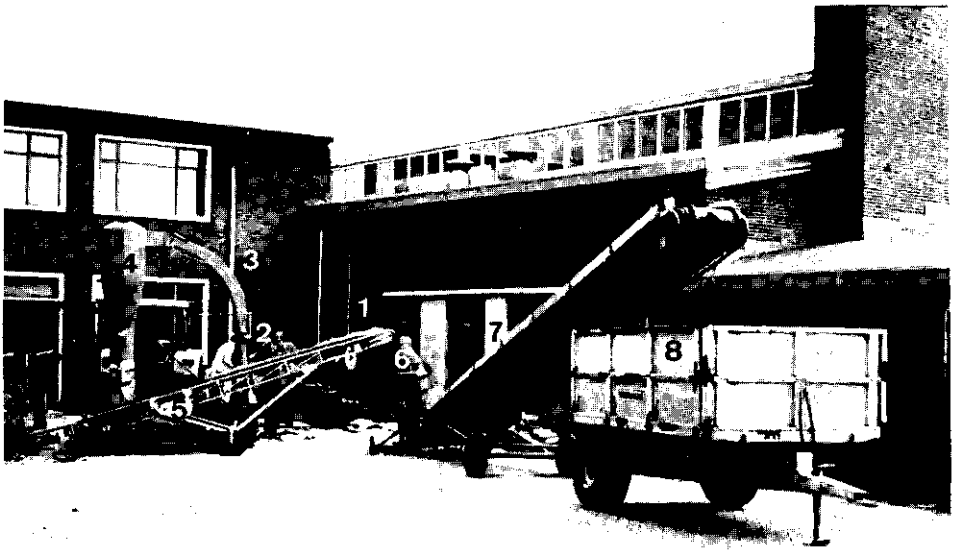


Fig. 7. Chopping procedure for samples of stover and husk + shank.
1 = balance; 2 = input; 3 = transport of chopped material by jet of air;
4 = cyclone; 5 = conveyor belt 1; 6 = concrete mixer; 7 = conveyor belt 2;
8 = waggon for wastes.
(Photograph by Dr.ir. B. Deinum)

Step 8. Drying

Drying in the oven must be rapid to prevent biological processes changing the chemical composition and reducing the dry weight of the sample. The temperature of the material, however, should not exceed 70°C if certain chemical analyses are required. Samples were therefore placed in pre-heated ovens immediately after fresh weighing of each individual sample. By spreading the samples thinly over large aluminium trays, maximum contact with the hot

air was achieved. If necessary, the material was shaken about during drying. The temperature of the oven was checked regularly. Each dried sample was weighed as soon as it had been taken out of the heated oven. Thus no acclimatization to the air occurred. Since samples were weighed after reaching constant weight at 70°C, the dry-matter content of the samples during weighing was approximately 99%.

Step 10. Bulking

To reduce the number of samples for chemical analysis, samples of the replicates were bulked per treatment and per fraction after assessing the dry weight. The sample size must be uniform to prevent overrepresentation of certain replicates. This is only relevant if block effects cannot be ignored.

Step 11. Grinding

Samples of a certain fraction must always be ground on the same mill, since the shape and size of the particles are important characteristics for subsampling and chemical and biological analyses.

During grinding, samples must be dry. If they are temporarily stored before grinding they should be re-dried to enable grinding without undesired heat generation. Re-drying is permissible because the dry weights are already determined and dry-matter contents are re-assessed in the chemistry laboratory. Rate of input is very important to prevent heat generation, to reduce fractionation and to obtain uniform and small particles. Grinding should not be too short, i.e. should last until the mill is completely empty. Standardizing of the duration of grinding produces systematic errors! Like the chopping machines, the hammer mills used for grinding select and fractionate. Different structures and tissues show different resistance to grinding. Cobs, midribs, shanks and rind are hard to grind, whereas leaf mesophyll and pith pass through the 1 mm sieves very rapidly. In addition, differential sedimentation occurs because of differences in specific gravity. Before resampling this selection, fractionation and differential sedimentation must be overcome by mixing.

Step 12. Sampling and storage of the ground material

Careful mixing of the meal after grinding is necessary. When the bulk of meal is too large and if the meal is not too dusty, it can be subsampled using a proper dividing device.

The sample bags or flasks should be made of an inert material impervious

to all chemical components. The samples should be stored in chambers with low relative humidity of the air and free from pests and other kinds of damaging organisms. If long-term storage is desired, the chambers should be decontaminated regularly with gaseous disinfectants. Insects are particularly selective in their choice of samples to infest: starch content, for example, proved to be predictable on the basis of the number of larvae in the sample after protracted storage in sealed plastic bags.

Step 13. Subsampling and chemical analysis

Another crucial step in subsampling is carried out in the chemistry laboratory. The shape, volume and degree of filling of the sample bags or flasks determine the possibility of mixing and therefore affect the accurate subsampling of the meal. The error made during this final subsampling is probably predominantly random.

Most of the analyses were finally done with 0.5 g of material. This 0.5 g is believed to be representative of dozens of kilograms of harvested material. It therefore goes without saying that all stages of sampling require great accuracy, alertness and continuous criticism: sampling is certainly the major source of errors and inaccuracies in the entire procedure. The random errors made during chemical and biological analyses are very minor in comparison with other sources of variation. Some systematic errors may be made, e.g. during analysis of cell-wall components (see e.g. Van Soest & Robertson, 1980), content of non-structural carbohydrates and organic-matter digestibility. The latter will be discussed in the next section of this thesis.

4.2. *Evaluation of quality*

4.2.1. Introduction

The evaluation of forages for their quality is mostly based on methods of estimating the indigestible mass fraction. The absolute digestibility can only be ascertained by means of digestion trials with animals. These trials are expensive, laborious and time-consuming, and the amounts of forage required are large. In addition, standard deviations are high, especially in the case of forage maize, because of large variation between animals (Deinum et al., 1983).

Therefore, numerous laboratory procedures have been developed to estimate the indigestible fraction. Below I shall discuss why I mainly evaluated quality in terms of in vitro digestibility and cell-wall content.

A plant is composed of cell walls and cellular contents. The cellular contents are almost completely digestible (e.g. Van Soest, 1967); this means that the indigestible matter is located in the plant cell wall. Digestibility can therefore be estimated by chemical analyses involving crude fibre, cell walls or cell-wall components. Of these analyses, determinations of acid-detergent fibre give the highest correlations with digestibility (e.g. Van Soest, 1965; Mertens, 1973; Marten et al., 1975). By means of regression models using summative calculations a fair estimate of crop quality can be made (Lucas et al., 1961; Van Soest, 1967; Deinum & Van Soest, 1969; van der Koelen & van Es, 1973). Because of the numerous analyses involved, these methods are unpractical: they are not sufficiently accurate to be applied for quality prediction in this study.

However, chemical analysis cannot reveal the digestibility of a forage, since there is no chemical method that will fractionate the carbohydrates of the cell wall into digestible and indigestible fractions, and since structural features of the cell wall also affect the digestibility (Van Soest, 1976).

Therefore biological procedures involving the in vitro incubation of forage material in rumen liquor have been developed enabling forage digestibility to be accurately predicted. The most popular techniques are those of Tilley & Terry (1963) and Van Soest et al. (1966). Both systems need calibration as described by van der Meer (1980). The method of Van Soest et al. is the most elegant, for it yields the indigestible fraction of the cell walls and thus the true digestibility of the cell walls can also be estimated when cell-wall content and ash content are known. In vitro rumen fermentation methods have been recognized as the most suitable methods for predicting in vivo digestibility (e.g. Deinum & Van Soest, 1969; van der Koelen & van Es, 1973; Schmid et al., 1975; Van Soest, 1976; Aerts et al., 1977; van Es, 1979; Marten & Barnes, 1980). However, the in vitro technique results in a final value for crop quality that gives no inkling of the origins of the differences in digestibility observed. Further chemical analysis must reveal these causes. Moreover, at high levels of feed intake, feed efficiency and rate of digestion are more relevant than possible extent of digestion. Intake is related more to the cell-wall content (e.g. Van Soest, 1965, 1976; Van Soest & Robertson, 1980; Waldo & Jorgensen, 1981), rate of digestion (Donefer et al., 1960; Van Soest, 1976; Van Soest et al., 1978; Waldo & Jorgensen, 1981) or cell-wall bulk density (van der Aar et al., 1981) than to the extent that the feedstuff is digested (i.e. its digestibility).

New developments in the evaluation of feed quality are:

- the use of enzyme preparations (e.g. McQueen & Van Soest, 1975; Jones, 1976; Barthiaux-Thill et al., 1980a,b; Marten & Barnes, 1980; Dowman & Collins, 1982)
- near-infrared reflectance (e.g. Norris et al., 1976; Shenk et al., 1979; Barton & Burdick, 1981; Shenk et al., 1981; Templeton et al., 1981)
- gas production during incubation with rumen liquor (Menke et al., 1979; Dinkelaker et al., 1980).

The merits of these procedures need further evaluation.

Because it is accurate, elegant, reliable and tried, I used the method of Van Soest et al. (1966) as the basic technique for evaluating quality.

4.2.2. Restrictions of the in vitro digestibility technique

The sampling problems described in 4.1. had to be overcome to ensure that the results of chemical and biological analyses were reliable. In addition, all procedures had to be precisely standardized. Nevertheless, some sources of variation and inaccuracy probably remained and limited the reliability of the data on digestibility:

- Differences between in vitro runs.
  To prevent this, all samples of a harvest have to be analysed within one run. Sometimes a small, but significant difference was found between the values of certain samples analysed in different runs, even after calibration.
- Differences within in vitro runs.
  Standard samples of known in vivo digestibility should be re-analysed several times throughout one run. It was found that values of these standard samples were sometimes lower at the end of the run than at the beginning, especially for samples with a low digestibility. Repeated analysis of one sample 10 times throughout a run showed that differences within a run are not consistently relevant (CV only approx. 1.5%; n = 10). Nevertheless, the effects of such small differences for the calibration curve can be considerable.
- Standard deviations of digestibility of the organic matter of poorly digestible samples were often larger than standard deviations found for very digestible samples. The opposite was true for digestibility of cell walls, since this is calculated from the residue of undigested cell-wall components. This residue is small - and thus afflicted with a great relative error - when digestibility is high.
- Standard samples and experimental samples should be from the same plant

species; standard samples should cover the entire range of the experimental samples. Unfortunately, this is not always possible.

- At least five (reliable!) standard samples should be analysed in each run, preferably in triplicate or quadruplicate.
- Severe contamination with soil (e.g. occurring in harvests of very young plants) may result in a smaller reproducibility.
- The ratio of sample size: amount of inoculum, and the mean particle size and the particle-size distribution may affect the rate and extent of digestion, especially in very fibrous material.

Nevertheless, if the regression line between in vitro and in vivo digestibility can be assessed accurately, the in vitro data will be more reliable and more reproducible then the in vivo data. It is therefore essential to have many standard samples whose in vivo digestibility is indisputable.

5. REFERENCES

Aar, P.J. van der, H. Boer, B. Deinum & G. Hof, 1981. Bulk volume: a parameter for measuring forage quality and its influence on voluntary intake. In: J.A. Smith & V.W. Hays (eds.), Proc. XIVth int. Grassld Congr., Lexington, Ky, pp. 502-505.

Aerts, J.V., D.L. De Brabander, B.G. Cottyn & F.X. Buysse, 1977. Comparison of laboratory methods for predicting the organic matter digestibility of forage. Anim. Feed Sci. Technol. 2: 337-349.

Barthiaux-Thill, N., R. Biston & J. Fabry, 1980a. Estimation in vitro de la digestibilité de l'herbe de prairie permanente par la cellulase. 1. Examen de quelques facteurs susceptibles de modifier l'importance de l'attaque cellulasique. Bull. Rech. Agron. Gembloux 15: 277-296.

Barthiaux-Thill, N., J. Fabry, R. Biston & M. Boukharta, 1980b. Estimation in vitro de la digestibilité de l'herbe de prairie permanente par la cellulase. 2. Corrélations avec la digestibilité mesurée in vivo ou estimée in vitro selon Tilley et Terry. Bull. Rech. Agron. Gembloux 15: 297-308.

Barton, F.E. II & D. Burdick, 1981. Prediction of forage quality with NIR reflectance spectroscopy. In: J.A. Smith & V.W. Hays (eds.), Proc. XIVth int. Grassld Congr., Lexington, Ky, pp. 532-534.

Becker, W.R., 1976. Mais. Een handleiding voor de teelt van korrel- en snijmais. P.A. publicatie nr. 21, pp. 1-84.

Beerepoot, L.J., 1981. De genetische variatie in verteerbaarheid van snijmais. Scriptie Vakgroep Landbouwplantenteelt & Graslandkunde, Agric. Univ., Wageningen, pp. 1-43.

Blanco, J.L., 1976. Selection objectives for maximum yields of feed with hybrid maize. Anim. Feed Sci. Technol. 1: 245-250.

Bonnett, O.T., 1966. Inflorescences of maize, wheat, rye, barley and oats: their initiation and development. Univ. Ill. agric. Exp. Stn Bull. 721, pp. 5-30.

Breeze, V.G. & G.M. Milbourn, 1981. Inter-plant variation in temperate crops of maize. Ann. appl. Biol. 99: 335-352.

Bunting, E.S., 1980. History of the maize crop in N.W. Europe. In: E.S. Bunting (ed.), Production and utilization of the maize crop. Proc. First European Maize Congress, Cambridge, England, Hereward & Stourdale Press, Ely, pp. 3-13.

Daynard, T.B. & W.G. Duncan, 1969. The black layer and grain maturity in corn. Crop Sci. 9: 473-476.

Daynard, T.B. & J.F. Muldoon, 1983. Plant-to-plant variability of maize plants grown at different densities. Can. J. Plant Sci. 63: 45-59.

Deinum, B., 1981. The influence of physical factors on the nutrient content of forages. Mededelingen Landbouwhogeschool Wageningen 81-5, pp. 1-18.

Deinum, B. & J.J. Bakker, 1981. Genetic differences in digestibility of forage maize hybrids. Neth. J. agric. Sci. 29: 93-98.

Deinum, B., A. Steg & G. Hof, 1983. Measurement and prediction of digestibility of forage maize in The Netherlands. Anim. Feed Sci. Technol. 8 (in press).

Deinum, B. & P.C. Struik, 1980. Harvesting field experiments for silage maize. In: J. Dijkstra & A. van Santen (eds.), Proc. 5th int. Conf. on Mechanization of Field Experiments, Wageningen, pp. 231-236.

Deinum, B. & P.C. Struik, 1982. Productivity and nutritive value of forage maize. In: H.J. Oslage & R. Daccord (eds.), Proc. Seminar on COST-PROJECT 82 'Maize as basic feed for beef production', Grangeneuve, Switzerland, pp. 8-16.

Deinum, B. & P.J. Van Soest, 1969. Prediction of forage digestibility from some laboratory procedures. Neth. J. agric. Sci. 17: 119-127.

Dinkelaker, J., K.H. Menke, F. Gross, W.G. Pollmer & D. Klein, 1980. Evaluation of the feeding value of maize for silage use by the gas production method. Preliminary results. In: W.G. Pollmer & R.H. Phipps (eds.), Improvement of quality traits of maize for grain and silage use. Martinus Nijhoff, The Hague, pp. 477-489.

Donefer, E., E.W. Crampton & L.E. Lloyd, 1960. Prediction of the nutritive value index of a forage from in vitro rumen fermentation data. J. Anim. Sci. 19: 545-552.

Dowman, M.G. & F.C. Collins, 1982. The use of enzymes to predict the digestibility of animal feeds. J. Sci. Food Agric. 33: 689-696.

Duncan, W.G., 1975. Maize. In: L.T. Evans (ed.), Crop physiology. Some case histories. Cambridge University Press, London, pp. 23-50.

Ebskamp, A.G., 1981. Het cultuurwaardeonderzoek van snijmaisrassen in Nederland. (II). Criteria bij de beoordeling van snijmaisrassen. Bedrijfsontwikkeling 12: 269-275.

Edmeades, G.O. & T.B. Daynard, 1979. The development of plant-to-plant variability in maize at different densities. Can. J. Plant Sci. 59: 561-576.

Es, A.J.H. van, 1979. International workshop on the standardization of techniques in feedingstuffs analysis, Ottawa, 12-14 March 1979. Intern Rapport no. 129, I.V.V.O. 'Hoorn', Lelystad, pp. 1-15.

Galinat, W.C., 1971. The origin of maize. Ann. Rev. Genetics 5: 447-478.

Gallais, A., M. Pollacsek & L. Huguet, 1976. Possibilités de sélection du maïs en tant que plante fourragère. Ann. Amélior. Plantes 26: 591-605.

Gallais, A. & P. Vincourt, 1983. Possibilités d'amélioration du rendement en matière sèche du maïs ensilage. Colloque 'Physiologie du maïs', Royan 15-17 Mars 1983.

Glenn, F.B. & T.B. Daynard, 1974. Effects of genotype, planting pattern, and plant density on plant-to-plant variability and grain yield of corn. Can. J. Plant Sci. 54: 323-330.

Jones, D.I.H., 1976. Fungal cellulases and hemicellulases and their application to the analysis of forage. In: Carbohydrate research in plants and animals. Misc. Papers no. 12, Agric. Univ., Wageningen, pp. 67-77.

Kiesselbach, T.A., 1949. The structure and reproduction of corn. Res. Bull. Univ. Nebr. agric. Exp. Stn 161.

Kiesselbach, T.A. & E.R. Walker, 1952. Structure of certain specialized tissues in the kernel of corn. Amer. J. Bot. 39: 561-569.

Koelen, C.J. van der & A.J.H. van Es, 1973. A comparison of some laboratory techniques for the estimation of the digestibility of the organic matter in forage samples. Neth. J. agric. Sci. 21: 199-205.

Lucas, H.L., Jr., W.W.G. Smart, Jr., M.A. Cipollini & H.D. Gross, 1961. Relations between digestibility and composition of feeds and foods. S-45 Report, North Carolina State College (Mimeo).

Marten, G.C. & R.F. Barnes, 1980. Prediction of energy digestibility of forages with in vitro rumen fermentation and fungal enzyme systems. In: W.J. Pigden, C.C. Balch & M. Graham (eds.), Proc. Workshop Ottawa. Standardization of analytical methodology for feeds. IDRC - 134e Int. Develop. Res. Centre, Ottawa, pp. 61-71.

Marten, G.C., R.D. Goodrich, A.R. Schmid, J.C. Meiske, R.M. Jordan & J.C. Linn, 1975. Evaluation of laboratory methods for determining quality of corn and sorghum silages. II. Chemical methods for predicting in vivo digestibility. Agron. J. 67: 247-251.

McQueen, R.E. & P.J. Van Soest, 1975. Fungal cellulase and hemicellulase prediction of forage digestibility. J. Dairy Sci. 58: 1482-1491.

Meer, J.M. van der, 1980. Determination of the 'in vitro' digestibility for the prediction of the 'in vivo organic matter digestibility coefficient' of feeds for ruminants. Documentation report no. 67, I.V.V.O. 'Hoorn', Lelystad, pp. 1-12.

Menke, K.H., L. Raab, A. Salewski, H. Steingass & W. Schneider, 1979. The estimation of the digestibility and metabolizable energy content of ruminant feedingstuffs from the gas production when they are incubated with rumen liquor in vitro. J. agric. Sci., Camb. 93: 217-222.

Mertens, D.R., 1973. Application of theoretical mathematical models to cell-wall digestion and forage intake in ruminants. Ph.D. thesis, Cornell Univ., Ithaca, N.Y.

Miller, E.C., 1919. Development of the pistillate spikelet and fertilization in *Zea mays* L. J. agric. Res. 28: 255-265.

Norris, K.H., R.F. Barnes, J.E. Moore & J.S. Shenk, 1976. Predicting forage quality by infrared reflectance spectroscopy. J. Anim. Sci. 43: 889-897.

Rijksinstituut voor het Rassenonderzoek van Cultuurgewassen (RIVRO), 1963 up to and including 1983. 38e t/m 58e Beschrijvende rassenlijst voor landbouwgewassen, Leiter-Nypels, Maastricht.

Roth, L.S., G.C. Marten, W.A. Compton & D.D. Stuthman, 1970. Genetic variation of quality traits in maize forage (*Zea mays* L.). Crop Sci. 10: 365-367.

Scheijgrond, W., 1978. Ontwikkelingen in het rassensortiment van landbouwgewassen sedert de oprichting van de Studiekring voor Plantenveredeling. Zaadbelangen 32: 226-231.

Schmid, A.R., R.D. Goodrich, G.C. Marten, J.C. Meiske, R.M. Jordan & J.L. Halgerson, 1975. Evaluation of laboratory methods for determining quality of corn and sorghum silages. I. Biological methods for predicting in vivo digestibility. Agron. J. 67: 243-246.

Schuster, W., W. Schreiner & G.R. Müller, 1977. Über die Ertragssteigerung bei einigen Kulturpflanzen in den letzten 24 Jahren in der Bundesrepublik Deutschland. Z. Acker- u. PflBau 145: 119-141.

Shenk, J.S., I. Landa, M.R. Hoover & M.O. Westerhaus, 1981. Description and evaluation of a Near Infrared Spectro-Computer for forage and grain analysis. Crop Sci. 21: 355-358.

Shenk, J.S., M.O. Westerhaus & M.R. Hoover, 1979. Analysis of forages by infrared reflectance. J. Dairy Sci. 62: 807-812.

Struik, P.C., 1982. Production pattern, chemical composition and digestibility of forage maize (*Zea mays* L.). Mededeling no. 64, LH, Vakgroep Landbouwplantenteelt & Graslandkunde, Wageningen, Netherlands, pp. 1-28.

Templeton, W.J., Jr., J.S. Shenk, K.H. Norris, G.W. Fissel, G.C. Marten, J.H. Elgin, Jr. & M.O. Westerhaus, 1981. Forage analysis with Near-Infrared Reflectance Spectroscopy: Status and outline of national research project. In: J.A. Smith & V.W. Hays (eds.), Proc. XIVth int. Grassld Congr., Lexington, Ky, pp. 528-531.

Tilley, J.M.A. & R.A. Terry, 1963. A two-stage technique for the in vitro digestion of forage crops. J. Brit. Grassld Soc. 18: 104-111.

Van Soest, P.J., 1965. Symposium on factors influencing the voluntary intake of herbage by ruminants: Voluntary intake in relation to chemical composition and digestibility. J. Anim. Sci. 24: 834-843.

Van Soest, P.J., 1967. Development of a comprehensive system of feed analyses and its application to forages. J. Anim. Sci. 26: 119-128.

Van Soest, P.J., 1976. The estimation of digestibility from chemical composition. In: Carbohydrate research in plants and animals. Misc. Papers nr. 12, Agric. Univ., Wageningen, pp. 137-145.

Van Soest, P.J., D.R. Mertens & B. Deinum, 1978. Preharvest factors influencing quality of conserved forage. J. Anim. Sci. 47: 712-720.

Van Soest, P.J. & J.B. Robertson, 1980. Systems of analysis for evaluating fibrous feeds. In: W.J. Pigden, C.C. Balch & M. Graham (eds.), Standardization of analytical methodology for feeds. IDRC-134e Int. Develop. Res. Centre, Ottawa, pp. 49-60.

Van Soest, P.J., R.H. Wine & L.A. Moore, 1966. Estimation of true digestibility of forages by the in vitro digestion of cell walls. Proc. Xth int. Grassld Congr. Helsinki, pp. 438-441.

Velde, H.A. te, 1983. Constraints on maize production in northern latitudes. Proc. 2nd int. Summer School in Agriculture, "Cereal production". (ed.) E. Gallagher, Royal Dublin Society (in press).

Waldo, D.R. & N.A. Jorgensen, 1981. Forages for high animal production: nutritional factors and effects of conservation. J. Dairy Sci. 64: 1207-1229.

Wilson, J.R., 1982. Environmental and nutritional factors affecting herbage quality. In: J.B. Hacker (ed.), Nutritional limits to animal production from pastures. Farnham Royal U.K., Commonwealth Agricultural Bureaux, pp. 111-131.

Zuber, M.S., T.R. Colbert & L.L. Darrah, 1980. Effect of recurrent selection for crushing strength on several stalk components in maize. Crop Sci. 20: 711-717.

CHAPTER 1
PRODUCTION PATTERN, CHEMICAL COMPOSITION AND DIGESTIBILITY OF FORAGE MAIZE (*ZEA MAYS* L.)

P.C. Struik
Department of Field Crops and Grassland Science
Agricultural University
Wageningen, Netherlands.

Key words: forage maize, production pattern, yield, chemical composition, quality, digestibility, sowing time, hybrid, brown midrib

Summary

Four silage-maize hybrids, differing in rate of grain filling and whole-crop digestibility were sown on two dates. Production and quality traits were estimated five times during the growing season. Differences in yield between hybrids were relatively small. Differences in quality were caused by differences in cell-wall quality and arose during the construction of the vegetative organs. Differences in yield and quality between the crops sown on the two sowing dates were mainly caused by differences in the amount of carbohydrates produced in the post-silking period. This period was approximately two weeks shorter for the later-sown crops.

In a concomitant trial, two contrasting commercial hybrids and three brown-midrib (bm_3) hybrids were grown. The plants were separated into ten morphological fractions, which were analysed for dry-matter content, yield and quality. The dry-matter content of the fractions varied greatly within one plant and between hybrids. Inter-hybrid differences in the proportion of dry matter in the fractions were of minor importance for the quality of the whole crop. Except for the kernels, the *in-vitro* digestibility of the organic matter differed greatly for all fractions and was mostly best for bm_3 genotypes. Differences between the two commercial hybrids, however, were also relevant. These differences resulted from differences in cell-wall content and cell-wall quality. The digestibility of the cell walls was the main factor that determined the whole-crop digestibility of each hybrid, although differences between brown-midrib genotypes were completely attributable to differences in cell-wall content. *In-vivo* digestion trials confirmed these results.

Introduction

The area under forage maize has expanded rapidly in North-West Europe in recent decades. Initially, all the hybrids available were for grain production. Even now, several European countries do not have special variety lists for forage maize. Yet the requirements for a grain crop are not the same as those for a forage crop because they are used for very different purposes and they are grown in different ways. Much attention has been paid to the relevance of ear development and grain filling for the yielding ability and quality (dry-matter content, digestibility, feed intake etc.) of forage maize (Bunting, 1975, 1976, 1977; Deinum & Knoppers, 1979; Gross, 1980). These studies suggest that the effects of grain filling on yield are minor in most years; the whole-crop digestibility of a grainless crop may be lower, and the dry-matter content of the whole crop is positively influenced by grain filling. Ear development and subsequent grain filling are less important in North-West Europe than in the U.S.A. or in tropical or subtropical regions. The ratio of non-structural carbohydrates to structural material, which is affected by cell-wall production and total production, changes during grain filling. Because the digestibility of the non-structural carbohydrates is almost 100% and the digestibility of the structural material (cell-wall constituents: hemicellulose, cellulose, lignin and silica) is much lower, this could have a great impact on the digestibility of the whole crop. But the quality of the structural material is not constant. Cell-wall digestibility is strongly affected by climatic factors (mainly temperature), cutting date, genotype and cultural practice. Fig. 1 shows an example of the development over time of the main plant characters that influence whole-crop digestibility.

Cell-wall content increases until flowering, remains constant for a while after this stage and decreases during later stages of grain filling. The digestibility of the organic matter declines rapidly in the pre-silking period and then, in this example, increases slightly. The decline in cell-wall digestibility is less after flowering than before. In Fig. 1 this decline is compensated for by the increase in ear content, which causes the content of the less digestible cell walls to decrease. Genotypic differences in this pattern are likely.

Recently, breeding programmes to improve the quality of the vegetative parts of maize have been started in several countries. Striking results have been obtained from the brown-midrib genes, which lower the lignin content and therefore improve the digestibility of the cell walls. In the Netherlands,

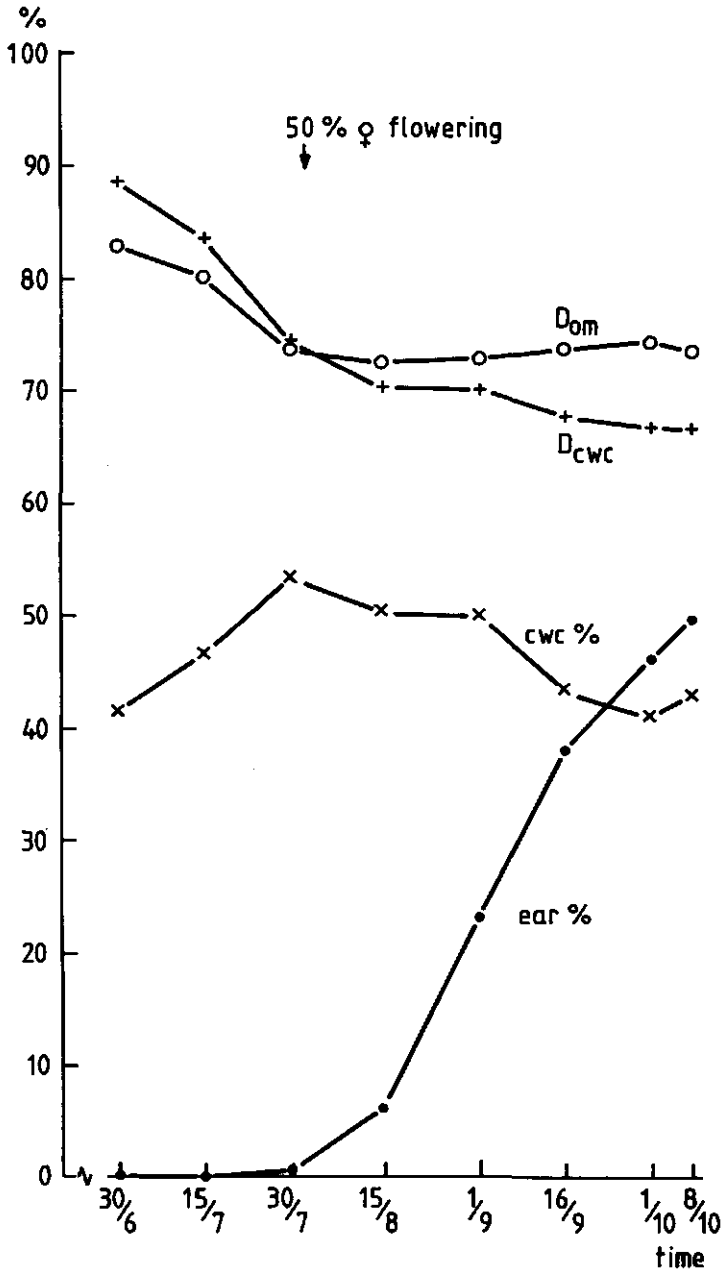


Fig. 1. Ear content (ear%), cell-wall content in dry matter (cwc%), apparent digestibility of organic matter (D_{om}) and cell-wall digestibility (D_{cwc}) as a function of time. Hybrid LG 11; location Achterberg, Netherlands; year 1980; plant density 10 m^{-2}.

a research programme has been started to investigate the relationship between production pattern and quality of forage maize under different climatic conditions. In one of the first trials, we investigated how production and quality developed during the growing season in four hybrids sown on two different dates. At the same location, two commercial hybrids and three bm_3 synthetics were grown and separated into a number of morphological fractions so that the most important quality differences could be identified. This paper reports on these trials.

Materials and methods

Trial 1. Four hybrids were selected on the basis of their whole-crop digestibility and dry-matter content of the ear. For many years LG 11 and Fronica were the dominant varieties in the Netherlands. Eta Ipho is used on limited scale. Nicco is not of any practical importance under Dutch conditions, since the dry-matter content of the whole crop is normally too low to make good silage. All four hybrids are described by the Bundessortenamt in 1980. The hybrids were sown in sandy soil on two dates: 26 April and 28 May 1979, in a split-plot design, with sowing time as main treatment and with six replicates. Fertilization (both organic and inorganic), weed and disease control were optimum. Originally the plant density was 16 m^{-2} (row distance 75 cm). The number of seedlings was reduced to 10 m^{-2} 3 - 4 weeks after emergence. The plants that had been removed were used for the first sample. On four other sampling dates one row 6 m long (i.e. 4.5 m^2 or about 45 plants) was harvested from each plot. Plot size was 9 m x 10 m with two border rows on both sides of the plot and one row separating the rows intended for sampling. One extra net row was used for additional measurements at final sampling.

Before the estimation of the fresh weight, samples were separated into four fractions: top ear, lower ears if visible in the axils of the leaf blades, husks + shanks, and stover (stem, tassel and leaves). With earlier samplings whole plants were chopped with a vegetable cutter. With later samplings the ears were chopped with the same machine but the husks + shanks and the stover were chopped with a stationary ordinary 1-row Fahr MH 70 chopper (tractor-mounted). The chopped material was blown in a jet of air over a conveyor belt, which transported it into a concrete mixer. Subsamples were taken from the stream of material while emptying the mixer. Although time-consuming, this method gave minimal random and systematical errors in estimating the

dry-matter content of the whole crop (see Deinum & Struik, 1980) and provided much additional information.
After subsampling, the material was dried to constant weight in forced ventilated ovens at 70 °C. Samples of the six replicates were bulked per plant part and per treatment and ground in hammer mills with 1 mm sieves. Samples were analysed for true digestibility *in-vitro* of the organic matter, using the method of Van Soest et al. (1966). By recourse to a series of standard maize samples with known *in-vivo* digestibility for sheep, conversion could be made to apparent digestibility of organic matter (D_{om}). Cell-wall constituents (cwc) were estimated according to Van Soest's (1977) method. Cell-wall digestibility was calculated from true digestibility, cell-wall content and ash content.
Further analysis revealed the contents of crude protein (N % x 6.25), water-soluble carbohydrates (with ferricyanide), total non-structural carbohydrates (starch + water-soluble carbohydrates), Ca, P, K and residue (100-(crude protein + ash + total non-structural carbohydrates + cell walls)).
Some additional information was collected during the growing season. Leaf area was measured at silking, using the length * maximum width * 0.75 method (Montgomery, 1911). Because the area of all leaf numbers was estimated, the post-silking duration of leaf area could be estimated by counting the number of green leaves weekly. Leaf angles were estimated with a clinometer (Whigham & Woolley, 1974).
Plant height and number of leaves were measured weekly. Length and maximum width of the top ear were estimated once during grain filling.

Trial 2. At the same location, large plots of the following genotypes were sown on 26 April: Eta Ipho, Circé (both described by Rijksinstituut voor het Rassenonderzoek van Cultuurgewassen, 1982), INRA 240 bm_3, INRA 188 bm_3 and LG 11 bm_3. Seed of the bm_3 genotypes was kindly provided by Dr A. Gallais (INRA, France). For the description of these genotypes, see Gallais et al., 1980.
The density was 7 $pl.m^{-2}$. For each genotype 20 plants were harvested on 11 October and separated into tassel, kernel of the top ear, rachis of the top ear, kernel of lower ears, rachis of lower ears, husk + shank, leaf midribs, rest of leaf blades, leaf sheath, stem rind, stem pith and tiller. Material was chopped in a vegetable cutter and dried at 70 °C. Dried samples were treated as described for Trial 1. Top ears and lower ears were analysed

separately, but the results will be presented together.
The crops left on the plots after sampling were used for making silage from Eta Ipho, Circé and bm_3 material for *in-vivo* digestion studies.

Results and discussion

Weather. The 1979 season was cool with excessive rain during May and June (Table 1). Moreover, the precipitation in June was concentrated in short periods (once 100 mm fell in 2 days). The other months were dry. Radiation was about average. Damaging frosts did not occur at the trial site.

Table 1. Weather at Wageningen in 1979 and means over the period 1931-1960 at De Bilt.

Month	Solar irradiance J. cm^{-2}		Average temperature °C		Rainfall mm	
	mean	1979	mean	1979	mean	1979
May	51779	51593	12.4	11.7	52	75.7
June	53108	49272	15.5	15.0	57	148.4
July	47754	46118	17.0	15.8	78	31.4
August	41525	40918	16.8	15.3	89	84.8
September	30390	33225	14.3	13.2	71	17.8
October	17707	19399	10.0	10.8	72	36.6

Trial 1

Plant measurements: Early development, as expressed by number of visible leaves and plant height, was faster for Eta Ipho and Fronica than for LG 11 and Nicco. Table 2 shows some plant characteristics. Differences between sowing dates are not of great relevance for these characteristics except for the ear size. Eta Ipho appeared to be a tall genotype with small ears; this was especially apparent in the later-sown crop. The leaf area was rather small. Its upper leaves had relatively large leaf angles and were stiff. Eta Ipho thus showed the typical leaf arrangement of the ideotype described by Mock & Pearce (1975). LG 11 was short with a small leaf area. Since the leaves of this hybrid also died earlier, the post-silking duration of leaf area was much shorter for LG 11 than for the other hybrids. For the later sowing date these differences were less pronounced. Fronica was tall

and had a large leaf area and showed a slow but good ear development. Nicco proved to be a stocky hybrid with wide leaves and large ears.

Table 2. Final plant height, number of leaves, leaf area and ear size of four hybrids sown on 26 April and 28 May.

Hybrid	Eta Ipho	LG 11	Fronica	Nicco
Sowing date: 26/4				
Plant height (cm)	238	217	238	208
Number of leaves	14.5	14.2	15.2	14.4
Leaf area at silking (m^2/m^2)	3.73	3.48	4.78	4.28
Post-silking duration of leaf area (m^2/m^2.days)	204	153	227	203
Length of top ear (cm)	16.2	17.0	16.6	18.0
Maximum width of top ear (cm)	4.1	4.3	4.6	4.7
Sowing date: 28/5				
Plant height (cm)	232	214	236	207
Number of leaves	14.4	14.0	15.0	14.1
Leaf area at silking (m^2/m^2)	3.88	3.84	4.80	4.25
Post-silking duration of leaf area (m^2/m^2.days)	182	176	228	199
Length of top ear (cm)	14.9	16.6	16.8	18.6
Maximum width of top ear (cm)	3.8	4.1	4.1	4.5

One of the original criteria for selecting hybrids for this trial was the dry-matter content of the top ear. For each of the sowing dates, the same pattern in dry-matter content of the top ear was apparent with Eta Ipho achieving the highest dry-matter content and Nicco the lowest, in both treatments (Fig. 2).

Table 2 shows the maximum diameter and length of the top ears. The volume of the top ear can be roughly estimated using the formula $1/3.\pi.(\frac{1}{2} * \text{width})^2.$ length. The volumes correlated negatively with the dry-matter contents presented in Fig. 2. (at final sampling: $r^2 = 0.97$ for early sowing and $r^2 = 0.95$ for late sowing). Therefore the dry-matter yields of the ear were not significantly different for the hybrids on any sampling date. This agrees with the official variety tests of 1979.

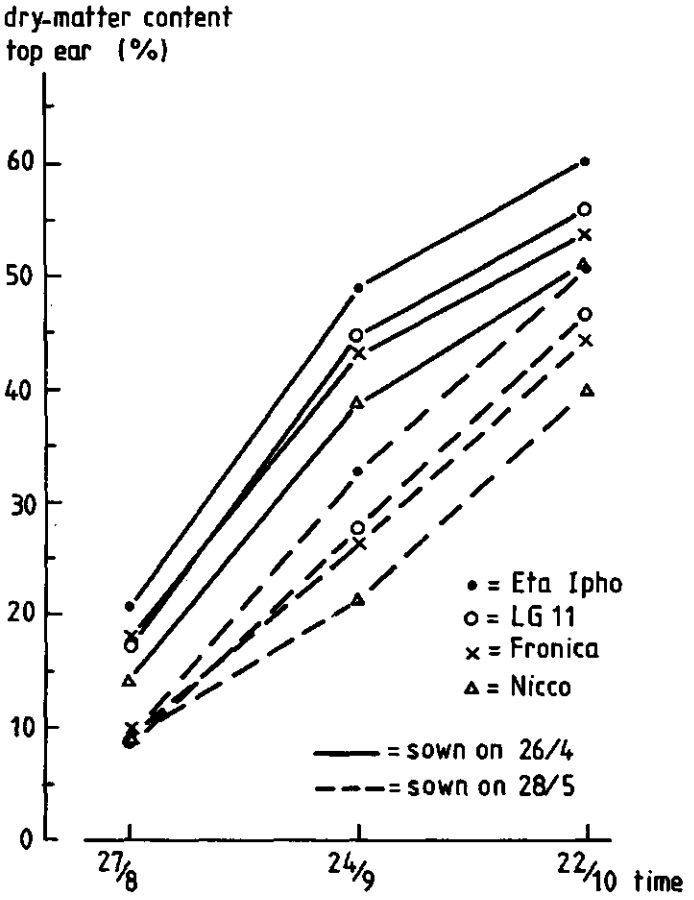


Fig. 2. Course of the dry-matter content of the top ear for four hybrids, sown on two dates.

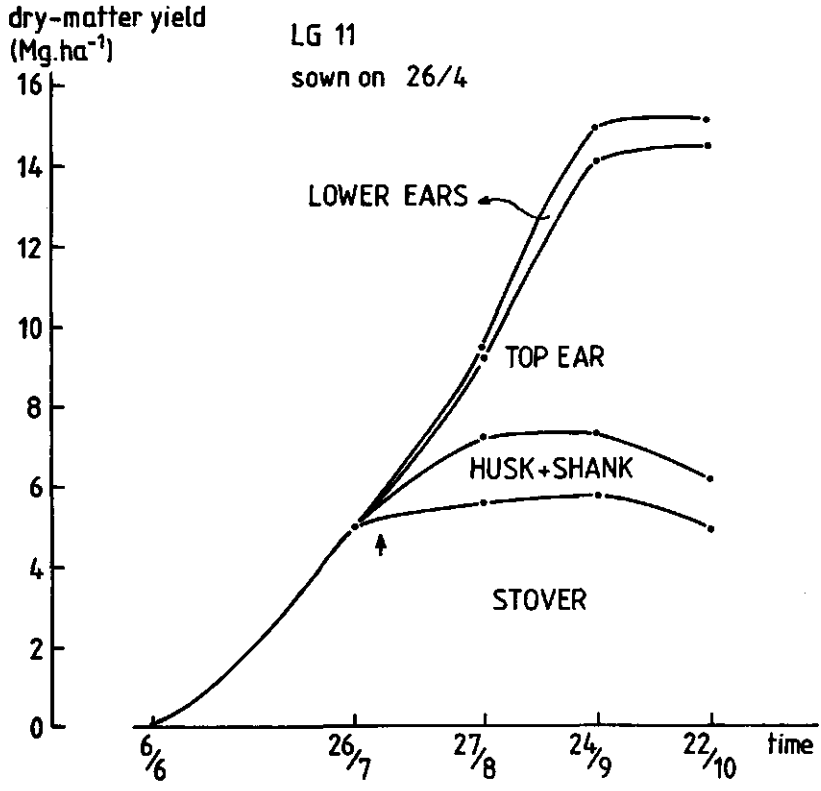
Sowing date had a considerable effect: at final sampling (22 October) the difference in dry-matter yield between the early and late sown crops was still about 2 $Mg.ha^{-1}$ for all hybrids (hybrid means were 9.17 $Mg.ha^{-1}$ at early sowing and 7.08 $Mg.ha^{-1}$ at late sowing).

Production pattern: As stated, the four selected high-yielding hybrids showed no differences in ear yield. The results from this trial suggest that the climatic conditions influenced the rate of assimilate flow to the ear, regardless of ear volume and genotype. Extending the grain-filling period by postponing the final harvest date would probably have resulted in Nicco achieving the highest ear yields.

Total dry-matter yields were significantly different between sowing dates and hybrids on all but the last sampling date. At the end of October, no significant hybrid effect could be discerned, but the sowing-time effect was still very significant. Early samplings showed hybrid effects on yield, because of an effect on yield of stover and of husks + shanks. For both sowing dates and on all sampling dates, Fronica gave the largest stover yield and Nicco the largest husk + shank yield. In the pre-silking period, Fronica had the highest production rate. Nicco had the highest post-silking production capacity. The flowering dates of all the hybrids were very similar Although the late sowing was 32 days later than the early one, later-sown crops achieved 50% emergence only 19 days later than early-sown crops. The anthesis and silking of the later-sown crops were delayed by only 14 days. The effects of sowing date were less than have been previously reported (Becker, 1976), probably because of the low temperatures during May and the use of modern hybrids in this experiment.

To illustrate the general production pattern, Fig. 3 shows the distribution of the dry matter in LG 11 for the two sowing dates. After flowering the yield of the non-reproductive parts continued to increase, but during the last four weeks, grain filling occurred partially at the expense of dry mass (probably mainly carbohydrates) stored in the stover, husks and shanks. This is a normal pattern under Dutch conditions. The productivity of the later-sown crop was higher during the last four weeks, because its remaining leaf area was larger and more productive. The pattern was exactly the same for all hybrids.

So, despite differences in plant traits (ear volume, plant height etc.), production and distribution of dry matter only showed slight differences between hybrids.



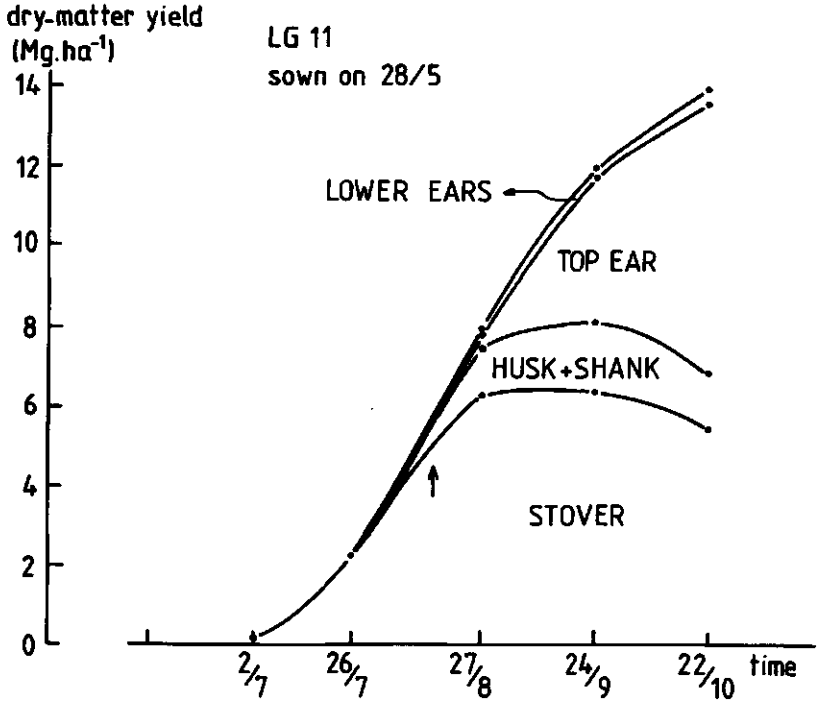


Fig. 3. Production pattern for LG 11, sown on two dates. ↑ indicates 50% ♀ flowering.

Quality. By way of example, the yields of the different chemical constituents of the dry matter in LG 11 have been plotted against time (Fig. 4). Cell-wall production stopped some time after flowering for the early sowing, but seemed not to have been completed at the final sampling of the late sowing. The amounts of water-soluble carbohydrate, ash and crude protein were at their peak on 24/9. Most of the non-structural carbohydrates were produced after flowering. The marked decline in the amount of water-soluble carbohydrates clearly illustrates the redistribution of short carbohydrates from the non-reproductive parts to the ear, where they are converted to starch. This redistribution occurred in both sowings. The pattern shown in Fig. 4 was also true for the other hybrids.

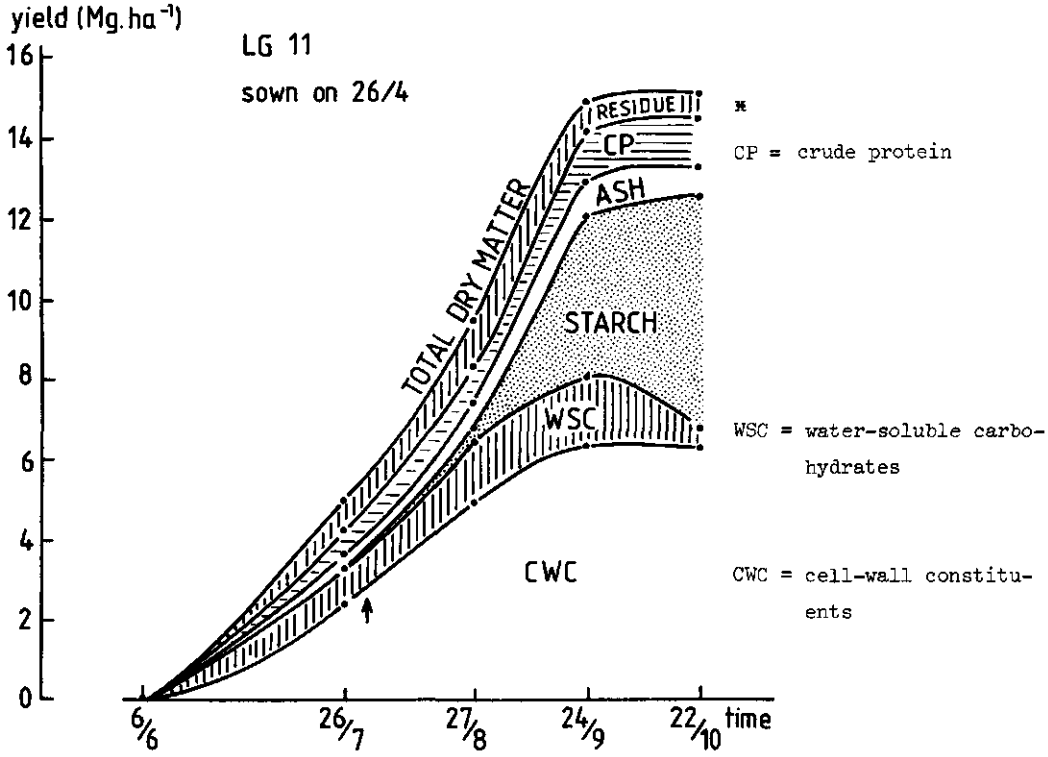
The proportions of the different constituents present were very similar in all the hybrids on each sampling date. The hybrid ranges in yields of the constituents are listed in Table 3. The ranges are small, except for the estimated residue, which is subject to the greatest error. The yields of all constituents are lower for late sowing, except for those of water-soluble carbohydrates (because grain filling was less advanced) and those of the residue (because of a smaller decrease in leaf area).

The mean effect of sowing time on dry-matter yield at final sampling was 1.67 $Mg.ha^{-1}$. This difference mainly resulted from the difference in yield of non-structural carbohydrates (about 1400 $kg.ha^{-1}$): it decreased by 1 $Mg.ha^{-1}$ during the last four weeks.

Table 3. Ranges in yields of constituents at final sampling ($Mg.ha^{-1}$).

Sowing time	26/4	28/5
Dry matter	15.1 - 16.7	13.9 - 15.0
Cell-wall constituents	6.25 - 6.94	6.16 - 6.69
Water-soluble carbohydrates ($C_6H_{12}O_6$)	0.50 - 0.77	0.83 - 1.24
Starch $(C_6H_{10}O_5)_n$	5.42 - 5.99	3.91 - 4.09
Total non-structural carbohydrates	6.17 - 6.66	4.90 - 5.18
Ash	0.70 - 0.84	0.64 - 0.76
Crude protein	1.20 - 1.40	1.08 - 1.25
Residue	0.61 - 1.18	0.80 - 1.33

Table 4 shows some quality factors at final sampling. Eta Ipho was considerably



* residue includes organic acids (in leaves), fats and oils (in ears) and estimation errors

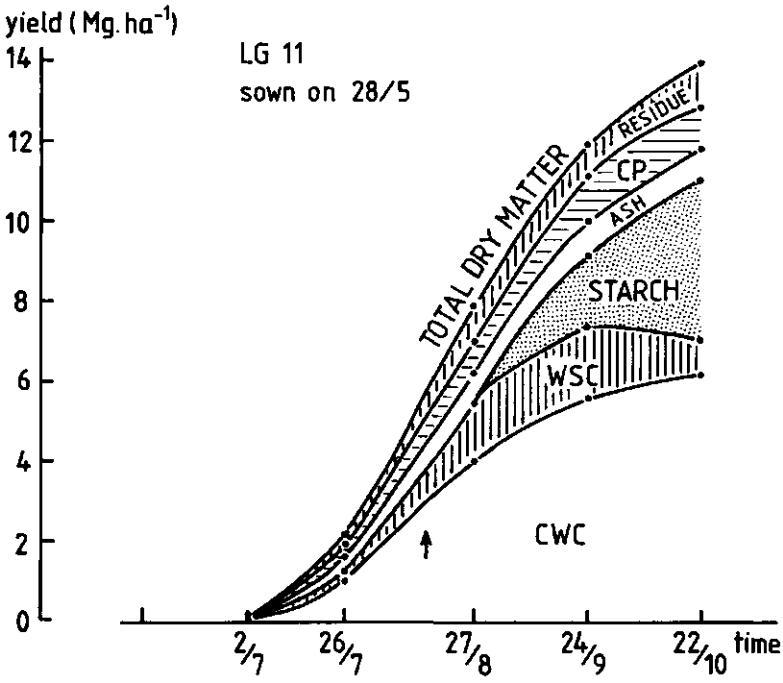


Fig. 4. Dry-matter composition over time for LG 11. ↑ indicates 50% ♀ flowering.

less digestible than the other three hybrids. This genotypic difference was mainly effected by differences in cell-wall digestibility, but was also amplified by differences in cell-wall content, especially in the later sowing. Sowing date only showed slight effects on digestibility: the higher cell-wall contents for later-sown crops were compensated for by the higher cell-wall digestibilities.

Both cell-wall content and cell-wall digestibility are related to physiological age. Fig. 5 shows that in this trial the cell-wall quality of both sowing dates was completely comparable if time is expressed in days after 50% emergence. It is also evident that the poorer digestibility of the cell walls of Eta Ipho results from the more rapid decrease in quality during the formation of the large leaves (with their thick midribs) and stem elongation. During these processes the rate of cell-wall production is very rapid and the quality of the cell walls produced is poorer. This is why genotypic differences arise in these stages. Similarly, the cell walls produced in the ear parts of Eta Ipho after flowering were of poorer quality and again these differences arose during the rapid elongation of the cob. The cell-wall digestibility of the husks + shanks depended on the physiological stage of the ear.

Table 4. Dry-matter yield of the whole plant (dm yield), ear content (ear%), apparent digestibility of organic matter (D_{om}), percentage of cell-wall constituents in dry matter (cwc%), cell-wall digestibility (D_{cwc}) and dry-matter content (dm%) on 22/10.

	sown on 26/4				sown on 28/5			
	Eta Ipho	LG 11	Fronica	Nicco	Eta Ipho	LG 11	Fronica	Nicco
dm yield ($Mg.ha^{-1}$)	16.15	15.11	16.21	16.66	13.97	13.87	15.02	14.61
ear% (%)	57.5	59.2	56.4	56.6	50.4	51.2	47.8	48.6
D_{om} (%)	70.3	74.2	73.4	75.0	69.5	74.2	74.4	74.6
cwc% (%)	42.7	41.4	42.0	41.6	46.6	44.4	44.6	43.4
D_{cwc} (%)	58.4	65.6	64.2	67.5	60.2	67.8	68.3	68.0
dm% (%)	38.2	38.9	33.8	31.4	29.7	27.3	25.7	23.6

Thus in this trial, the hybrids differed mainly in the yield of the non-reproductive organs, in the dry-matter contents of the ears and of the whole

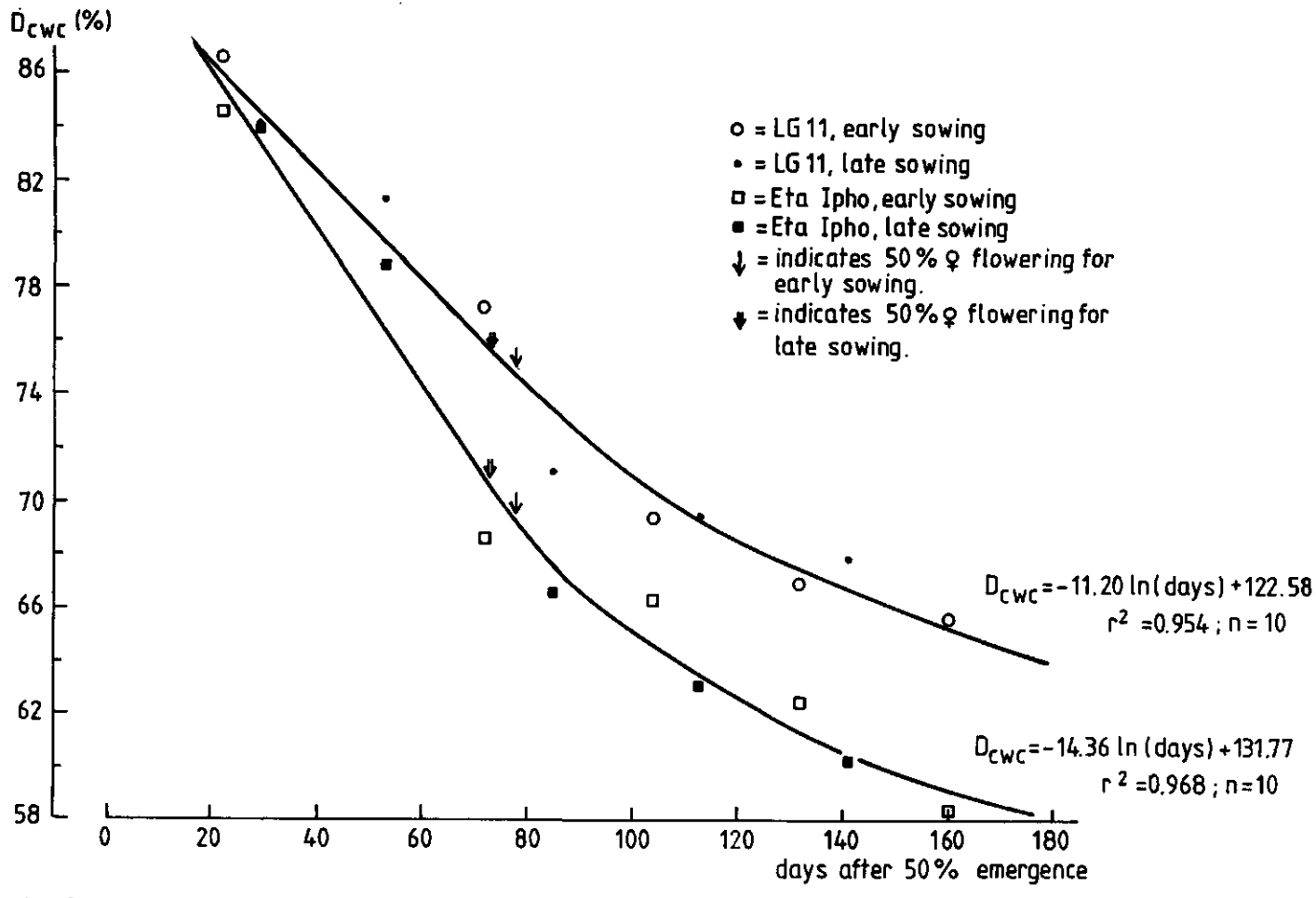


Fig. 5. Cell-wall digestibility (D_{cwc}) of two early hybrids, both sown on two dates, plotted against the number of days after 50% emergence.

crop, and in the quality of the cell walls. The effects of sowing date on crop quality were connected with the difference in date of emergence and were not caused by differences in climatic conditions during any stage of development. Within the range of genotypic variation present, the pre-silking period appeared to be important for quality. Differences in digestibility were effected relatively quickly.

Digestibility can be modified after flowering: it can increase, decrease or remain constant, depending on the climate but only slightly on genotype. The course of the digestibility after flowering in this trial was approximately the same for all hybrids. In tropical climates, digestibility may increase considerably after flowering. The decline during stem elongation is great, because the high temperatures stimulate lignification. However, high irradiance and good ear development will guarantee a strong "dilution" of the cell walls. In the sombre autumn climate of North-West Europe a decrease in digestibility is common. Digestibility is already good because of the good cell-wall quality, and the increase in starch content cannot always compensate for the decrease in cell-wall digestibility because starch is partly formed from sucrose, stored temporarily elsewhere in the plant. Indeed, in the literature increasing, decreasing and constant post-silking digestibilities have been reported, depending on latitude and year (Daynard & Hunter, 1975; Sheldrick, 1975; Andrieu, 1976, McAllan & Phipps, 1977; Aerts et al., 1978; Phipps, 1978; Weaver et al., 1978; Deinum & Knoppers, 1979; Gross, 1979; Phipps & Weller, 1979; Sheldrick, 1979; White & Winter, 1979; Wilkinson & Phipps, 1979; Wermke & Theune, 1980). These different possibilities are illustrated in Fig. 6, which shows that grain filling is crucial for the silage crop to be of good quality under tropical conditions, but is less important under temperate conditions. Variation in earliness and in duration of leaf area after silking are not taken into account in this figure. In early genotypes, the decline in digestibility before silking may be shorter and therefore digestibility may increase more rapidly after silking. A high leaf-area duration after flowering (because of earlier flowering or better longevity of leaves) also favours whole-plant digestibility, especially in the tropics.

Trial 2

Dry-matter distribution. The percentages of dry matter accounted for by 10 morphological fractions are presented in Fig. 7, together with the dry-matter contents of those fractions. One of the most striking phenomena

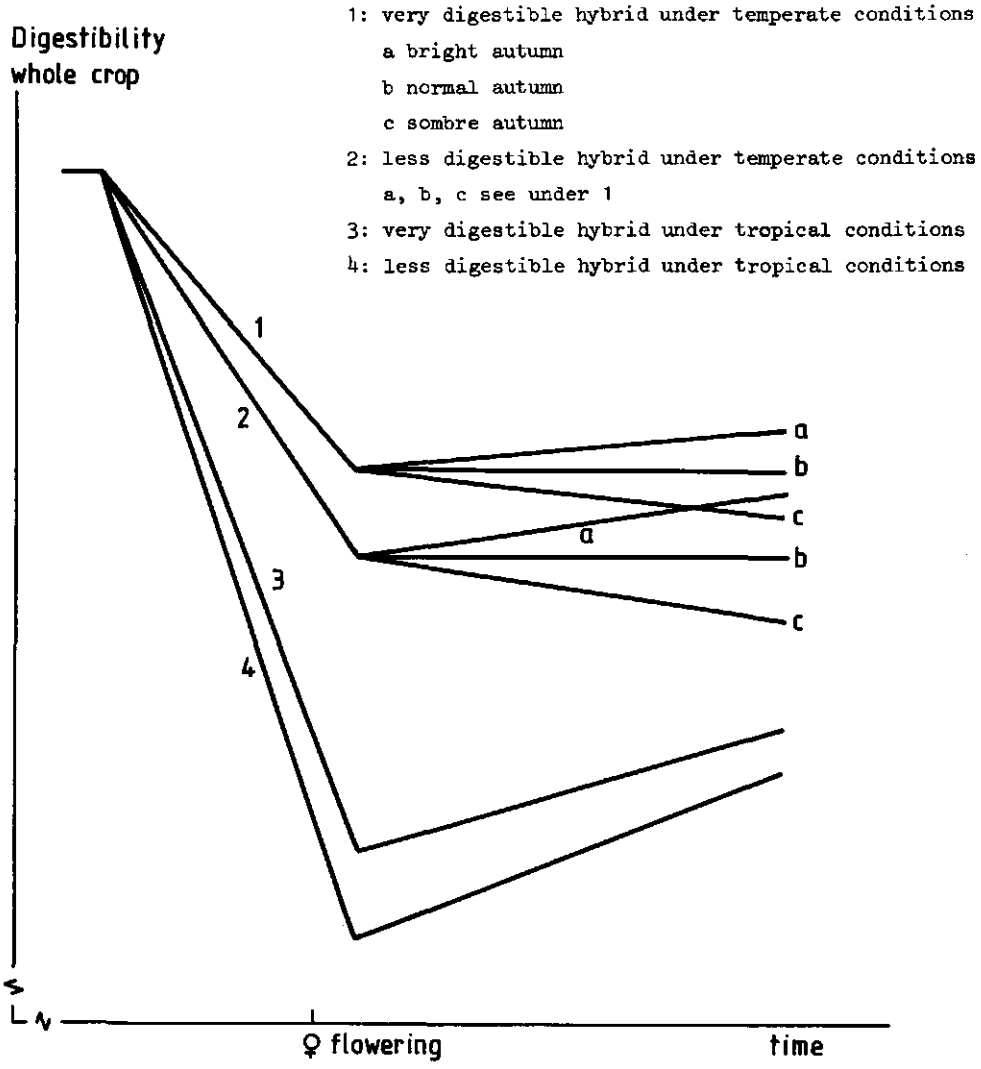


Fig. 6. Hypothetical course of digestibility over time for different situations.

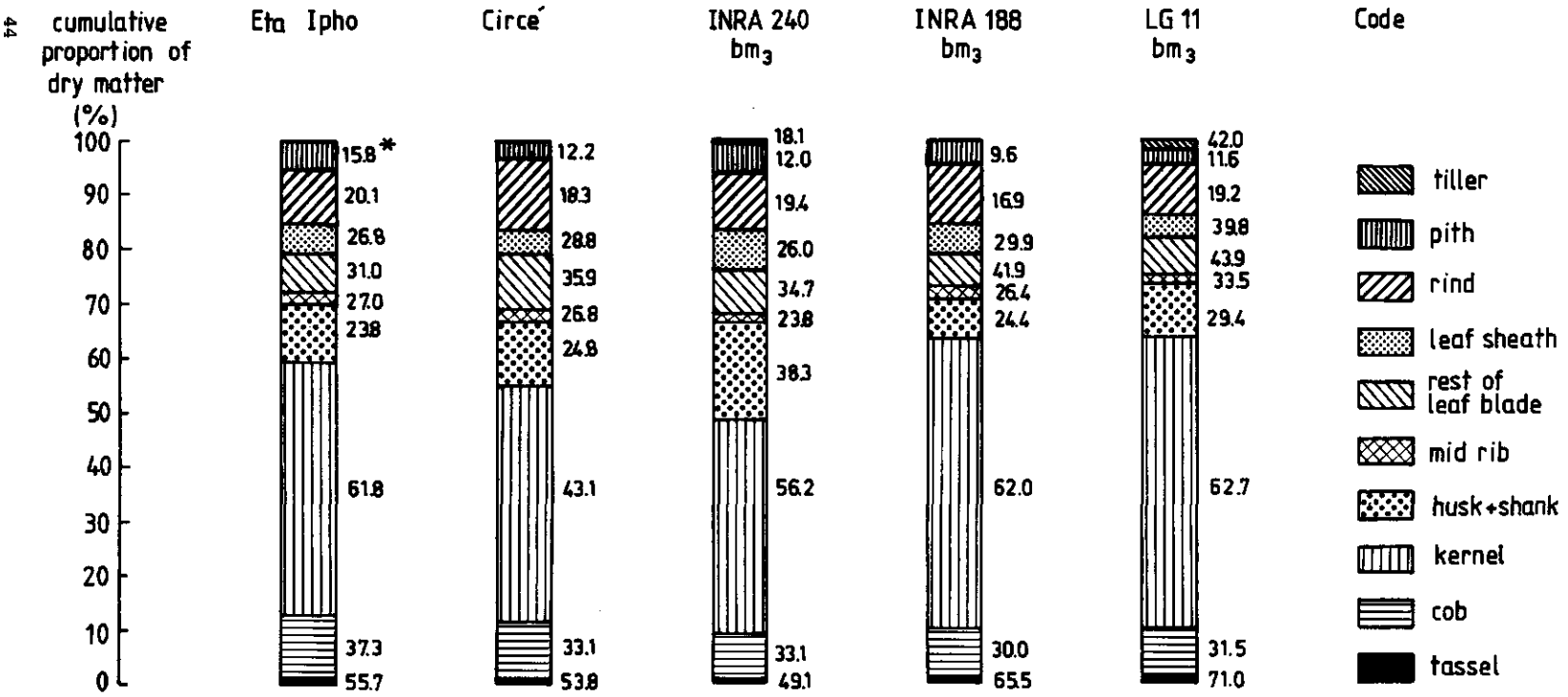


Fig. 7. The percentages of dry matter accounted for by ten morphological fractions in five genotypes.
100% = 196, 168, 189, 161 and 169 g/pl for Eta Ipho, Circé, INRA 240 bm_3, INRA 188 bm_3 and LG 11 bm_3, respectively.
* Numbers indicate the dry-matter content of the fractions (in %).

shown in this figure is the enormous range in the dry-matter contents of the different fractions within one plant. After fresh material has been chopped, the shape and specific gravity of the various fractions will vary so that stratification and selection are inevitable. This illustrates the problems encountered when attempting to take adequate samples from a chopped maize crop for estimating the dry-matter content. Similar or even greater problems are encountered when investigating quality traits.

The proportions of dry matter did not vary greatly between the five genotypes but:

- shelling percentage was high for brown-midrib genotypes
- INRA 240 bm_3 had a high portion of husk + shank and of leaf sheath
- Circé showed characteristics of a late hybrid and had a thick rind
- LG 11 bm_3 was early; it had a high proportion of grain but the amounts of pith and leaf blades were low.

In this trial, Eta Ipho and INRA 240 bm_3 yielded more than the other three genotypes. The dry-matter distribution of Eta Ipho was similar in both trials. In Trial 2, the maturity and the dry-matter distribution of LG 11 bm_3 were similar to those of its normal counterpart, which was grown at the same location and in the same plant density, but has not been mentioned elsewhere in this paper.

Quality. The digestibility of the fractions was very variable both between fractions and between genotypes (Table 5). The apparent digestibility ranged from 44.0 (the tassel of Eta Ipho) to 88.9% (kernel of INRA 240 bm_3). This range is wider than the range of the standard samples, so the extreme values may be deviations that have arisen because the extrapolated relationship is not a straight line. Very low values of digestibility were normally repeatable within on in-vitro run, but not always between runs. Large inter-hybrid differences existed for all fractions, except for the kernels. In all its fractions, Circé was more digestible than Eta Ipho. The three brown-midrib genotypes had higher digestibility values than the two commercial hybrids except for the "kernel" and "rest of the leaf blade" fractions.

In Fig . 8 the digestibility of each fraction has been plotted against the cell-wall content of the dry matter. There was a wide range of digestibility at a given cell-wall content, especially when the cell-wall contents were high. Some of the differences in digestibility, however, can be attributed to differences in cell-wall content (r^2 = 0.447; RSD = 9.12). At the same cell-wall content, Eta Ipho shows the lowest D_{om} and bm_3 genotypes shows

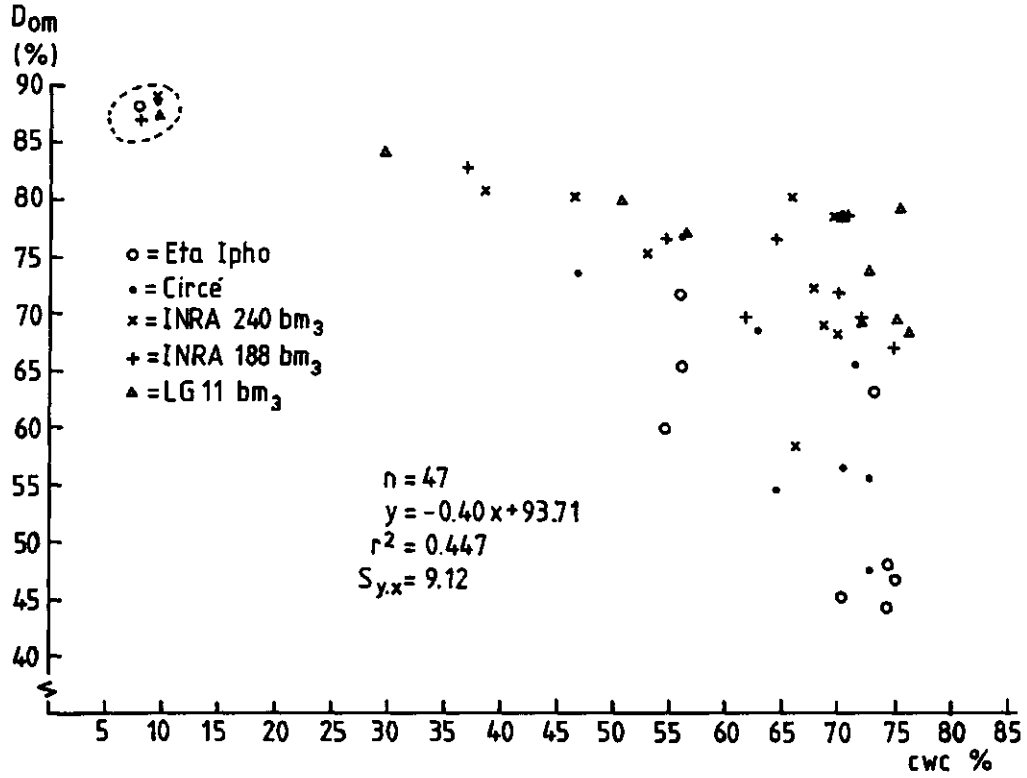


Fig. 8. Relation between the cell-wall content of the dry matter (cwc%) and the apparent digestibility of the organic matter (D_{om}). Data on ten morphological fractions of five genotypes.
The data on the kernel fractions are encircled. Because of the low cwc%, there is little variation in their D_{om} between genotypes.

Table 5. Apparent digestibility of the organic matter of ten morphological fractions for five genotypes, expressed as %.

Fraction \ Genotype	Eta Ipho	Circé	INRA 240 bm_3	INRA 188 bm_3	LG 11 bm_3
Tassel	44.0	47.6	72.1	66.9	69.3
Cob	59.7	68.4	78.4	77.6	78.4
Kernel	88.1	88.6	88.9	87.0	87.3
Husk + shank	63.1	65.5	80.3	78.5	78.9
Midrib	46.4	56.3	68.3	71.8	73.4
Rest of leaf blade	71.6	76.7	75.3	76.5	77.1
Leaf sheath	47.7	55.6	68.7	69.2	68.3
Rind	44.9	54.4	58.8	69.7	69.1
Pith	65.3	73.6	80.7	82.7	79.7
Tiller	--	--	80.3	--	83.9

the highest D_{om}, except for the kernels. Differences between hybrids were especially large for material with a high cell-wall content.

Thus, cell-wall content influenced the quality negatively but was not the only determinant; cell-wall quality was also variable. In Fig. 9 the digestibility of the organic matter has been plotted against the cell-wall digestibility. The relation is linear with a high correlation and a relatively low RSD. (Note that these two parameters were not estimated independently!). Eta Ipho and Circé had predominantly low D_{cwc} values. The linear correlation between cell-wall content and cell-wall digestibility was relatively low (r^2 = 0.187), but was also significant. Deinum & Bakker (1981) found high correlations between cell-wall digestibility and the digestibility of the organic matter when examining a number of hybrids.

In our experiment fractions from different hybrids also had a very high correlation, although the range in cell-wall content was much wider. If these high correlations between cell-wall digestibility and organic-matter digestibility are common (even if cell-wall contents vary greatly), then it will be difficult to estimate the quality of forage maize from crude-fibre content or from cell-wall content.

Table 6 shows the different characteristics for the whole crop, calculated from the data of the fractions. Note that Eta Ipho performed differently in

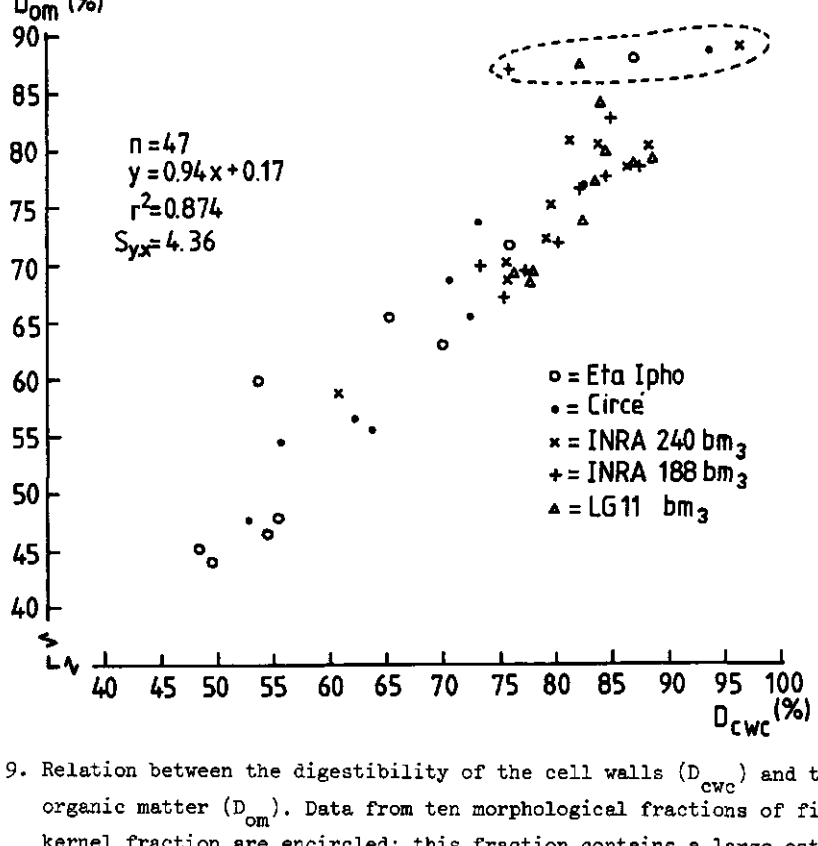


Fig. 9. Relation between the digestibility of the cell walls (D_{cwc}) and the apparent digestibility of the organic matter (D_{om}). Data from ten morphological fractions of five genotypes. The data on the kernel fraction are encircled; this fraction contains a large estimation error, because the true digestibility is almost 100% and the cell-wall content is very low.

the two trials because of differences in sampling date, plant density and *in-vitro* runs (compare Table 6 with Table 4). The calculated digestibilities agree with the *in-vivo* digestibilities estimated from adult wethers fed at maintenance on silages made from the same crops. These estimates of digestibility were done by the Institute for Animal Feeding and Nutrition Research, Lelystad, Netherlands (personal communication, A. Steg, 1980). The apparent digestibilities of the organic matter were: Eta Ipho 72.6%; Circé 75.6%; mixture of brown-midrib genotypes 80.1%. The improvement in the quality attributable to the recessive bm_3 gene is impressive. Genotypes varied in earliness, as can be seen from differences in dm% and cwc%. Regardless of their cwc%, bm_3 genotypes had a much better whole-crop digestibility than commercial hybrids, because of their larger D_{cwc}. In addition, Eta Ipho was less digestible than Circé, because its D_{cwc} was lower (see also Deinum & Bakker, 1981), and INRA 240 bm_3 was less digestible than the other bm_3 genotypes, because its cell-wall content was greater. The relatively low digestibilities of its rind and midribs indicate that the digestibility of INRA 240 bm_3 might be improved by further alteration of its genotype. The differences observed are relevant even in the Netherlands, where the cell-wall digestibility is already good because lignification is less extensive but where the cell-wall contents are also very large. Improving the cell-wall quality by decreasing the lignin content is even more important for tropical regions, as lignification is more pronounced in warmer climates (Deinum, 1976).

Table 6. Dry-matter content (dm%), apparent digestibility of the organic matter (D_{om}), cell-wall content (cwc%) and cell-wall digestibility (D_{cwc}) of the whole crop for five genotypes, calculated from the fractions and expressed as %.

Genotype	Eta Ipho	Circé	INRA 240 bm_3	INRA 188 bm_3	LG 11 bm_3
dm%	34.8	29.3	32.7	33.3	38.8
cwc%	38.5	40.4	41.7	33.2	36.6
D_{om}	71.8	75.4	79.8	81.4	81.8
D_{cwc}	62.6	70.7	81.1	80.1	83.0

The agronomic disadvantages of brown-midrib genotypes, however, are considerable, and improving a commercial hybrid by introducing a bm gene is a time-consuming process (Gallais et al., 1980): therefore the yielding ability of a brown-midrib hybrid is usually less than that of the latest introductions.

The variation in and heritability of the digestibility of several forage crops in the Gramineae family are good (Ross et al., 1970; Burton & Monson, 1972; Ross et al., 1975; Quesenberry et al., 1978; Dangi et al., 1979; Monson & Burton, 1980; Pedersen et al., 1980; Vogel et al., 1981a, b). A preliminary test has shown that high heritability values can be obtained for maize too (Beerepoot, 1980; personal communication). There is sufficient unexploited genetic variation to obtain digestibility values as high as those of the bm_3 genotypes without recourse to bm genes and thus maybe without their agronomic disadvantages. Firstly, however, it should be irrefutably established that the known differences in quality have a positive effect on the digestibility, intake or feed efficiency of different classes of livestock under practical feeding and producing levels. Methods must be standardized and -as stated by Gallais (1980)- international co-operation must be established because of the high costs involved.

Mineral content and mineral uptake. In Trial 1 no great differences were found between hybrids in the uptake of N, P, K and Ca although Nicco showed a somewhat greater accumulation of minerals than the other three hybrids; later sowing resulted in less mineral uptake (Table 7) but mineral contents were as high as for early sowing.

Table 7. Mineral accumulation in above-ground plant parts at final sampling, in $kg.ha^{-1}$.

	Sown on 26/4		Sown on 28/5	
Mineral	Hybrid range	mean	Hybrid range	mean
N	192 - 225	203	172 - 199	184
P	25 - 32	29	23 - 25	24
K	148 - 194	170	140 - 182	165
Ca	34 - 39	37	30 - 33	31
Total ash	701 - 839	758	643 - 760	706

The mineral contents of the fractions from Trial 2 were also analysed. The metabolic roles of the different nutrients determine in which plant part they accumulate. According to Pain (1978) the distribution of nutrients can be summarized as follows:

- Nitrogen, being an essential constituent of protein, enzymes and chlorophyll, reaches high levels in the leaves; a considerable amount of N, present in vegetative parts is translocated to the ear after grain set.
- Although phosphorus (an important constituent in the cell nucleus) is initially fairly uniformly distributed in the different plant tissues, translocation from vegetative parts to developing kernels occurs.
- Though not incorporated in any organic compound of the plant, maize requires large amounts of potassium. Potassium contributes to the strengthening of the sclerenchyma in the fibres and has many other functions in transport, photosynthesis, stomata closure etc. At the end of the growing season, potassium may accumulate in stem parts.
- Calcium is required in cell-wall formation and in neutralizing organic acids. It tends to accumulate in the leaves.

In confirmation of the above, we found that

- the N content was highest in the mesophyll
- the P content was fairly constant, but was lower in fixed organs such as cob, tassel, rind and pith
- the K content was relatively low in the ear but high in the pith and midrib
- Ca was barely detectable in cob and kernels, but reached high levels in tassel, leaf blade, pith and rind.

Ca content was significantly correlated with cell-wall content. However, very low Ca contents were found in the cobs, although cobs were rich in cell walls. The absence of Ca in cob-cell walls suggests that the structure of the latter is different.

Concluding remarks

Silage made from whole plants of forage maize is composed of very digestible plant parts with a low cell-wall content (kernels, pith) and of plant parts with much higher cell-wall contents and variable cell-wall digestibility (e.g. rind, tassel, midrib). It could be said that the forage obtained is a mixture of roughage and concentrates. The roughage is mainly produced during June, July and August, while the concentrates are mainly produced during July, August, September and October. Moderate temperatures during

early summer and a bright autumn encourage high yields of forage maize and boost the proportion of concentrates and the quality of the roughage. Since cell-wall content and cell-wall quality show a wide range within one plant and between genotypes and since the proportion of the different plant parts can be changed by selection, breeders are able to boost the proportion of the concentrates and to increase the quality of the roughage, even without undesirable repercussions on any other agronomic property.

References

Aerts, J.V., B.G. Cottyn, D.L. De Brabander, Ch.V. Boucqué & F.X. Buysse, 1978. Digestibility and feeding value of maize. Proceedings of the European Maize Meeting held at Louvain-La-Neuve (Belgium) ed. J.-F. Ledent, pp. 106-128

Andrieu, J., 1976. Factors influencing the composition and nutritive value of ensiled total maize plant. Symposium on the maize crop as a basic feed for beef production. Commission of the European Communities - Novi Sad - Yugoslavia

Becker, W.R., 1976. Mais. Een handleiding voor de teelt van korrel- en snijmais. P.A. publicatie nr. 21, pp. 1-84

Bundessortenamt, 1980. Beschreibende Sortenliste 1980. Getreide, Mais, Ölfrüchte und Hackfrüchte ausser Kartoffeln. Alfred Strothe Verlag, Hannover

Bunting, E.S., 1975. The question of grain content and forage quality in maize: Comparison between isogenic fertile and sterile plants. J. agric. Sci., Camb. 85: 455-463

Bunting, E.S., 1976. Effects of grain formation on dry matter distribution and forage quality in maize. Expl. Agric. 12: 417-428

Bunting, E.S., 1977. Maize physiology in relation to breeding for a northern climate. Ann. Appl. Biol. 87: 250-254

Burton, G.W., & W.G. Monson, 1972. Inheritance of dry matter digestibility in Bermuda grass, Cynadon dactylon (L.) Pers. Crop Sci. 12: 375-378

Dangi, O.P., G.P. Lodhi & Y.P. Luthra, 1979. Inheritance of in vitro dry matter digestibility in forage sorghum. Forage Research 5: 75-77

Daynard, T.B. & R.B. Hunter, 1975. Relationship among whole-plant moisture, grain moisture, dry matter yield and quality of whole-plant corn silage. Can. J. Plant Sci. 55: 77-84

Deinum, B., 1976. Effect of age, leaf number and temperature on cell wall and digestibility of maize. In: Carbohydrate research in plants and animals. Misc. Papers nr. 12, Agric. Univ., Wageningen, pp. 29-41

Deinum, B. & J.J. Bakker, 1981. Genetic differences in digestibility of forage maize hybrids. Neth. J. agric. Sci. 29: 93-98

Deinum, B. & J. Knoppers, 1979. The growth of maize in the cool temperate climate of The Netherlands: Effect of grain filling on production of dry matter and on chemical composition and nutritive value. Neth. J. agric. Sci. 27: 116-130

Deinum, B. & P.C. Struik, 1980. Harvesting field experiments for silage maize. Proc. fifth international conference on mechanization of field experiments, Wageningen, eds. J. Dijkstra & A. van Santen, pp. 231-236

Gallais, A., 1980. Summaries by chairmen. In: Improvement of quality traits of maize for grain and silage use, eds. W.G. Pollmer & R.H. Phipps, Martinus Nijhoff, The Hague, p. 493

Gallais, A., L. Huguet, H. Berthet, G. Bertin, B. Broqua, A. Mourguet & R. Traineau, 1980. Preliminary evaluation of brown midrib maize hybrids for their feeding and agronomic value in France. In: Improvement of quality traits of maize for grain and silage use, eds. W.G. Pollmer & R.H. Phipps, Martinus Nijhoff, The Hague, pp. 319-339

Gross, F., 1979. Futter qualität wird bei der Ernte festgelegt. Massnahmen zur Verbesserung des Futterwertes und der Futterqualität von Silomais. Mais. Zeitschrift über Forschung, Produktionstechnik, Verwertung und Ökonomik 7 (4): 12-13

Gross, F., 1980. Content and in vivo digestibility (sheep) of nutrients in maize varieties harvested at different stages for silage. In: Improvement of quality traits of maize for grain and silage use, eds. W.G. Pollmer & R.H. Phipps, Martinus Nijhoff, The Hague, pp. 429-445

McAllan, A.B. & R.H. Phipps, 1977. The effect of sample date and plant density on the carbohydrate content of forage maize and the changes that occur on ensiling. J. agric. Sci., Camb. 89: 589-597

Mock, J.J. & R.B. Pearce, 1975. An ideotype of maize. Euphytica 24: 613-623

Monson, W.G. & G.W. Burton, 1980. Forage quality evaluations in Pearl Millet. 1980 Agronomy Abstracts, American Society of Agronomy, Madison (WI), p. 127

Montgomery, F.G., 1911. Correlation studies of corn. Nebr. agric. Exp. Stat. Ann. Rep. 24: 108-159

Pedersen, J.F., H.J. Gorz, F.A. Haskins & R.A. Britton, 1980. Inheritance of forage and silage quality traits in forage sorghum hybrids. 1980 Agronomy Abstracts, Agronomy Society of America, Madison (WI), p. 127

Pain, B.F., 1978. Nutritional requirements of forage maize. In: Forage maize, eds. E.S. Bunting, B.F. Pain, R.H. Phipps, J.M. Wilkinson & R.E. Gunn, Agricultural Research Council, London, pp. 87-116

Phipps, R.H., 1978. The quality of maize silage. Proceedings of the European Maize Meeting held at Louvain-La-Neuve (Belgium) ed. J.-F. Ledent, pp. 74-79

Phipps, R.H. & R.F. Weller, 1979. The development of plant components and of their effects on the composition of fresh and ensiled forage maize. I. The accumulation of dry matter, chemical composition and nutritive value of fresh maize. J. agric. Sci., Camb. 92: 471-483

Quesenberry, K.H., D.A. Sleper & J.A. Cornell, 1978. Heritability and correlations of IVOMD, maturity and plant height in Rhodes grass. Crop Sci. 18: 847-850

Rijksinstituut voor het Rassenonderzoek van Cultuurgewassen, 1982. 57e Beschrijvende Rassenlijst voor Landbouwgewassen 1982. Leiter-Nypels, Maastricht

Ross, J.G., S.S. Bullis & K.C. Lin, 1970. Inheritance of in vitro digestibility in Smooth Broomegrass. Crop Sci. 10: 672-673

Ross, J.G., R.T. Thaden & W.L. Tucker, 1975. Selection criteria for yield and quality in big bluestem grass. Crop Sci. 15: 303-306

Sheldrick, R.D., 1975. Optimum cutting periods for silage maize in Western Kenya. E. Afr. For. J. 40: 394-399

Sheldrick, R.D., 1979. Growing maize for silage. Information leaflet no. 6. Grassland Research Institute, Hurley. pp. 1-8

Van Soest, P.J., 1977. Modified procedure for determining plant cell wall by the neutral detergent procedure. Paper presented at the Annual Meeting of the American Society of Animal Science

Van Soest, P.J., R.H. Wine & L.A. Moore, 1966. Estimation of the true digestibility of forages by the in vitro digestion of cell walls. Proc. 10th int. Grassl. Congr. (Helsinki) pp. 438-441

Vogel, K.P., H.J. Gorz & F.A. Haskins, 1981a. Heritability estimates for forage yield, in vitro dry matter digestibility, crude protein and heading date in Indiangrass. Crop Sci. 21: 35-39

Vogel, K.P., F.A. Haskins & H.J. Gorz, 1981b. Divergent selection for in vitro dry matter digestibility in Switchgrass. Crop Sci. 21: 39-41

Weaver, D.E., C.E. Coppock, G.B. Lake & R.W. Everett, 1978. Effect of maturation on composition and in vitro dry matter digestibility of corn plant parts. J. of Dairy Sci. 61: 1782-1788

Wermke, M. & H.H. Theune, 1980. Influence of variety, developmental stage, year and location upon the quality of silage maize. In: Improvement of quality traits of maize for grain and silage use, eds. W.G. Pollmer & R.H. Phipps, Martinus Nijhoff, The Hague. pp. 411-427

Whigham, D.K. & D.G. Woolley, 1974. Effect of leaf orientation, leaf area and plant densities of corn production. Agron. J. 66: 482-486

White, R.P. & K.A. Winter, 1979. Effects of harvest date on yield, dry matter content, plant nutrient content and in-vitro digestibility of various parts of forage maize plants in a short season environment. Paper presented at the Euromais Congress, 1979, Cambridge

Wilkinson, J.M. & R.H. Phipps, 1979. The development of plant components and their effect on the composition of fresh and ensiled forage maize. II. The effect of genotype, plant density and date of harvest on the composition of maize silage. J. agric. Sci., Camb. 92: 485-491.

from microbial degradation in the fore-stomachs of polygastric animals (see, e.g.: MINSON, 1976; AKIN and BURDICK, 1981, HARTLEY, 1981). In some forage species, plant silica may play the same role as lignin in the microbial degradation of cell walls (VAN SOEST and JONES, 1968; HARTLEY, 1981).

There is, however, another temperature effect on cell-wall digestibility independent of lignin content (DIRVEN and DEINUM, 1977; DEINUM, 1979). This effect is probably connected with the organization characteristics of the cell walls, such as the manner in which hemicellulose is associated with polyphenol esters (CHESSON, 1982), the crystallinity of hemicellulose and cellulose (BAILEY et al., 1976; DEINUM, 1979), the interactions between hemicellulose and cellulose (BAILEY et al., 1976), the occurrence of O-acetyl groups (BAILEY et al., 1976), whether bacteria are physically impeded from adhering (cf. RICHARDS, 1976) or the available surface of the cell walls and their fragility (SMITH et al., 1971).

These two effects of temperature on cell-wall digestibility may be distinguished by estimating the potential cell-wall digestibility and the rate of cell-wall digestion. Lignin and silica affect the potential extent of cell-wall digestibility, but lignin content, the ratio of lignin to cellulose or of lignin to acid-detergent fibre do not correlate with the rate at which potentially digestible cell walls can be digested (SMITH et al., 1971; SMITH et al., 1972; WALDO et al., 1972; MERTENS, 1977). The rate of disappearance of digestible fibre is related to the morphological and physical nature of the cell walls (MERTENS, 1977; GOODRICH and MEISKE, 1979), although SMITH et al. (1971) have stated that the content of cell solubles (or 100 – cell-wall content!) may also be relevant for cell-wall digestion kinetics during in vitro fermentation. Other factors limiting rates of degradation, such as the pH in the rumen, are not relevant in the in vitro technique.

Literature about the effects of temperature on maize digestibility is scarce. DEINUM (1976) found that higher temperatures caused a slight increase in cell-wall content, but a strong decline in the cell-wall digestibility of leaf blades, leaf sheaths and stems. Data on the effects of temperature on whole-plant digestibility of forage maize have previously been based on comparisons made under uncontrolled conditions (e.g. CUMMINGS and DOBSON, 1973; ANDRIEU, 1976). This paper deals with the effects of temperature during certain stages of growth, partly in combination with low light intensity, on the development, production and quality of forage maize under controlled conditions.

MATERIALS AND METHODS

Three experiments were carried out in greenhouses in 1979, 1980 and 1981. To obtain high and relatively constant light intensities for all treatments during periods in which the area of green leaf was large, experiments were started in March or April. Four seeds were sown per plastic pot containing 10 l of a mixture of equal volumes of sandy soil and peat. After emergence, the seedlings were reduced to 2 per pot. Nutrient solution, adjusted to soil type, and water were

provided adequately. Weeds were removed by hand or controlled by applying a low dose of atrazin. Plants (including their root systems) were kept as healthy as possible and were finally arranged in a density of 10 m^{-2} with a row distance of 75 cm, a plant arrangement similar to cultural practice in The Netherlands. Thus it was possible to place 8 rows of 26 pots (i.e. 416 plants including the border rows) in each greenhouse.

In early stages of growth, supplemental light was provided with 0.8 Philips HPLR 400 W mercury lamps per m^2 for 14 (1979 and 1980) or 16 (1981) hours per day. During vegetative development, the photoperiod was extended to 16 h by means of 12 incandescent bulbs (100 W) per 40 m^2, except for hybrid Dara in the 1979 trial. Relative humidity was kept at 75%.

Pollination in greenhouses may be suboptimal because air currents are locally strong and always flow in the same direction. Therefore, pollen was collected and sprinkled over the silks by hand daily. The date on which silk extrusion was first visible was noted for each plant in all experiments. In the 1981 experiment the dates of the first visible extrusion of anthers were noted as well. Plants were checked twice daily every day.

Prior to treatment, plants were rearranged to cancel out any differences that might have arisen in different greenhouses during pre-treatment growth.

In 1979, the hybrid Dara was sown one week earlier than Ula. In combination with different photoperiods, this ensured a better synchronized silking for the early and late genotypes.

Treatments

Maize development can be divided into four physiologically distinct periods:

1. from sowing until the double-ridge stage of the shoot apex (approx. 6.5-leaf stage)
2. from double-ridge stage until 50% ♂ flowering
3. from 50% ♂ flowering until onset of linear dry-matter accumulation in kernels
4. grain-filling period.

These phases differ greatly in duration.

In this paper, experiments are described in which temperature was varied in period 2 or 4. Data from the literature or unpublished results on the influence of temperature during periods 1 and 3 will be mentioned. Comparisons will be made with maize grown in the field under different conditions. In addition to temperature, light intensity was also varied during period 4 in the 1979 and 1980 experiments. Each greenhouse was divided into two compartments, separated by shading nets. The outer glass of low-light compartments was sprayed with temperzon (Hermadix). Care was taken to ensure, that the light was reduced by the same amount in all temperature treatments. The hybrids were chosen according to the aims of the experiments. Only LG 11 is in current use in The Netherlands. Ula, LG 11 and Nicco have been described in earlier reports (STRUIK, 1982b; STRUIK and DEINUM, 1982). Dara is a late, dent hybrid registrated in France.

In Table 1, climatic conditions are presented for each of the three experiments

and for normal Dutch conditions. The data of normal conditions are based on average climatic data and on average rate of crop development. The treatments have been coded according to the day/night temperature during the period in which the temperature was varied and with the relative amount of light or according to whether they were shaded or unshaded. Treatment 18/12 represents average temperature conditions in The Netherlands during periods 2, 3 and 4. Treatment 24/18 represents an extremely warm year, while treatment 30/24 reflects American and tropical or subtropical conditions. Average light intensity during period 4 was calculated as follows:

$$\frac{\text{cumulative outdoor irradiance in period 4 (J . cm}^{-2})}{\text{duration of period 4 (days)}} \times 0.75 \times a$$

in which 0.75 accounts for the light reduction, caused by the greenhouse itself
a accounts for the light reduction obtained by shading.
$a = 1.00$ for unshaded treatments and $a = 0.40$ (1979) or 0.33 (1980) for shaded treatments.

For Experiment 1 the same procedure was followed for period (3 + 4).

Light intensity was relatively low for treatment 18/12 in 1981 and treatment 24/18 in 1980 and was relatively high for treatment 30/24 in 1979. In all years the radiation received by unshaded treatments exceeded or was similar to the amounts of radiation maize crops would normally receive under field conditions in The Netherlands during grain filling.

Data on crop development

The number of visible leaves per plant and the plant height were estimated twice weekly to record and monitor rates of development in different greenhouses. The surface area of fully expanded leaves was calculated from the equation length × maximum width × 0.75 (MONTGOMERY, 1911). The maximum diameter of the middle of the second above-ground stem internode was measured with a marking gauge, to provide an estimate of stem thickness. Leaf angles were estimated with a clinometer (WHIGHAM and WOOLLEY, 1974). At each sampling date after female flowering, the ear length, number of unshrivelled kernels and total number of visible kernels or florets per ear were estimated for all ears arising from leaf axils. Plant height and flowering date were also noted.

Light extinction was measured using a 97.5 cm long light meter containing silicon cells and calibrated against a solarimeter.

Yield estimates

Plants were cut off at soil level, separated into stover (i.e. tassel + stem + leaves + leaf sheaths), husk + shank, top ear and lower ears and cut into pieces by hand. After recording their fresh weight, fractions were dried for each plant separately and without subsampling at 70 °C in forced ventilation ovens. After reaching constant weight, they were re-weighed. For the uppermost ears, shelling percentage (dry grain weight divided by whole-ear weight) was estimated in 1979

and 1980. In 1980, the root systems of six plants per treatment and per sampling date were also analysed.

In Experiment 1, 40 plants were harvested at the 6.5-leaf stage. For each temperature treatment, 40 plants were harvested 4 times during period 2, at 50% ♂ flowering and 4 weeks after 50% ♂ flowering. The final sample was taken 8 weeks after 50% ♂ flowering and comprised 30 plants.

In Experiment 2, 32 plants of each hybrid were harvested prior to climate differentiation. 20 plants from each treatment were sampled some time thereafter and 20 plants were harvested at the first visible black-layer formation in normal kernels for Ula and the next day for Dara.

In Experiment 3, 36 plants were harvested at initiation of treatment: 6 harvests

TABLE 1. Climatic conditions in Experiments 1, 2 and 3 and estimated normal conditions in The Netherlands.*

Experiment and hybrid	Day/night temperatures (°C)				Shading treatment during period 4	Estimated mean light intensity ($J\text{-}cm^{-2}.day^{-1}$) during periods 3+4 or 4
	period 1	period 2	period 3	period 4		
Experiment 1 (1981) LG 11 (FAO 260)	18/12	18/12 24/18 30/24	18/12	18/12	unshaded	1031 1090 1086
Experiment 2 (1979) Ula (FAO 190)	20/15	20/15	20/15	18/12	unshaded shaded	1206 482
				24/18	unshaded shaded	1197 479
				30/24	unshaded shaded	1305 522
Dara (FAO 320)	20/15	20/15	20/15	18/12	unshaded shaded	1202 481
				24/18	unshaded shaded	1178 471
				30/24	unshaded shaded	1300 520
Experiment 3 (1980) Nicco (FAO 300)	20/15	20/15	20/15	18/12	unshaded shaded	1107 365
				24/18	unshaded shaded	1031 340
				30/24	unshaded shaded	1080 356

Normal conditions	period 1	period 2	period 3	period 4
Mean light intensity ($J.cm^{-2}.day^{-1}$)	1650	1650	1350	1000
Mean air temperature (°C)	11.8	16.0	17.3	14.3

* Calculations of normal conditions are based on climatic data (source: KNMI, The Bilt) and on the average rate of development of a standard crop.

of 20 plants from each treatment were taken after climate differentiation and the final harvest was at the end of the grain-filling period. The samples from one intermediate harvest of treatment 30/24 were lost, because of a malfunction of the oven.

Experiments 2 and 3 differed in frequency of sampling, hybrid choice (and thus crop structure and crop reaction), and light reduction for shaded crops.

Chemical analyses

Samples were bulked per fraction and per treatment at each sampling, ground with hammer mills and subsampled. Subsamples were analysed for true digestibility in vitro of organic matter, using the method described by VAN SOEST et al. (1966). These values were standardized and converted to apparent digestibility by means of a series of standard samples of fresh maize, ensiled maize and parts of the maize plant with known apparent in vivo digestibility (sheep).

All the digestibilities of organic matter presented in this paper are standardized values, unless otherwise stated.

Digestibility of the whole plant was calculated from digestibilities of the fractions and their proportions of organic matter. According to JOANNING et al. (1981) it is permissable to calculate the in vivo digestibility of a feed from the in vivo digestibility of its components at feeding levels below 1.5–2 times maintenance. The calculations done by van DONSELAAR and STEG (1980) agree with this. Therefore I assumed that such calculations are permissable for the in vitro technique too.

Organic cell-wall content in dry matter (neutral-detergent fibre) after removal of the starch was estimated according to VAN SOEST's (1977) method. In vitro cell-wall digestibility (D_{cwc}) was calculated from true digestibility (D_{true}), cell-wall content (cwc%) and ash content (ash%), using the formula:

$$D_{cwc} = 100 - \frac{(100\text{-}D_{true}) \times (100\text{-ash}\%)}{cwc\%}.$$

Acid-detergent fibre, cellulose, lignin and insoluble ash were estimated according to the methods described by GOERING and VAN SOEST (1970). Hemicellulose was calculated as the difference between neutral-detergent fibre and acid-detergent fibre. Rates of cell-wall digestion were estimated as described by SMITH et al. (1971) and GOODRICH and MEISKE (1979), assuming that the maximum extent of digestion was reached at a retention time of 96 h. For ear samples this assumption was certainly true, as was evident from the calculations of maximum extent of digestion done according to the method described by MERTENS and VAN SOEST (1972). For some stover samples, indigestibility was probably slightly overestimated. The potential extents of cell-wall digestibility after 96 h of incubation in a certain amount of rumen liquor are thus not strictly comparable with potential digestibilities after several weeks of incubation in mixed rumen microorganisms (see, e.g. PRINS et al., 1981), or with potential digestibility after long-term incubation with refreshed inoculum (e.g. WILKINS, 1969). Water-soluble carbohydrates were colorimetrically determined with an automatic ana-

lysing device using ferricyanide. To ascertain the total non-structural carbohydrates the same procedure was followed after hydrolizing the starch with amyloglucosidase.

N, P and Ca were determined after the dry material had been digested in a solution of salicylic and sulphuric acid with hydrogen peroxide. N and P were measured colorimetrically; Ca was measured by flame-emission spectrometry. Crude-protein content was calculated as N content times 6.25.

Results and discussion

Period 1. Some unpublished data

In this stage of growth, the growing point of the maize plant is still below the soil surface. Thus temperatures in the upper soil layer influence the processes in the shoot apex. Soil temperatures may increase by several degrees centigrade under field conditions if a plastic mulch is applied. This technique has already been practised by French growers for some years. Much of the resulting increase in yield, however, consists of structural material, as is illustrated in Table 2. This increase in cell-wall yield may result because more plant cells are produced, especially in the vegetative parts of the plant. The effect on digestibility of a small rise in temperature during early growth is therefore variable.

In the trials done by Deinum and Struik, the plastic cover caused the temperature in the upper soil layer during period 1 to rise by about 2 °C. Therefore there were only slight differences in the number of leaves (and thus the number of stem internodes) between mulched and unmulched treatments. If temperature rises more than this during early stages of growth, the increase in cell-wall yield will be much greater, because of an increase in number of stem internodes and thus an increase in duration of the period of cell-wall formation. In that case, whole-plant digestibility may even decline, especially if cell-wall digestibility is low.

Table 2. Dry-matter yield, cell-wall yield (cwc yield), cell-wall content (cwc%), apparent digestibility (D_{om}) and cell-wall digestibility (D_{cwc}) of hybrid LG 11 with and without plastic mulch. (Field conditions; Deinum and Struik, 1977; unpublished data).

Location and sowing date	Wageningen 28 April		Swifterbant 17 May	
	control	mulched	control	mulched
whole-crop yield ($Mg.ha^{-1}$)	15.86	18.37	13.56	16.40
ear yield ($Mg.ha^{-1}$)	7.19	8.95	5.51	7.13
cwc yield ($Mg.ha^{-1}$)	7.28	8.22	6.56	8.06
D_{om} (%)	73.5	74.1	72.0	70.8
cwc% (%)	45.9	44.8	48.4	49.2
D_{cwc} (%)	65.4	65.7	64.1	62.0

Period 2. Experiment 1.

Development

In Experiment 1, the effects of temperature on leaf number were deliberately avoided. The rate of development increased dramatically when temperature rose (Table 3); yet final differences in vegetative development were small. Plant height showed a maximum in the 24/18 treatment, but was not affected much (cf. BLONDON and GALLAIS, 1976). Stem thickness decreased markedly with a rise in temperature. Thus stem volume declined if temperature rose. The cumulative area of all leaves was somewhat greater in the 24/18 treatment than in the other treatments. Leaves just below and above the top ear were smaller in treatment 30/24 than in the other two treatments but the uppermost leaves were larger when temperatures were higher (Fig. 1). This pattern is similar to the one described by ALLISON and DAYNARD (1979), although the differences found in Experiment 1 were smaller, possibly because the temperature differentiation occurred at a later stage. Although leaf areas only showed minor differences between treatments, the maximum length and maximum width of the leaves differed greatly between temperature treatments. At lower temperatures, leaves were shorter and wider. This difference in shape may alter the ratio of rib to mesophyll and therefore may affect digestibility (DEINUM, 1976).

Reproductive development was greatly accelerated at higher temperatures but anthesis was hastened more than silking. In treatment 30/24 this resulted in a very long anthesis-to-silking interval, combined with a delayed ear development (cf. dry-matter content of top ear at final sampling) and in the severely limited development of second ears. The dominance of the terminal inflorescence is more marked at higher temperatures (BLONDON and GALLAIS, 1976) and inhibition of reproductive axillary buds may be greater if climatic conditions are altered in the very early stages of their development (STRUIK, 1982a). In addition, a high plant density may be unfavourable for a good synchronization (BUREN et al., 1974; EDMEADES and DAYNARD, 1979), thus emphasizing the effects of other adverse factors.

Dry-matter production

At first, the rate of dry-matter production increased with temperatures, but dry-matter production was stimulated less than development. Maximum dry-matter production rates were found during tassel emergence and were similar for all treatments (Fig. 2a).

Total dry-matter at 50% anthesis correlated negatively with temperature (Fig. 2b). Climatic conditions during period 2 affected production rates after anthesis: the decline in rate of dry-matter production was more rapid if temperatures during period 2 were higher, resulting in great differences between final whole-plant yields (cf. NELSON and TREHARNE, 1973). As a result of the above-mentioned effects of temperature on reproductive development, ear yields for treatments 18/12 and 24/18 were the same, but the ear yield of treatment 30/24 was only half as much.

TABLE 3. Effect of temperature treatment during the period from 6.5-leaf stage to 50% ♂ flowering on vegetative and reproductive development.

	Day/night temperatures during period 2 (°C)		
	18/12	24/18	30/24
Vegetative development			
rate of leaf appearance (leaves.day^{-1})	0.25	0.36	0.50
final number of leaves per plant*	14.85	14.80	14.80
final height of plant (cm)†	291	300	284
stem diameter (cm)§	2.48	2.23	1.97
cumulative leaf area (dm^2/pl)§	50.9	52.6	49.2
Reproductive development			
date of 50% anthesis (days after emergence)	73	57	50
portion of silking plants at 50% anthesis (%)	81	50	15
date of 50% silking (days after emergence)	72	57	63
number of kernels (top ear)†	413	481	452
length of top ear (cm)†	15.1	18.5	17.3
length of the second ear (cm)†	7.9	4.7	2.3
dry-matter content top ear at final sampling (%)	47.8	46.0	33.6

* average of 80 plants †average of 70 plants § average of 20 plants

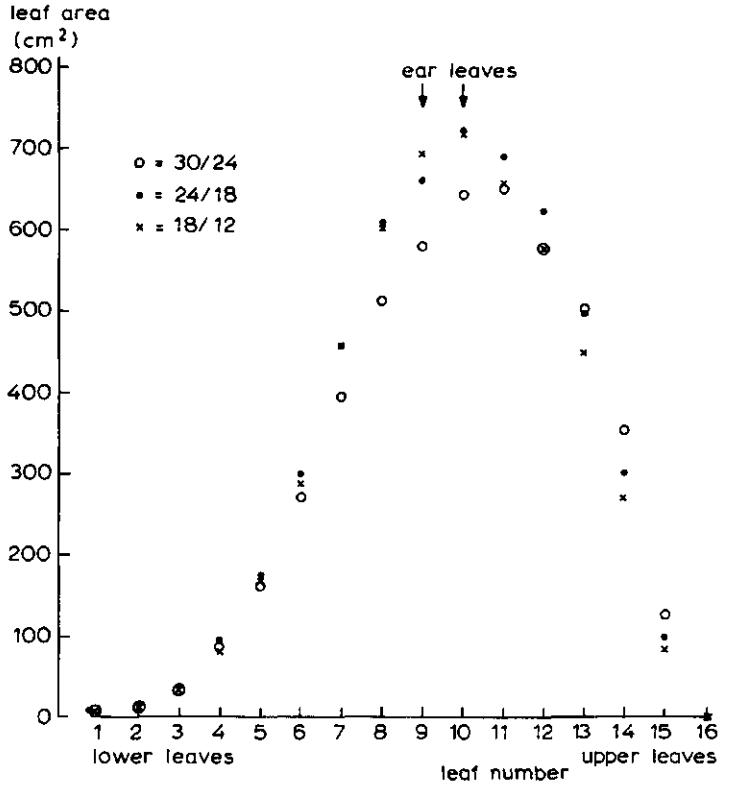


FIG. 1. Mean surface area of leaf laminae of plants grown at three different temperatures during period 2. Each point represents the mean of 20 leaves.

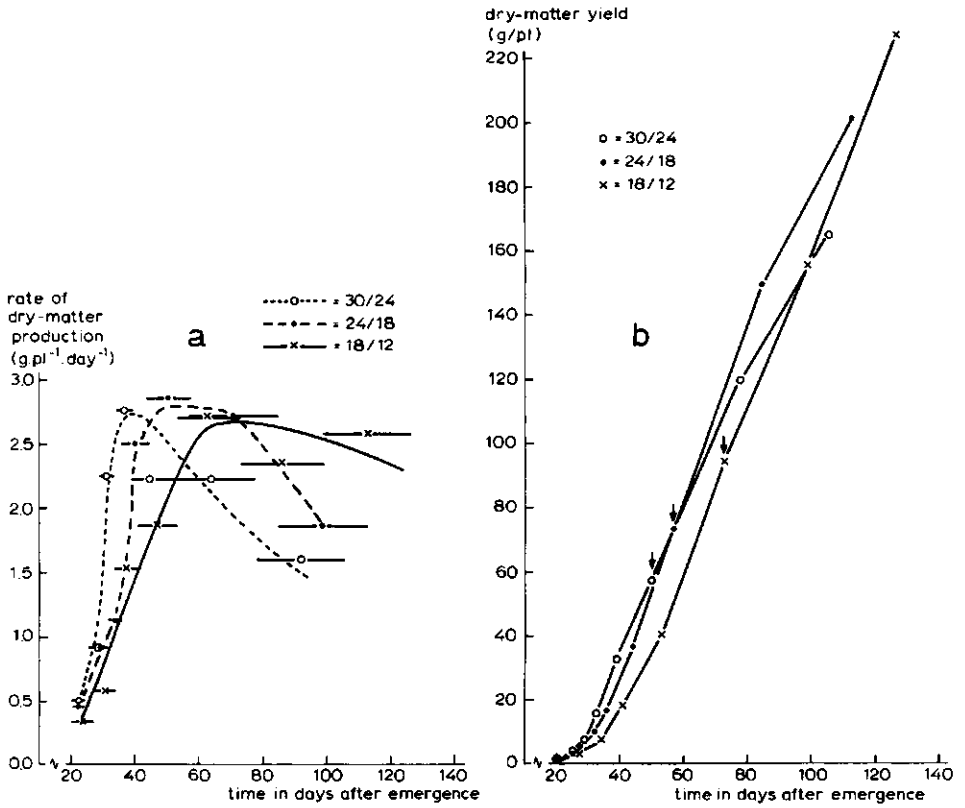


FIG. 2. Rate of dry-matter production (a) and dry-matter yield (b) in Experiment 1. Horizontal lines indicate the duration of the period, for which the production rate has been calculated. Arrows indicate 50% anthesis.

The course of quality up to anthesis

During period 2, maize generally shows a decline in the in vitro digestibility of the organic matter (D_{om}), because of an increase in cell-wall content and a decrease in the cell-wall digestibility (STRUIK, 1982b). In the present experiment, the increase in cell-wall content and the decrease in cell-wall digestibility were both stimulated by a rise in temperature, as occurs in other Gramineae (Table 4). This resulted in a marked temperature effect on D_{om} at 50% anthesis, as is shown in Fig. 3.

Temperature had a much greater effect on cell-wall digestibility than on cell-wall content, especially if ear shoots, including husks and shanks, are excluded (Table 4). The chemical composition of stover-cell walls was not greatly affected by temperature, although there were small temperature-induced effects on lignification and on silica content (insoluble ash). Yet, the cell-wall digestibility differed greatly, especially between treatments 30/24 and 24/18. Unidentified physical/chemical factors must have been responsible for most of the observed effects on digestibility. Incidentally, it is mainly these factors that prevent in vitro data being accurately extrapolated to in vivo parameters.

TABLE 4. Some quality parameters (all expressed as % of organic matter or cell walls) of the whole crop and of the stover in Experiment 1 at 50% anthesis.

		Day/night temperatures during period 2 (°C)		
		18/12	24/18	30/24
whole crop				
D_{om}		68.7	66.7	60.9
cwc%		59.5	61.3	62.9
D_{cwc}		68.2	66.1	58.7
stover				
D_{om}		67.2	65.4	60.3
cwc%		62.1	63.4	63.6
cell-wall composition:				
	hemicellulose	39.4	38.9	38.3
	cellulose	52.7	51.5	51.7
	lignin	7.7	8.7	8.7
	insoluble ash	0.2	0.9	1.3
D_{cwc}		67.4	65.4	58.4

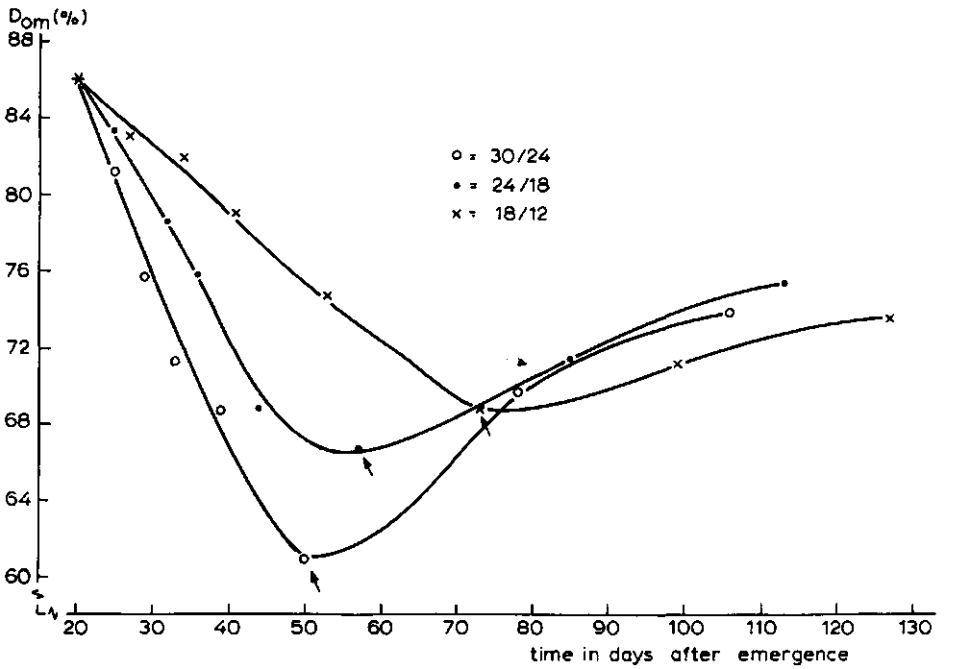


FIG. 3. Effect of temperature during period 2 on the apparent digestibility of the organic matter (D_{om}). Arrows indicate 50% ♂ flowering.

but not in the same direction as the digestibility of cell walls produced before anthesis. Cell walls present in husks, shanks and ears were almost completely formed during periods 3 and 4, i.e. after the three temperature treatments were reduced to one. The digestibility of cell walls present in husks and shanks was not affected by the temperature treatments. The D_{cwc} of upper ears increased as temperatures rose during period 2. During periods 3 + 4 the stover D_{cwc} did not decline in treatment 30/24, but fell markedly in treatments 24/18 and 18/12 (Fig. 5). On the basis of the whole crop, the most digestible cell-wall constituents produced after anthesis were those from treatment 30/24. Differences in the D_{cwc} of the whole crop therefore faded in the post-anthesis period.

The digestibility of stover-cell walls appeared to be strongly correlated with plant height (Fig. 6). The regression coefficient decreased slightly with increasing temperatures. However, the greatest deviations from the joint regression line were found at 50% anthesis, when mean plant height only ranged between 266 and 277 cm, but the digestibility of stover-cell walls ranged from 58.4% to 67.4%.

This relation is meaningful: it indicates that the decline in stover D_{cwc} is connected with stem elongation and that this decline stops when stem extension has ceased (Fig. 6). The more rapid decline of the D_{cwc} with increasing plant height at higher temperatures is caused by the effect of temperature on digestibility irrespective of morphological stage.

For leaves, stems and ears longitudinal growth exceeded growth in width and thickness at higher temperatures. FRIEND and POMEROY (1970) found for wheat that leaf length was stimulated by increasing temperatures over a wide range and that length increase was mainly due to an increase in cell length. The number of cells along the lamina could even decline with increasing leaf length. Extrapolating these findings for wheat leaves to all plant parts in the present maize trial, we might surmise, that at higher temperatures the stem, leaves and cobs had fewer cells along their longitudinal (and perhaps also along the lateral and radial) axes, and that these were longer, narrower and thinner. This would mean that the cell-wall content could be higher at higher temperatures since the ratio of surface area to volume increases when longitudinal growth dominates. This agrees with the data given in Table 4, but differences are very small, especially when the expected lower mass fraction of water-soluble carbohydrates is taken into account. This means that the cell walls must be thinner at higher temperatures. The possibilities for the formation of secondary walls are greater at lower temperatures since total area of cell walls is larger (because stem volume is larger and there are more cells). Thickening was also more pronounced at lower temperatures. Surface availability for microbial attack therefore declined when temperatures were lower during period 2.

The Q_{10} for lignin synthesis is higher than the Q_{10} for the synthesis of other cell-wall components. The lignin content is therefore higher at higher temperatures but the time lag between accretion of cellulose and hemicellulose and encrustation of lignin will also be smaller. A better synchronized lignin encrustation will give more opportunity for the formation of linkages and will therefore change the nature of the hemicellulose/cellulose fraction of the cell wall, especially when surface area of the primary cell wall is large. This structural effect will influence both potential digestibility and rate of cell-wall digestion and will be consistent throughout the growing season.

In an extra in vitro run, an attempt was made to gain more insight into these (partly hypothetical) influences of temperature by estimating potential digestibility of cell walls and the rate of digestion of potentially digestible cell walls.

Husk + shank samples were not investigated, since temperature during period 2

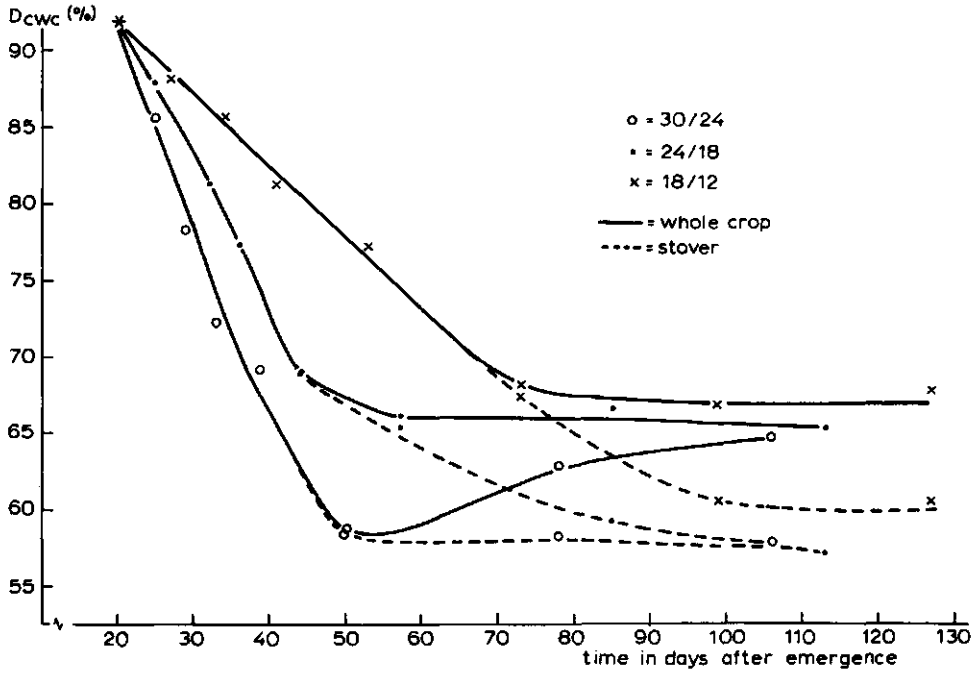


FIG. 5. Effect of temperature during period 2 on cell-wall digestibility (D_{cwc}) of the whole plant and of the stover.

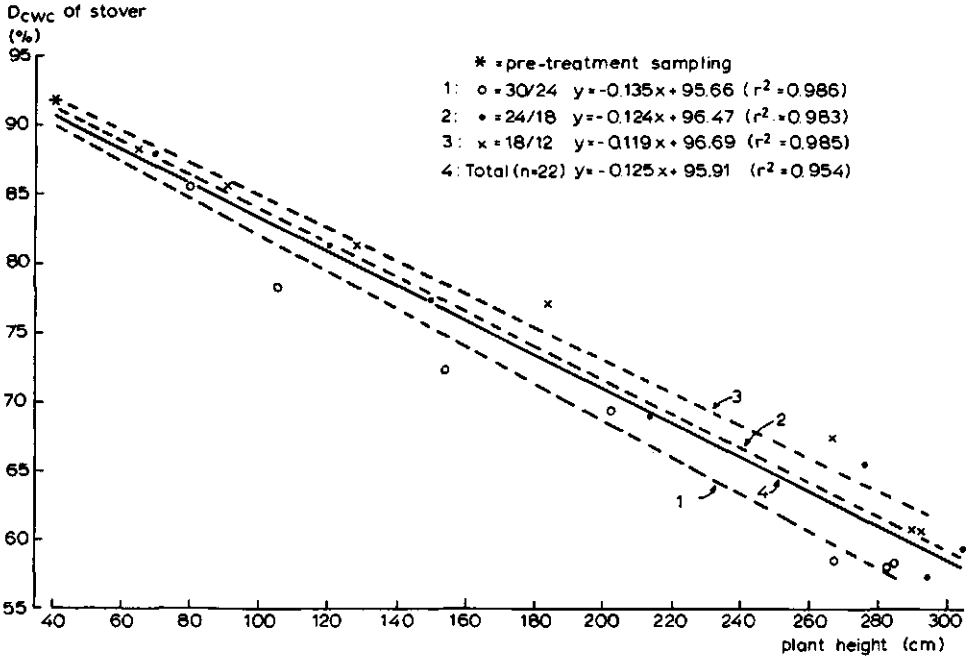


FIG. 6. Relation between plant height and cell-wall digestibility of the stover in Experiment 1.

did not affect their D_{cwc}. The data from ear samples will not be presented: their cell-wall digestion showed a considerable time lag, but was very rapid after 6 hours of incubation, so that accurate estimation of digestion rate was impossible. Stover samples taken about 2 weeks after temperature differentiation, at 50% ♂ flowering and 4 and 8 weeks after anthesis were analysed and gave workable results. Fig. 7 illustrates the method with stover samplings at 50% ♂ flowering and gives the relation between rate of cell-wall digestion and sampling date.

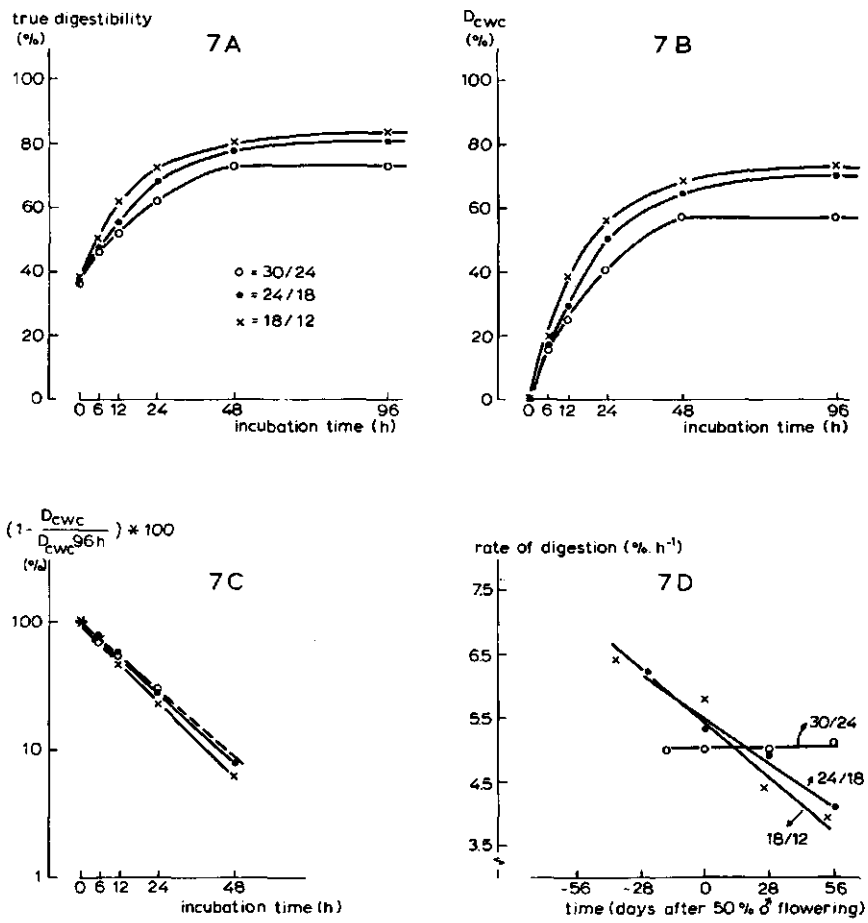


FIG. 7. Illustration of method for estimating digestion rate of potentially digestible cell walls.
7A. True digestibility in relation to incubation time; residues contain indigestible cell walls and potentially digestible cell walls that have not yet been digested.
7B. Digestibility of cell walls as a function of incubation time; D_{cwc} at 96 h is assumed to equal potential D_{cwc}. $1 - \frac{D_{cwc} \text{ at time t}}{D_{cwc} \text{ at 96 h}}$ indicates the fraction of the cell walls that have not been digested at time t, although they are digestible within 96 h of incubation.
7C. Semilog plot of fraction of potentially digestible cell walls that remained undigested versus incubation time; the regression coefficient is an estimator of the rate of digestion of potentially digestible cell walls.
7D. Rates of cell-wall digestion plotted against sampling date (cf. Table 6).

Table 6 shows the potential digestibilities of cell walls, the semilog regression equations and the correlation coefficients (all significant at $P < 0.01$; $n = 5$).

Potential digestibility depended on content of lignin and silica but even more on the structural organization of the cell-wall components. Differences in potential digestibility of cell walls achieved their maximum at 50% ♂ flowering and decreased during the first weeks of the post-anthesis period. Although for final samplings only slight differences were recorded after 48 h of incubation (Table 5), the potential digestibility of cell walls still differed considerably between temperature regimes. On the other hand, stover samples from early sampling dates showed smaller differences in D_{cwc} (96 h) than in D_{cwc} (48 h). This discrepancy is caused by differences in rate of cell-wall digestion (Table 6).

These digestion rates have been plotted against sampling date in Fig. 7D. The effect of temperature on lignification and structural organization apparently accelerated the maturity of the cell walls before flowering, which agrees with the above-described hypothesis. After anthesis, the content of cell solubles (i.e. 100 – cwc%) increased considerably in treatment 30/24, because ear development was inhibited. These increasing contents of cell solubles could have compensated for the normal decline in the rate of cell-wall digestion. SMITH et al. (1971, 1972) reported very significant positive correlations between the rate of cell-wall digestion and content of cell solubles.

TABLE 6. Potential cell-wall digestibilities (D_{cwc} after 96 h of incubation), and the regression equations and correlation coefficients (r) of the relation between $(1 - \frac{D_{cwc,\,t_i}}{D_{cwc,\,96\,h}}) \times 100\%$ and time of incubation, for stover samples taken on four sampling dates.

Temperature regime during period 2 (°C)	D_{cwc} after 96 h of incubation (%)	Regression equation	r
2 weeks after temperature differentiation			
30/24	76.1	$y = -0.050\,x + 4.544$	–0.99
24/18	81.7	$y = -0.062\,x + 4.489$	–0.98
18/12	84.5	$y = -0.064\,x + 4.431$	–0.96
at 50% ♂ flowering			
30/24	57.3	$y = -0.050\,x + 4.604$	–1.00[1])
24/18	70.0	$y = -0.053\,x + 4.643$	–1.00
18/12	72.6	$y = -0.058\,x + 4.583$	–1.00
4 weeks after 50% ♂ flowering			
30/24	63.7	$y = -0.050\,x + 4.580$	–1.00
24/18	65.3	$y = -0.049\,x + 4.569$	–1.00
18/12	69.6	$y = -0.044\,x + 4.502$	–0.99
8 weeks after 50% ♂ flowering			
30/24	63.2	$y = -0.051\,x + 4.591$	–0.99
24/18	64.7	$y = -0.041\,x + 4.520$	–0.98
18/12	70.0	$y = -0.039\,x + 4.495$	–0.99

[1]) $n = 4$, since the potential D_{cwc} had already been reached after 48 h of incubation.

Rates of digestion decreased for both other temperature treatments because of changes in the chemical composition of the cell walls after anthesis (cf. Tables 4 and 5) and because of a reduction of the surface availability. These effects reduced the rate of cell-wall digestion to such an extent that they overcompensated the still existing differences in physical structure.

The method illustrated in Fig. 7 clearly reveals the effect of temperature on digestibility as caused by its effect on the organization of the cell-wall components.

The dilution of cell walls with completely digestible organic matter was most efficient in treatment 24/18 and 30/24 (Table 5: $\triangle$ cwc%). The rate of the dilution process was determined by the cell-wall content present at anthesis, the cell-wall production after anthesis and the production rate of cell contents.

Résumé: *During period 2, the main processes that were dependent on temperature were leaf appearance, stem growth and reproductive development. High temperatures during period 2 led to lower amounts of dry matter at 50% ♂ flowering and a lower productivity thereafter. Temperature affected final digestibility by its effects on cell-wall content, cell-wall digestibility and amounts of cell wall. Its effects, however, were limited, since cell-wall production* after *anthesis was reduced by higher temperatures* before *anthesis and since most of the difference in cell-wall digestibility present at anthesis subsequently disappeared. Considerable differences in potential digestibility of cell walls remained at final samplings, but the rate of digestion of stover-cell walls was ultimately greater for the crop that received higher temperatures during period 2. This effect was probably partly caused by the high content of cell solubles in the stover that resulted from poor ear development.*

Period 3. Data and inferences from literature and unpublished research

The period from anthesis to grain set is a very critical period in the development of the maize crop. Stresses such as drought, low light intensity and heat produce very detrimental effects on ear development during this period. Although in Western Europe high temperatures are generally accompanied by high light intensity and high evaporation, in this discussion only temperature will be considered. High temperatures during pollination result in poor grain set because anther emergence is curtailed and pollen viability reduced (HERRERO and JOHNSON, 1980). According to these authors pollen viability remains almost unaffected up to 32 °C. JOVANOVIĆ and JOVANOVIĆ (1963) found that the success of pollination strongly depended on time of day associated with the concomitant temperature and the concomitant atmospheric humidity. Poorest grain set was obtained by pollination at 1 p.m. when the temperature was 26.4 °C and air humidity was 37%. Extremely high temperatures during silking are rare in The Netherlands. However, it is known that both pollen shed and silk extrusion may be inhibited by a succession of cool days (F. DE WOLFF, 1982; personal communication). Tolerance of cool weather during flowering shows great genotypic variability.

The effects of successful pollination on dry-matter production and D_{om} are illustrated in Fig. 8. In this example both yield and quality are greatly reduced by partial sterility of the ear. Smaller effects of sterility, however, have also been reported (e.g. BUNTING, 1975; DEINUM and KNOPPERS, 1979).

Fig. 4 illustrates that at least 43% of the cell-wall yield was attained after 50% anthesis. Much of this increase in cell-wall yield will occur during period 3. Thus during this stage too, an increase in temperature will reduce D_{om} by increasing the cell-wall content and reducing the cell-wall digestibility. The quantity of cell-wall constituents produced during period 4 will be little affected by the temperatures prevailing in period 3, unless adverse temperature reduces fertilization. In that case, cell-wall production during period 4 will be promoted (see above).

Period 4. Experiments 2 and 3

Developmental stage at climatic shift and climatic conditions

In Fig. 9 the physiological stages at which climatic differentiations took place are illustrated for all three hybrids in Experiments 2 and 3. Ula was treated at a later stage of kernel development than Nicco and Dara.

Rapid dry-matter accumulation in the kernels normally starts 12 to 18 days after silk emergence (JOHNSON and TANNER, 1972; DAYNARD and KANNENBERG, 1976; TOLLENAAR and DAYNARD, 1978), although cell division of the endosperm is not completed until 28 days after pollination (INGLE et al., 1965). Tip kernels

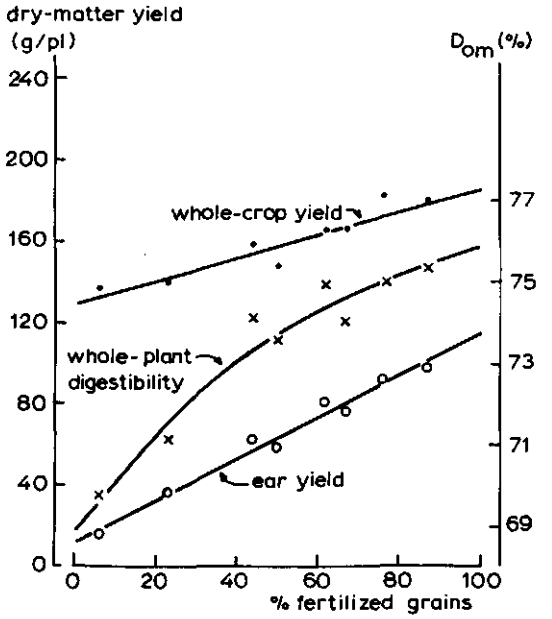


FIG. 8. Ear yield, whole-crop yield and whole-plant digestibility as affected by artificially prevented pollination. Plant density: 8.9 m^{-2}. (STRUIK, 1980; unpublished data).

TABLE 7. Length of the top ear (in cm) ± standard error of the mean, as affected by light intensity and temperature during period 4 (hybrid Nicco, 1980; means of 80 plants).

Day/night temperatures (°C)	Length of top ear at 100% rel. light intensity	Length of top ear at 33% rel. light intensity	Mean length of top ear
30/24	14.9 ± 0.31	13.9 ± 0.29	14.4
24/18	15.3 ± 0.28	13.8 ± 0.34	14.6
18/12	16.1 ± 0.23	15.2 ± 0.28	15.7
Mean length of top ear	15.4	14.3	

treatments 18/12 and 24/18 were greater than differences between treatments 24/18 and 30/24. The shading treatment showed a prompt and strong effect on the number of active kernels at all temperatures; the final differences between shaded and unshaded treatments were temperature-independent for Ula and Nicco, but not for Dara, where the shading effect was more pronounced at higher temperatures.

Leaf-area duration after grain set was temperature-dependent and was also affected by light intensity. An example of the leaf-senescence pattern is presented in Fig. 12. The pattern, however, varied between genotypes. The differences between light treatments in the number of green leaves per plant increased as temperatures fell. This was true for all genotypes, but the degree of the difference between the number of green leaves at final sampling for the shaded crop and the number of green leaves at final sampling for the unshaded crop depended on genotype. The difference was always large and positive for Ula. The differences were smaller, but still positive or zero for Nicco (Fig. 12). For Dara the difference declined from + 3.6 leaves at 18/12 to – 2.8 leaves at 30/24.

These differences in type of reaction may be connected with the physiological stage at which shading was applied (Fig. 9), or with genotypic background.

Dry-matter production

Ear. The final ear yields of unshaded crops were always highest in treatment 18/12, slightly lower in treatment 24/18 and much lower in treatment 30/24. For Ula and Dara this was also true for shaded crops; for hybrid Nicco a very low ear yield was found for the shaded crop in treatment 24/18. The duration of grain filling increased as temperature fell; grain-filling rate increased as temperatures rose, but not enough to compensate fully for the decrease in duration of filling. The growth rates of ears in Nicco are presented in Table 8. Ear growth can also be derived from Fig. 13. The penultimate harvest of the shaded crop in treatment 24/18 gave an atypical high ear yield, that arose because the average number of aborted kernels was low in that sample (see also Fig. 11). At a relative light intensity of 100%, rate of ear growth was higher in treatment 30/24 than in treatments 24/18 and 18/12. For shaded crops, however, the growth rate was

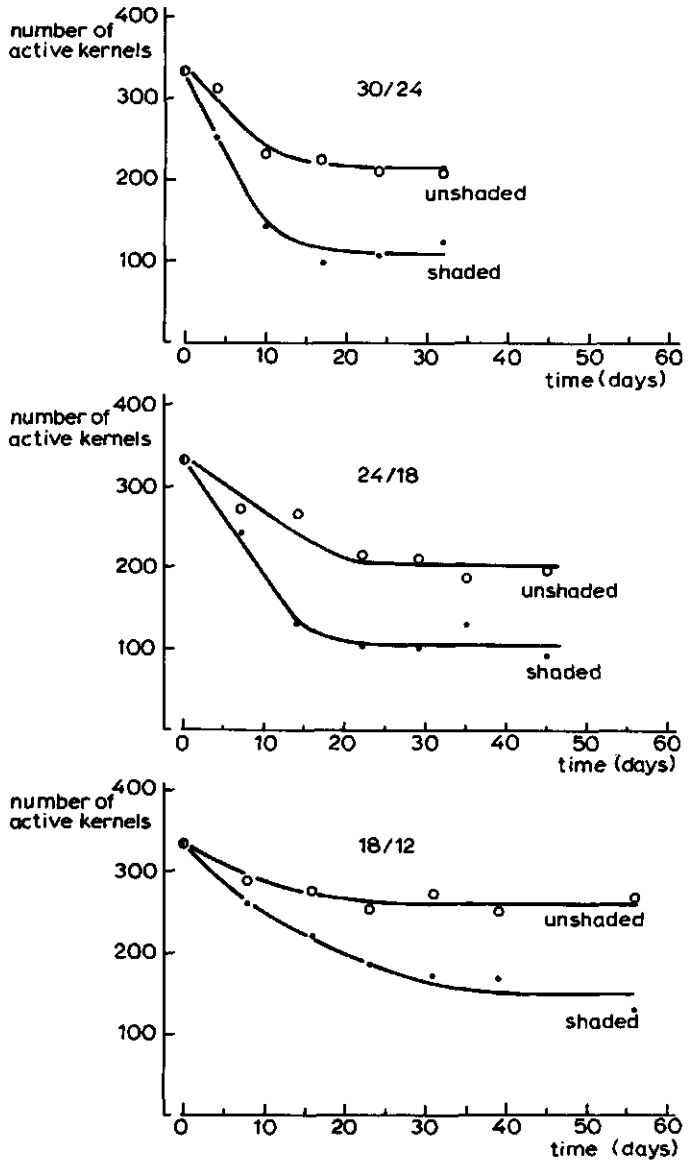


FIG. 11. Decline in the number of active kernels at three temperatures and two light treatments during period 4 (hybrid Nicco, 1980; means of 20 plants). Day 0 = date of initiation of treatment.

highest in treatment 18/12. The higher the temperature, the greater the negative effect of shading on the growth rate of ears was (cf. the lower the temperature the greater the positive effect of shading on leaf-area duration; see above). The effects of shading on duration of ear filling were inconsistent in these trials.

The final shelling percentages of the top ear were negatively affected by temperature but unaffected by light intensity in Ula and Dara; in Nicco no significant or consistent differences were found.

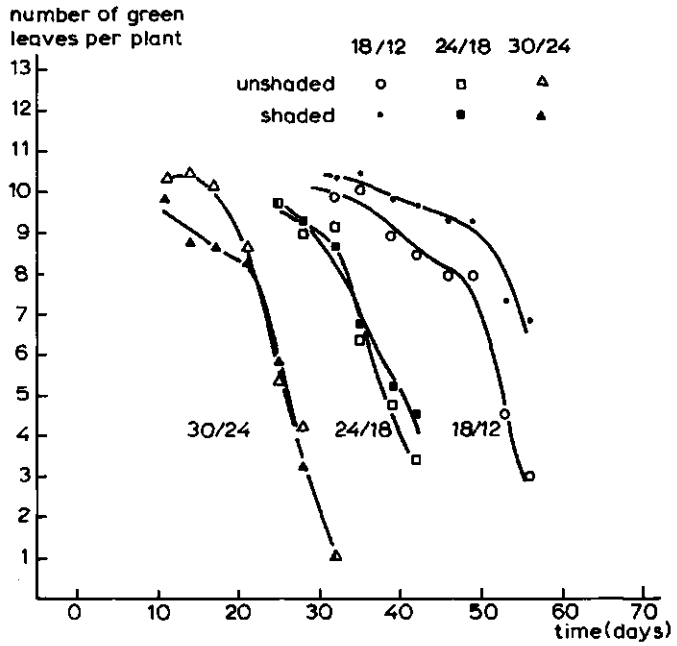


FIG. 12. Leaf senescence at three temperatures and two light intensities during period 4. Hybrid Nicco. Day 0 = date of initiation of treatment.

In all hybrids, ear yields were closely related to leaf-area duration during period 4 if data from the two light treatments were pooled separately.

Stover and husk + shank. A large portion of the dry matter present in the ears is produced after flowering. This portion may be 100% in regions with abundant irradiance and conditions that favour a long duration of leaf area (ALLISON

TABLE 8. Correlation coefficients (r) and regression coefficients (b) of the linear relation between ear yield and time for Nicco, grown under three temperature regimes and two light intensities during period 4.

Day/night temperatures (°C)	Relative light intensity (%)	n	r	90% interval of confidence of b (g.day^{-1})
30/24	100	5	0.99**	2.30 ± 0.42
	33	6[1])	0.99**	1.06 ± 0.13
24/18	100	6	0.99**	1.91 ± 0.34
	33	6	0.92**	0.85 ± 0.38
18/12	100	6	0.99**	1.82 ± 0.29
	33	6	0.99**	1.16 ± 0.17

[1]) This treatment did not reach a constant level of ear yield.
** = significant at $P < 0.01$.

and WATSON, 1966). In many other regions a significant reduction in weight of stem, leaves, husks and shanks has been recorded (DAYNARD et al., 1969; GENTER et al., 1970; DEINUM and DIRVEN, 1971; ADELANA and MILBOURN, 1972; BUNTING, 1976; AERTS et al., 1978; PHIPPS and WELLER, 1979; DEINUM and KNOPPERS, 1979; LUCAS, 1981; STRUIK, 1982b). This reduction is caused by redistribution of soluble carbohydrates, minerals and nitrogenous compounds (HAY et al., 1953; HANWAY, 1963; DAYNARD et al., 1969; GENTER et al., 1970; BEAUCHAMP et al., 1976; BELOW et al., 1981; STRUIK, 1982b). The intensity of redistribution depends on the difference between the rate of ear growth and that of crop growth. Since high temperature stimulates kernel growth more than crop growth, redistribution will be more intensive at higher temperatures, providing the light intensity is the same. In addition, low light intensity will dramatically increase the necessity for redistribution, unless complete ear abortion occurs.

Table 9 shows the final increases in dry matter, non-structural carbohydrate ($C_6H_{12}O_6$) and protein (N × 6.25) in non-ear parts at the 6 combinations of temperature and light intensity in Experiments 2 and 3. The rates of decline in component yield differed even more than final absolute values. Kernel abortion, induced by high temperatures or low light intensity, slowed down the redistribution of nitrogenous compounds (Table 9) and also of phosphorus (data not presented). Although the accumulation of N and P in the above-ground parts of the plant was reduced by shading (data not presented), the need for these minerals in the ear was reduced even more. If climatic conditions enable the plant to continue its ear growth successfully, N and P depletion in the stover occurs. This depletion may accelerate the senescence of the leaves under normal conditions.

The Ca content was also estimated. Ca plays a role in cell-wall formation and neutralization of organic acids. It tends to accumulate in the leaves (PAIN, 1978) where the light-dependent and organic-acid producing nitrate reduction

TABLE 9. Constituent yield in non-ear parts at final sampling minus constituent yield in non-ear parts at the climatic shift in g per plant for six climatic regimes during period 4 (means of three hybrids).

Temperature regime (°C)		30/24	24/18	18/12	*Mean*
dry matter	unshaded	− 7.1	− 4.9	+ 3.0	*− 3.0*
	shaded	−22.1	−20.4	−14.1	*−18.8*
	Mean	*−14.6*	*−12.7*	*− 5.6*	
non-structural carbohydrates	unshaded	− 5.6	− 1.3	+ 0.7	*− 2.1*
	shaded	−11.4	− 9.9	− 6.4	*− 9.2*
	Mean	*− 8.5*	*− 5.6*	*− 2.8*	
protein	unshaded	− 3.8	− 4.5	− 5.0	*− 4.5*
	shaded	− 3.6	− 3.5	− 3.8	*− 3.6*
	Mean	*− 3.7*	*− 4.0*	*− 4.4*	

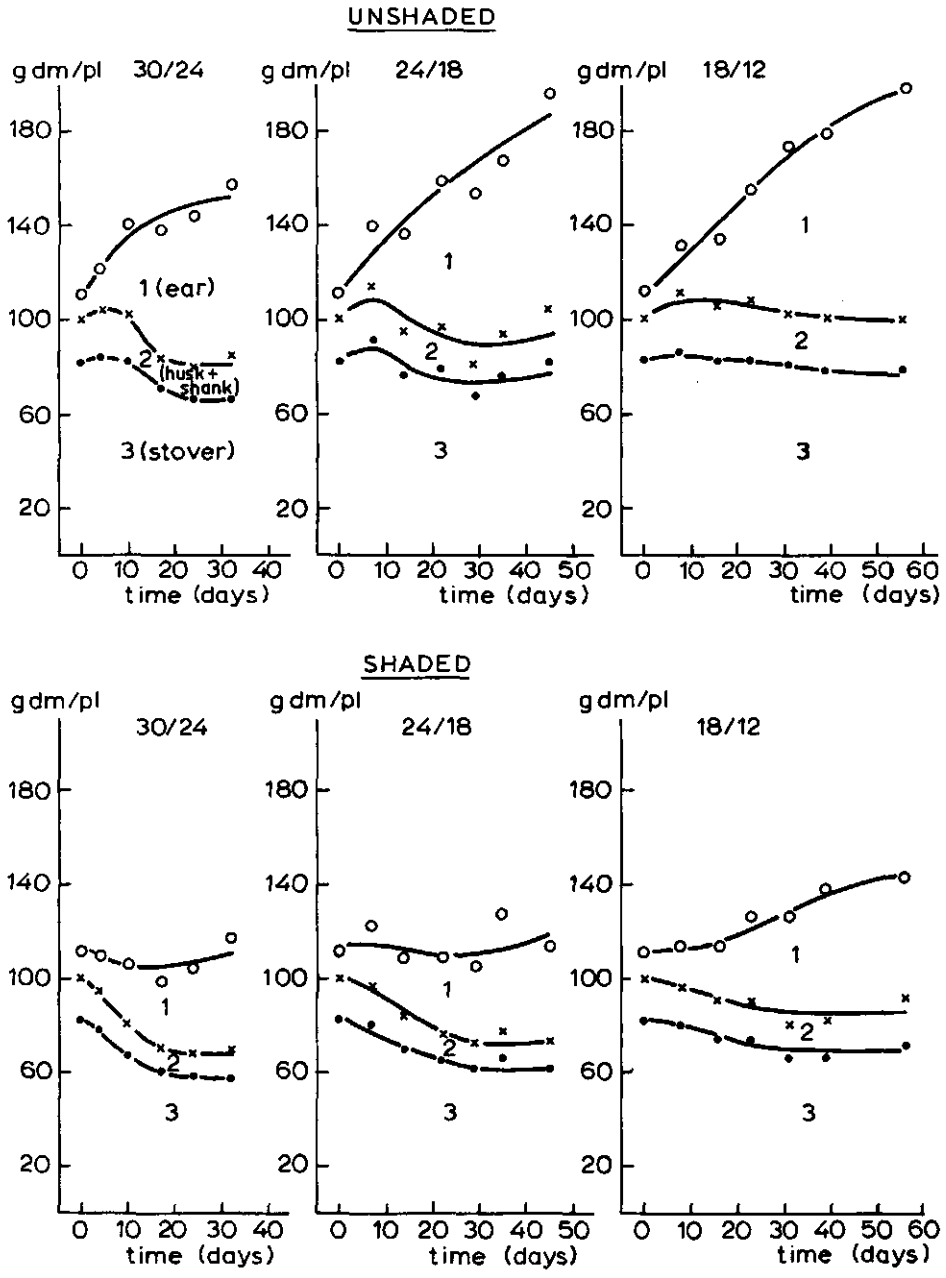


FIG. 13. Dry-matter production and distribution for all treatments in Experiment 3. Day 0 = date of initiation of treatment.

occurs. The accumulation of Ca in the above-ground parts of the plant was reduced by shading during period 4, but the amounts of Ca in ears were very low and it was not remobilized in the plant. Ca does not play a role in the redistribution pattern.

Kernel abortion also decreases the amount of carbohydrates that has to be translocated from the vegetative parts to the ears. The redistribution of carbohydrates, however, was still intensive. Much of the fraction that was not identified as ash, cell wall, non-structural carbohydrate or crude protein also left the vegetative parts if redistribution of other compounds was intensive.

Whole plant. As an example, Fig. 13 illustrates the dry-matter production and distribution of Nicco. Although fewer sampling dates were available for Ula and Dara, the general pattern was essentially similar. Since some data were deviant because there were few plants in the samples, curves were drawn using the cell-wall yield as a standardizing criterion. Final yields increased with falling temperature and increasing light intensity. Initially, the production rates of all hybrids in the unshaded treatments tended to increase with rising temperatures. If shaded, however, crop-production rate was highest in treatment 18/12.

Low light intensity resulted in a strong reaction during the first part of the grain filling, but dry-matter production rate was higher in the later part associated with a decrease in rate of redistribution. This is especially evident in treatment 18/12 (Fig. 13) but was also clear in Ula and Dara in treatments 24/18 and 30/24. This phenomenon of habituation to a growth-limiting climatic factor during a rather fixed, unplastic stage of the crop is conspicuous. The phenomenon might be explained by the hypothesis presented by STRUIK and DEINUM (1982), who stated that shading promptly curtailed root activity. Reduced root activity might have induced the observed kernel abortion. If abortion occurs early in the grain-filling period, a new balance might be obtained, since partial sterility favours translocation of sugars to the roots. When this new balance is achieved, the plants may function better than expected on the basis of their previous performance. Data from the root samples of Experiment 3 tended to support this hypothesis, but the difficulties of separating roots from root medium affected the reliability of the data. The linear correlation coefficient between non-structural carbohydrate content in the roots and number of active kernels, however, was highly significant ($P < 0.01$; $n = 35$).

Quality of the organic matter

Fig. 14 illustrates the trend in D_{om} of the most relevant plant parts in each treatment in Experiment 3. The development of the proportion of the most digestible part (i.e. the ear fraction) is also given.

Ear digestibility increased slightly during early stages of grain filling but subsequently remained constant. The same pattern was found in Experiment 2. This agrees with results obtained by PERRY and COMPTON (1977) and AERTS et al. (1978). Temperature did not influence ear digestibility. Continuous shading also barely affected ear digestibility, since shelling percentage and thus cell-wall con-

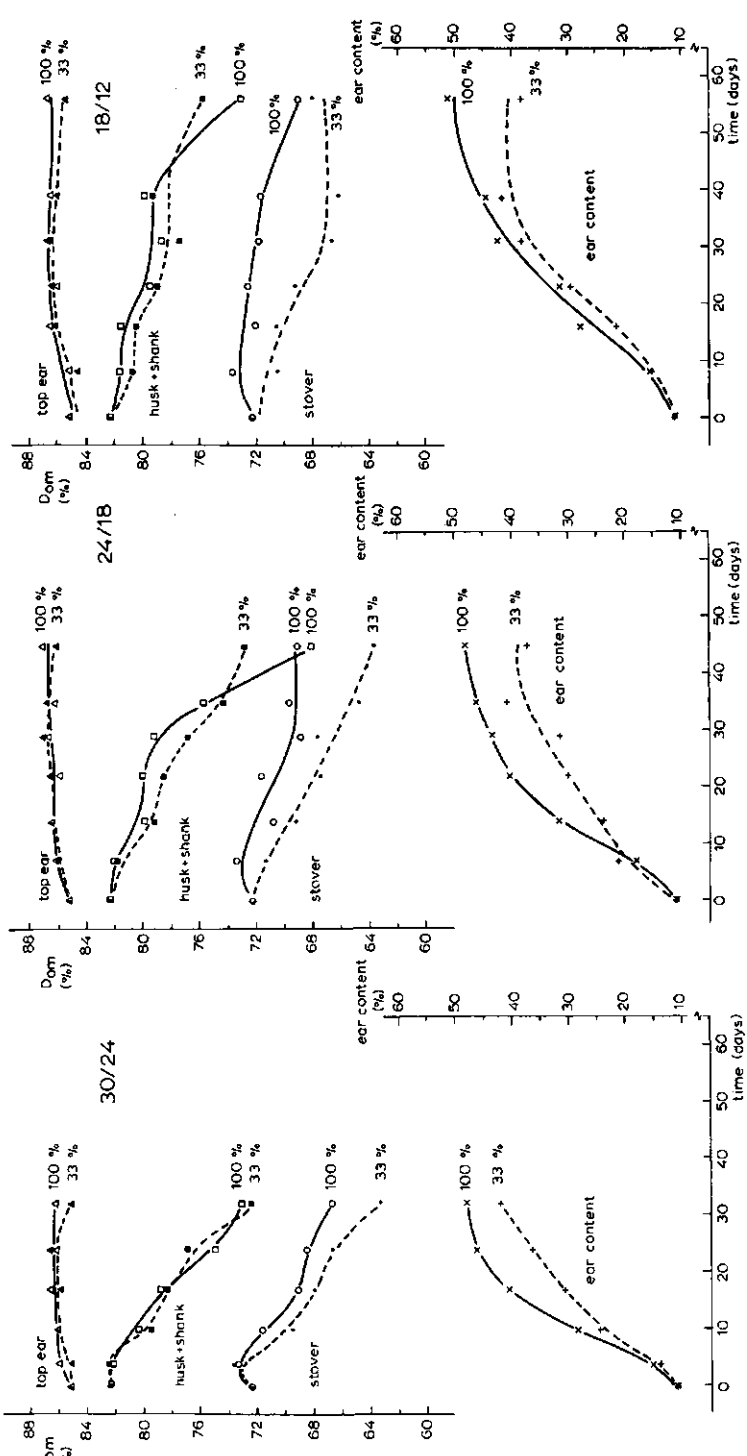


FIG. 14. Development of ear content and digestibility of the main plant parts over time after grain set for two light intensities at 30/24, 24/18 and 18/12 °C. Day 0 = date of initiation of treatment.

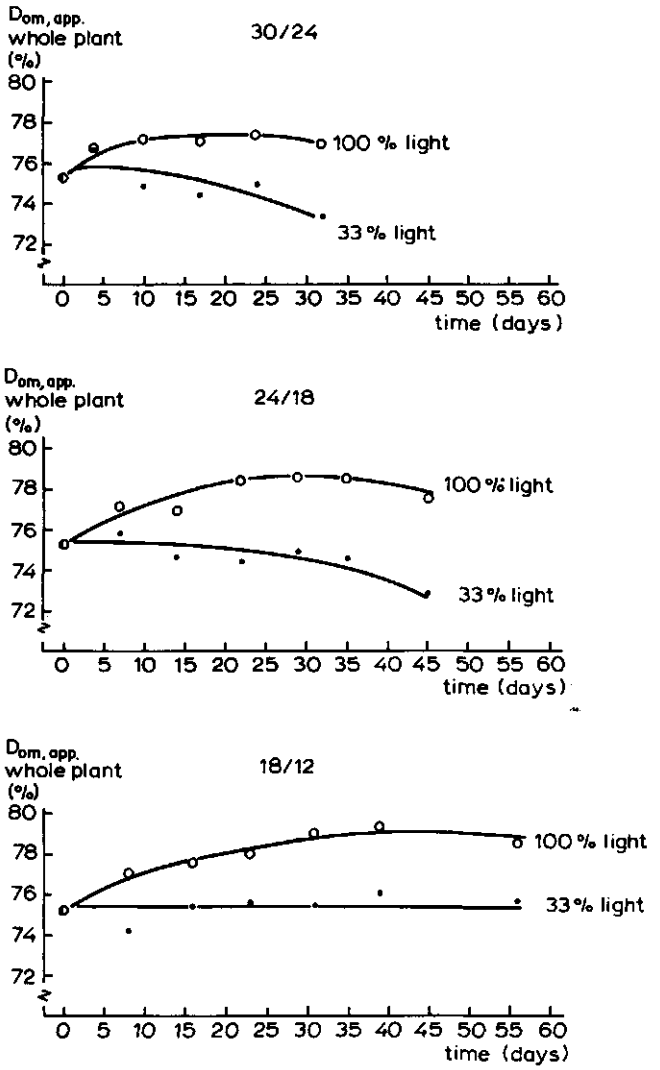


FIG. 15. Apparent digestibility of the whole plant plotted against time during period 4, for six temperature/light combinations. Day 0 = date of initiation of treatment.

tent were almost unaffected (see above). This agrees with field data obtained by STRUIK and DEINUM (1982). Shading, however, considerably reduced the proportion of organic matter in the ears.

The digestibility of husk + shank decreased during period 4. This decline was more rapid at higher temperatures but only slightly affected by radiation. In treatment 30/24 no consistent differences between shaded and unshaded plants could be identified.

In both lower temperature regimes, low light intensity initially produced lower D_{om}, but finally a much higher D_{om} was found. Also in Experiment 2 the digestibility of husk + shank in shaded crops was better: a prolonged increase in the

cell-wall content of the husks and shanks of unshaded crops caused this reversal. (This prolonged increase in cell-wall content probably occurred because redistribution from the husks to the kernels was necessary for a longer period).

Stover digestibility declined during period 4 and this decline was more rapid at higher temperature and at lower light intensity. In Experiment 2 some treatments originally showed a considerable increase in the digestibility of the stover before the decline set in. Otherwise the pattern was similar. Trends and differences in digestibility agree with the redistribution phenomena. Thus only the digestibility of vegetative parts and the proportion of ear parts were sensitive to temperature and light intensity during period 4.

These two effects of temperature and light intensity resulted in the patterns of whole-plant digestibility shown in Fig. 15. At 100% light, the increase in whole-plant digestibility continued for longer at lower temperatures, giving higher final digestibilities (Table 10). Similarly, D_{om} decreased less in shaded crops at lower temperatures. At higher temperatures, the small decline in D_{cwc} could not be compensated for by a concomitant decrease in the cell-wall content. In Experiments 2 and 3, light intensity during grain filling was relatively constant and fairly high. In practice in The Netherlands, diurnal amounts of light drop sharply during grain filling, so that a standard crop merges from the conditions experienced by the unshaded crops in these experiments to those experienced by the shaded crops. The pattern of digestibility in the unshaded crops in Experiments 2 and 3 is similar to the pattern found in Experiment 1, during the same period.

Differences in cell-wall digestibility had little effect on organic-matter digestibility. Plants had reached their maximum height before the climate shift. As Fig. 6 shows, an important differentiation in stover D_{cwc} is unlikely beyond that stage. The D_{cwc} of husk + shank was not affected by light intensity either. Its rate of decline in D_{cwc} was affected by temperature (as was plant development) but the final extent of the D_{cwc} decline (thus the D_{cwc} at the same physiological stage) was not.

Cell-wall production was affected both by temperature and light intensity and in the same direction as was dry-matter production. This limitation of cell-wall formation was very evident in husks + shanks and in ears, but was only small in the stover. In the husk + shank and in the ear fraction, the yield of cell walls from shaded plants was only approximately 70% of that of the unshaded plants, and plants in treatment 30/24 yielded about 30% fewer cell walls than plants in treatment 18/12. These reductions in the amounts of cell wall resulted in smaller effects of the treatments on the quality of ears and of husks + shanks than on the quality of stover. The most relevant factor in determining the digestibility of the vegetative parts was the extent of assimilate redistribution.

Thus in ears, dry-matter accumulation and cell-wall formation were equally affected by climatic conditions. In stover, the amounts of cell wall and their quality were barely affected, so that the necessity for redistribution was the over-

riding factor in stover quality. In the husk + shank fraction, cell-wall formation, the rate at which the cell-wall digestibility declined, and the extent and rate of translocation of metabolites all affected quality.

Since shading affected cell-wall formation in the plant organs with the best cell-wall quality, a small negative effect of shading on cell-wall digestibility of the whole plant must be expected. Table 10 confirms this supposition but also indicates that the greatest differences in cell-wall quality were found in Nicco. This hybrid showed a strong decline in D_{cwc} during the final part of the grain-filling period for shaded crops. Before this process started, the effects of shading on D_{cwc} were certainly not greater than in Ula and Dara. It is unlikely that Nicco's greater sensitivity to shading as expressed in decreasing digestibility is genetically determined.

Table 10 also presents the cell-wall contents of the whole crop at final sampling. In Experiments 2 and 3 digestibility was mainly related to this quality criterion, as is illustrated in Fig. 16 in which the whole-crop digestibility on each sampling date is plotted against the cell-wall content on the basis of the organic matter. Physiological age, temperature and light intensity all affected quality predominantly by their effects on cell-wall content. The data from the final samplings are underlined; in Ula and Dara they were equally distributed above and below the regression line, but in Nicco they were all below that line. Although also significant in both experiments, the linear correlation coefficient between D_{cwc} and D_{om} was much lower, especially in Experiment 2.

TABLE 10. Quality parameters of all treatments in Experiments 2 and 3 at final sampling (whole plant).

Day/night temperatures (°C)		30/24		24/18		18/12	
Light treatment		unshaded	shaded	unshaded	shaded	unshaded	shaded
D_{om} (%)	Ula	77.3	74.8	78.5	76.1	78.8	76.0
	Dara	76.3	74.0	78.7	75.4	77.3	76.4
	Nicco	76.9	73.3	77.5	72.8	78.5	75.6
	Mean	*76.8*	*74.0*	*78.2*	*74.8*	*78.2*	*76.0*
		75.4		*76.5*		*77.1*	
D_{cwc} (%)	Ula	68.3	64.7	66.2	66.4	68.4	67.4
	Dara	65.4	66.4	68.1	67.4	68.0	66.3
	Nicco	73.6	69.7	72.2	66.2	76.1	70.9
	Mean	*69.1*	*66.9*	*68.8*	*66.7*	*70.8*	*68.2*
		68.0		*67.8*		*69.5*	
cwc% (%)	Ula	39.8	46.4	33.5	41.1	34.8	39.4
	Dara	42.3	47.3	34.8	44.3	36.4	40.2
	Nicco	43.6	51.8	38.6	47.8	37.9	46.0
	Mean	*41.9*	*48.5*	*35.6*	*44.4*	*36.4*	*41.9*
		45.2		*40.0*		*39.1*	

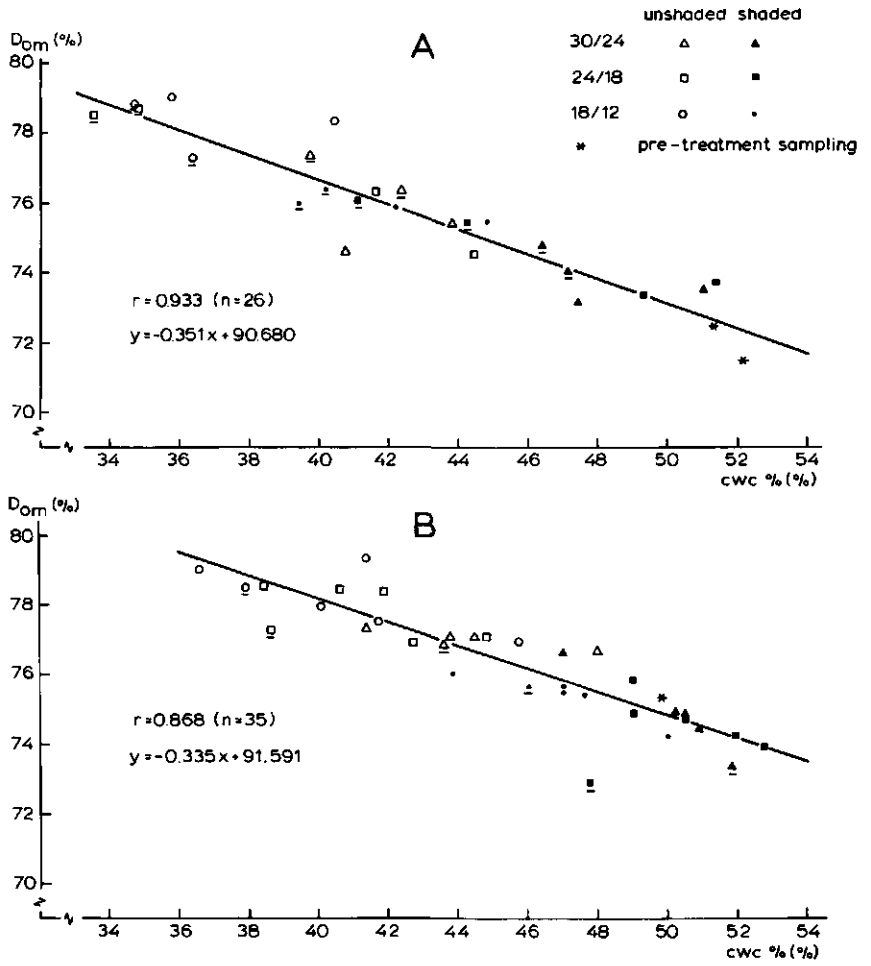


FIG. 16. Relation between cell-wall content of the organic matter (cwc%) of the whole plant and apparent digestibility of the organic matter (D_{om}) of the whole plant, in Experiment 2 (A) and Experiment 3 (B). Data from final samplings are underlined.

Résumé: *Increased temperatures during period 4 accelerated grain filling, the redistribution of certain metabolites, D_{cwc} decline and plant senescence, but curtailed the duration of grain filling and of leaf area, final ear yield, ear size and kernel activity, whole-plant yield, cell-wall yield and crop quality.*

In addition, low light intensity during period 4 stimulated the senescence of the ear and the redistribution of metabolites to the ear, and may have stimulated cell-wall maturation to some extent. Poor light conditions reduced cell-wall formation and sometimes slowed down leaf senescence.

Both temperature and light mainly affected quality by means of their effects on the proportion of ear in the whole plant and the cell-wall content of the vegetative parts, resulting in a strong correlation between crop digestibility and cell-wall content of the whole crop.

TABLE 11. Summary of effects of temperature during different stages of development on final dry-matter and cell-wall production, and on final quality parameters. Light intensity is assumed to be constant.

	Dry-matter production	Cell-wall production	Cell-wall content	Cell-wall digestibility	Organic-matter digestibility
Period 1	++	++	± or +	±	± or −
Period 2	−−	−−	±	−	−
Period 3	−−	− or ±	+	−	−
Period 4	−−	−	+	± or −	−
Entire growing season	−−	−	+	−	−

+ (+) indicates that a rise in temperature produces a (strong) positive effect.
± indicates that inconsistent or small effects are expected.
− (−) indicates that a rise in temperature produces a (strong) negative effect.

Comparisons with field data

Table 11 summarizes the findings of the above-described phytotron and desk research. It also presents the expected effects of temperature over the entire growing season. These expectations agree with data obtained by DEINUM (1976), although he did not present data on whole-crop quality.

In the years 1977, 1978, 1979, 1980 and 1981 the hybrid LG 11 was grown in the field at the same location and following the same cultural practices. Detailed data on temperature, crop development and quality were available, enabling the validity of the hypothesis to be tested. In Table 12 some relevant data are presented.

The number of leaves per plant differed significantly over the years. For example, in 1977, LG 11 had 1.5 leaves per plant more than in 1979, although the mean air temperature during the pre-tassel initiation period was almost the same. TOLLENAAR and HUNTER (1981), however, found that leaf number was determined during a short period to the tassel initiation. In the data presented in Table 12, the simple linear correlation coefficient between mean air temperature during the four days before the 6.5-leaf stage and the final number of leaves was 0.99 ($P < 0.01$). The regression coefficient was 0.28 leaves/°C, which agrees with the value of 0.2 found by TOLLENAAR et al. (1979). This temperature effect restricts the usefulness of maturity indexing systems that are based on the relationship between rate of crop development and temperature or heat unit.

The number of leaves, or rather the number of stem internodes, is crucial for final cell-wall yield and final cell-wall content. A significant linear relationship between number of leaves and cell-wall yield did indeed exist ($r = 0.97$; $n = 4$; $P < 0.05$). However, the cell-wall analysis of the 1978 crop was not available and most probably the cell-wall yield in that cool year was lower than expected on the basis of this relation. This supposition is supported by the good digestibility compared with the 1977 crop. The low height of the plant given the large number of stem internodes may be connected with this deviation. Climatic conditions during periods 2, 3 and 4 of the 1978 growing season were

TABLE 12. Crop descriptions of LG 11, grown at the same location for five years, together with the mean temperatures during different stages of growth for each year.

Year	1977	1978	1979	1980	1981
number of leaves per plant	15.3	15.7	13.8	14.2	14.9
height of plant (cm)	261	226	214	215	235
dry-matter yield ($Mg.ha^{-1}$)	15.4	13.4	12.8	14.1	17.0
cell-wall yield ($Mg.ha^{-1}$)	7.1	–	5.2	6.1	7.0
cell-wall content (% of organic matter)	49.3	–	42.2	44.8	42.4
digestibility (% of organic matter)	71.5	74.1[1])	74.8	73.6	74.3
cell-wall digestibility (%) after standardization of the true digestibility	61	–	61	61	61
T_1 (°C)	12.1	12.9	12.0	11.7	12.5
T_f (°C)	19.8	20.6	13.8	15.9	17.6
T_2 (°C)	16.2	14.7	15.3	15.5	15.2
T_3 (°C)	16.4	15.5	16.0	17.8	19.0
T_4 (°C)	13.0	12.8	13.7	14.5	14.9
T_m (°C)	14.1	13.8	14.0	14.4	14.8

T_1 = mean temperature during period 1.
T_f = mean temperature during 4 days prior to the 6.5-leaf stage.
T_2 = mean temperature during period 2.
T_3 = mean temperature during period 3.
T_4 = mean temperature during period 4.
T_m = mean temperature during the entire growing season.
[1]) Ear samples were not analysed in this year. Digestibility was calculated assuming that the digestibility and ash content of the ear were equal to the means of the years 1977, 1979, 1980 and 1981.

clearly unfavourable for dry-matter production and cell-wall formation.

Thus, the annual variation in cell-wall yield can largely be explained by variation in air temperature just prior to the 6.5-leaf stage. Extreme climatic conditions during the post-tassel initiation period, however, may cause deviations from this general pattern.

The cell-wall content also depends on the dilution of the cell walls with non-structural carbohydrates after silking. During the autumn in The Netherlands, prevailing temperatures are mostly below the optimum for dry-matter production. Therefore, an increase in temperature during period 4 will mostly benefit dry-matter production and thus crop quality. This means that the 1981 crop diluted its amounts of cell wall much more than the 1977 crop, although the cell-wall yields were approximately the same. The light intensity also plays an important role during this stage and is closely correlated with temperature under uncontrolled conditions.

Mean air temperatures during periods 2 and 3 varied considerably between years, but the mean temperatures during the period from 6.5-leaf stage until the grain-filling period ranged between 14.8–16.2 °C only. This range is much too small to induce differences in cell-wall digestibility. The D_{cwc} of all crops

for which the cell-wall analysis was available, was the same, resulting in a significant linear correlation between cell-wall content and digestibility of organic matter ($r = -0.99$; $n = 4$; $P < 0.01$).

High temperatures during grain filling make the crop suitable for ensiling at an earlier date or cause higher dry-matter contents at harvest if the harvest date is not advanced. This aspect of suitability for ensiling has not been taken into account in this analysis, but certainly plays an important role in areas at the limits of the range of maize.

The practical implications of the results obtained will be discussed in the author's doctoral thesis.

Summary

The effects of temperature on the growth, development, dry-matter production, dry-matter distribution and digestibility of forage maize were analysed.

Higher temperatures during the *period before tassel initiation* stimulated whole-crop yield without affecting its quality. During this period, however, temperature may affect the number of stem internodes and thus the plant's ability to form cell walls. High temperatures during early growth may therefore reduce crop quality, especially when the digestibility of cell walls is poor.

Higher temperatures during the *period from tassel initiation to anthesis* greatly accelerates plant development, without affecting leaf number. Stem diameter decreased as temperature rose but the final plant height in the various temperature treatments was similar. The interval between anthesis and silking was dramatically lengthened by high temperatures during this period. Initially, dry-matter production was more rapid at higher temperatures, but total dry matter at anthesis and productivity after anthesis decreased as temperatures rose. The digestibility of organic matter and of cell walls before anthesis declined more rapidly at higher temperatures, because temperature affected the rate of development, the cell-wall content, the encrustation of lignin and of silica and other physical/chemical processes. The latter were ascertained by estimating potential cell-wall digestibility and the rate of digestion of potentially digestible cell walls. Differences disappeared during the post-anthesis period, during which the temperature was the same for all treatments in this experiment.

The temperature *during flowering* may affect production and quality by its influence on anther emergence, pollen viability, silk emergence and grain set. In addition, temperature may affect the intensity of the ongoing cell-wall formation and the quality of the cell walls.

High temperatures *during grain fill* not only accelerated grain filling but also leaf senescence: they also reduced kernel viability, the duration of grain filling, and final plant yield. Crop quality was affected because temperature influenced the proportion of ear in the whole plant and the cell-wall content of the stover. Low light during this period influenced crop quality in the same way as high

temperature. Leaf senescence, however, was sometimes retarded by shading.

When these results were compared with field data it appeared that in practice it is mainly the temperature just prior to tassel initiation that is critical for crop quality.

Acknowledgments

I thank Mrs L. M. van Ravenswaaij and Mrs T. de Vent for their share in handling the experiments and collecting the data. Thanks are due to Mrs E. van Heusden, Mrs J. G. M. Miechels, Mrs I. A. M. Reurink and Mrs C. de Wit for skilful chemical analysis.

I am very indebted to Prof. Dr J. Bruinsma, Dr Ir B. Deinum, Prof. Ir J. G. P. Dirven, Prof. Dr Ir A. J. H. van Es, Prof. Ir M. L. 't Hart and Prof. Ir L. J. P. Kupers for their valuable and constructive criticism.

I gratefully acknowledge the 'Stichting Nederlands Graan-Centrum' for a grant permitting the employment of a full-time assistant.

References

Adelana, B. O. and G. M. Milbourn: 1972. The growth of maize. II. Dry-matter partition in three maize hybrids. J. agric. Sci., Camb., **78**: 73–78.

Aerts, J. V., B. G. Cottyn, D. L. De Brabander, Ch. V. Boucqué and F. X. Buysse: 1978. Digestibility and feeding value of maize. Proc. European Maize Meeting, Louvain-La-Neuve (Belgium), (ed.) J.-F. Ledent, pp. 106–128.

Akin, D. and D. Burdick: 1981. Relationships of different histochemical types of lignified cell walls to forage digestibility. Crop Sci., **21**: 577–581.

Allison, J. C. S. and T. B. Daynard: 1979. Effect of a change in time of flowering, induced by altering photoperiod or temperature on attributes related to yield in maize. Crop Sci., **19**: 1–4.

Allison, J. C. S. and D. J. Watson: 1966. The production and distribution of dry matter in maize after flowering. Ann. Bot. N.S., **30**: 365–381.

Andrieu, J.: 1976. Factors influencing the composition and nutritive value of ensiled whole-crop maize. Animal Feed Science and Technology, **1**: 381–392.

Bailey, R. W., J. A. Monro, S. E. Pickmere and A. Chesson: 1976. Herbage hemicellulose and its digestion by the ruminant. In: Carbohydrate research in plants and animals. Misc. Papers nr. 12, Agric. Univ. Wageningen, pp. 1–15.

Beauchamp, E. G., L. W. Kannenberg and R. B. Hunter: 1976. Nitrogen accumulation and translocation in corn genotypes following silking. Agron. J., **68**: 418–422.

Below, F. E., L. E. Christensen, A. J. Reed and R. H. Hageman: 1981. Availability of reduced N and carbohydrates for ear development of maize. Plant Physiol., **68**: 1186–1190.

Blacklow, W. M.: 1972a. Mathematical description of the influence of temperature and seed quality on imbibition by seeds of corn (*Zea mays* L.). Crop Sci., **12**: 643–646.

Blacklow, W. M.: 1972b. Influence of temperature on germination and elongation of the radicle and shoot of corn (*Zea mays* L.). Crop Sci., **12**: 647–650.

Blondon, F. and A. Gallais: 1976. Influence de la température, de la valeur de l'éclairement et de la photopériode sur le développement floral de quatre génotypes de maïs. Ann. Amélior. Plantes, **26**: 195–213.

Breuer, C. M., R. B. Hunter and L. W. Kannenberg: 1976. Effects of 10- and 20-hour photoperiod treatments at 20 and 30 C on rate of development of a single-cross maize (*Zea mays*) hybrid. Can. J. Plant Sci., **56**: 795–798.

BROUWER, R., A. KLEINENDORST and J. TH. LOCHER: 1973. Growth responses of maize plants to temperature. In: Plant response to climatic factors. Proc. Uppsala Symp., 1970. UNESCO, Paris, pp. 169–174.

BUNTING, E. S.: 1975. The question of grain content and forage quality in maize: comparisons between isogenic fertile and sterile plants. J. agric. Sci., Camb., **85**: 455–463.

BUNTING, E. S.: 1976. Effects of grain formation on dry matter distribution and forage quality in maize. Expl Agric., **12**: 417–428.

BUREN, L. L., J. J. MOCK and I. C. ANDERSON: 1974. Morphological and physiological traits in maize associated with tolerance to high plant density. Crop Sci., **14**: 426–429.

CHESSON, A.: 1982. Degradation of plant cell walls by rumen organisms. Livestock Prod. Sci. (in press).

CHOWDHURY, S. I. and I. F. WARDLAW: 1978. The effect of temperature on kernel development in cereals. Aust. J. agric. Res., **29**: 205–223.

COLIGADO, M. C. and D. M. BROWN: 1975a. A bio-photo-thermal model to predict tassel-initiation time in corn (*Zea mays* L.). Agric. Met., **15**: 11–31.

COLIGADO, M. C. and D. M. BROWN: 1975b. Response of corn (*Zea mays* L.) in the pre-tassel initiation period to temperature and photoperiod. Agric. Met., **14**: 357–367.

CUMMINGS, D. G. and J. W. DOBSON JR.: 1973. Corn for silage as influenced by hybrid maturity, row spacing, plant population and climate. Agron. J., **65**: 240–243.

DAYNARD, T. B. and L. W. KANNENBERG: 1976. Relationships between length of the actual and effective grain filling periods and the grain yield of corn. Can. J. Plant Sci., **56**: 237–242.

DAYNARD, T. B., J. W. TANNER and D. J. HUME: 1969. Contribution of stalk soluble carbohydrates to grain yield in corn (*Zea mays* L.). Crop Sci., **9**: 831–834.

DEINUM, B.: 1974. Structural inhibitors of quality in forage. Proc. Eur. Grassl. Fed. 5th Gen. Meeting, Växtodling, 1973, pp. 42–52.

DEINUM, B.: 1976. Effect of age, leaf number and temperature on cell wall and digestibility of maize. In: Carbohydrate research in plants and animals. Misc. Papers nr. 12, Agric. Univ. Wageningen, pp. 29–41.

DEINUM, B.: 1979. Invloed van uitwendige omstandigheden op produktie en celwandsamenstelling van gras. Proc. Symp. 'Ruwe celstof of voedingsvezel?', organized by Contactcommissie Celwand en celwandvertering, NRLO, Wageningen, pp. 27–33.

DEINUM, B.: 1981. The influence of physical factors on the nutrient content of forages. Mededelingen Landbouwhogeschool Wageningen **81-5**, pp. 1–18.

DEINUM, B. and J. G. P. DIRVEN: 1971. Climate, nitrogen and grass. 4. The influence of age on chemical composition and in vitro digestibility of maize (*Zea mays* L.) and tall fescue (*Festuca arundinacea* Schreb.). Neth. J. agric. Sci., **19**: 264–272.

DEINUM, B. and J. G. P. DIRVEN: 1975. Climate, nitrogen and grass. 6. Comparison of yield and chemical composition of some temperate and tropical grass species grown at different temperatures. Neth. J. agric. Sci., **23**: 69–82.

DEINUM, B. and J. G. P. DIRVEN: 1976. Climate, nitrogen and grass. 7. Comparison of production and chemical composition of *Brachiaria ruziziensis* and *Setaria sphacelata* grown at different temperatures. Neth. J. agric. Sci., **24**: 67–78.

DEINUM, B. and J. KNOPPERS: 1979. The growth of maize in the cool temperate climate of the Netherlands: Effect of grain filling on production of dry matter and on chemical composition and nutritive value. Neth. J. agric. Sci., **27**: 116–130.

DIRVEN, J. G. P. and B. DEINUM: 1977. The effect of temperature on the digestibility of grasses. An analysis. Forage Res., **3**: 1–17.

DONSELAAR, B. van and A. STEG: 1980. Voederwaardebepaling en voederwaardeberekening van mengvoer voor melkvee. Rapport no. **132**, Instituut voor Veevoedings Onderzoek 'Hoorn', Lelystad, pp. 1–12.

DUNCAN, W. G.: 1975. Maize. In: Crop physiology. Some case histories. (ed.) L. T. EVANS, Cambridge University Press, London, pp. 23–50.

DUNCAN, W. G. and J. D. HESKETH: 1968. Net photosynthetic rates, relative leaf growth rates and leaf numbers of 22 races of maize grown at eight temperatures. Crop Sci., **8**: 670–674.

EDMEADES, G. O. and T. B. DAYNARD: 1979. The development of plant-to-plant variability in maize at different planting densities. Can. J. Plant Sci., **59**: 561–576.

FRIEND, D. J. C. and Marion E. POMEROY: 1970. Changes in cell size and number associated with the effects of light intensity and temperature on the leaf morphology of wheat. Can J. Bot., **48**: 85–90.

GENTER, C. F., G. D. JONES and M. T. CARTER: 1970. Dry matter accumulation and depletion in leaves, stems, and ears of maturing maize. Agron. J., **62**: 535–537.

GMELIG MEYLING, H. D.: 1973. Effect of light intensity, temperature and daylength on the rate of leaf appearance of maize. Neth. J. agric. Sci., **21**: 68–76.

GOERING, H. K. and P. J. VAN SOEST: 1970. Forage fiber analysis; apparatus, reagents, procedures and some applications. USDA Agric. Handbook No. **359**.

GOODRICH, R. D. and J. C. MEISKE: 1979. Rate and extent of digestion. Aids for explaining some nutritional observations. Proc. 1979 Minnesota Nutrition Conference: 51–64.

GROBBELAAR, W. P.: 1963. Responses of young maize plants to root temperatures. Mededelingen Landbouwhogeschool **63-5**, Agric. Univ. Wageningen, pp. 1–71.

GRZESIAK, S., S. B. ROOD, S. FREYMAN and D. J. MAJOR: 1981. Growth of corn seedlings: Effects of night temperature under optimum soil moisture or under drought conditions. Can. J. Plant Sci., **61**: 871–877.

HACKER, J. B. and D. J. MINSON: 1981. The digestibility of plant parts. Herbage Abstracts, **51**: 459–482.

HANWAY, J. J.: 1963. Growth stages of corn (*Zea mays* L.). Agron. J., **55**: 487–492.

HARTLEY, R. D.: 1981. Chemical constitution, properties and processing of lignocellulosic wastes in relation to nutritional quality for animals. Agric. Environm., **6**: 91–113.

HAY, R. E., E. B. EARLY and E. E. DETURK: 1953. Concentration and translocation of nitrogen compounds in the corn plant (*Zea mays*) during grain development. Plant Physiol., **28**: 606–621.

HERRERO, M. P. and R. R. JOHNSON: 1980. High temperature stress and pollen viability of maize. Crop Sci., **20**: 796–800.

HUNTER, R. B., M. TOLLENAAR and C. M. BREUER: 1977. Effects of photoperiod and temperature on vegetative and reproductive growth of a maize (*Zea mays*) hybrid. Can. J. Plant Sci., **57**: 1127–1133.

INGLE, J., D. BEITZ and R. H. HAGEMAN: 1965. Changes in composition during development and maturation of maize seeds. Plant Physiol., **40**: 835–839.

JOANNING, S. W., D. E. JOHNSON and B. P. BARRY: 1981. Nutrient digestibility depressions in corn silage-corn grain mixtures fed to steers. J. Anim. Sci., **53**: 1095–1103.

JOHNSON, D. R. and J. W. TANNER: 1972. Calculation of the rate and duration of grain filling in corn (*Zea mays* L.). Crop Sci., **12**: 485–486.

JONES, R. J., B. G. GENGENBACH and V. B. CARDWELL: 1981. Temperature effects on in vitro kernel development of maize. Crop Sci., **21**: 761–766.

JOVANOVIĆ, B. and Ž. JOVANOVIĆ: 1963. The effect of temperature and relative air humidity on corn fertilization. Review of research work at the Faculty of Agriculture, Univ. of Belgrade, Yugoslavia. Year 11 no. **355**, pp. 1–11.

LUCAS, E. O.: 1981. Remobilization of stem assimilates in maize varieties grown under tropical conditions, Maydica, **26**: 287–292.

MERTENS, D. R.: 1977. Dietary fiber components: relationship to the rate and extent of ruminal digestion. Federation Proc., **36**: 187–192.

MERTENS, D. R. and P. J. VAN SOEST: 1972. Estimation of the maximum extent of digestion. J. Anim. Sci., **35**: 286 (Abstr.).

MINSON, D. J.: 1973. Effect of fertilizer nitrogen on digestibility and voluntary intake of *Chloris gayana, Digataria decumbens* and *Pennisetum clandestinum*. Austr. J. Exp. Agric. and Anim. Husbandry, **13**: 153–157.

MINSON, D. J.: 1976. Relation between digestibility and composition of feed. A review. In: Carbohydrate research in plants and animals. Misc. Papers nr. 12, Agric. Univ. Wageningen, pp. 101–114.

MINSON, D. J. and M. N. MCLEOD: 1970. The digestibility of temperate and tropical grasses. Proc. XI. Int. Grassl. Congress, Queensland, Australia, (ed.) M. J. T. NORMAN, pp. 719–722.

MONTGOMERY, F. G.: 1911. Correlation studies of corn. Nebr. agric. Exp. Stn ann. Rep., **24**: 108–159.
NELSON, C. J. and K. J. TREHARNE: 1973. Temperature adaptation in *Festuca arundinacea*. Report Welsh Breeding Station for 1973, University College of Wales, Aberystwyth, p. 11.
PAIN, B. F.: 1978. Nutritional requirements of forage maize. In: Forage maize. (eds) E. S. BUNTING, B. F. PAIN, R. H. PHIPPS, J. M. WILKINSON and R. E. GUNN, Agricultural Research Council, London, pp. 87–116.
PERRY, L. J. JR. and W. A. COMPTON: 1977. Serial measures of dry matter accumulation and forage quality of leaves, stalks and ears of three corn hybrids. Agron. J., **69**: 751–755.
PHIPPS, R. H. and R. F. WELLER: 1979. The development of plant components and their effects on the composition of fresh and ensiled forage maize. I. The accumulation of dry matter, chemical composition and nutritive value of fresh maize. J. agric. Sci., Camb., **92**: 471–483.
PITMAN, W. D., D. M. VIETOR and E. C. HOLT: 1981. Digestibility of kleingrass forage grown under moisture stress. Crop Sci., **21**: 951–953.
PRINS, R. A., W. C. CLINÉ-THEIL and A. TH. VAN 'T KLOOSTER: 1981. An in vitro procedure for the estimation of in vivo digestibility of roughage plant cell wall components in herbivores using mixed rumen microorganisms. Agric. Environm., **6**: 183–194.
RICHARDS, G. N.: 1976. Search for factors other than 'lignin-shielding' in protection of cell-wall polysaccharides from digestion in the rumen. In: Carbohydrate research in plants and animals. Misc. Papers nr. 12, Agric. Univ. Wageningen, pp. 129–135.
SMITH, L. W., H. K. GOERING and C. H. GORDON: 1972. Relationships of forage composition with rates of cell wall digestion and indigestibility of cell walls. J. Dairy Sci., **55**: 1140–1147.
SMITH, L. W., H. K. GOERING, D. R. WALDO and C. H. GORDON: 1971. In vitro digestion rate of forage cell wall components. J. Dairy Sci., **54**: 71–76.
SOFIELD, I., L. T. EVANS and I. F. WARDLAW: 1974. The effect of temperature and light on grain filling in wheat. In: Mechanisms of regulation of plant growth. Bull. Royal Soc. N.Z. **12**: 909–915.
SPIERTZ, J. H. J.: 1974. Grain growth and distribution of dry matter in the wheat plant as influenced by temperature, light energy and ear size. Neth. J. agric. Sci., **22**: 207–220.
SPIERTZ, J. H. J.: 1977. The influence of temperature and light intensity on grain growth in relation to the carbohydrate and nitrogen economy of the wheat plant. Neth. J. agric. Sci., **25**: 182–197.
STRUIK, P. C.: 1982a. Effect of a switch in photoperiod on the reproductive development of temperate hybrids of maize. Neth. J. agric. Sci., **30**: 69–83.
STRUIK, P. C.: 1982b. Production pattern, chemical composition and digestibility of forage maize (*Zea mays* L.). Mededeling no. **64**, Vakgroep Landbouwplantenteelt en Graslandkunde, Agric. Univ. Wageningen, pp. 1–28.
STRUIK, P. C. and B. DEINUM: 1982. Effects of light intensity after flowering on the productivity and quality of silage maize. Neth. J. agric. Sci., **30**: 297–316.
TOLLENAAR, M. and T. B. DAYNARD: 1978. Kernel growth and development at two positions on the ear of maize (*Zea mays*). Can. J. Plant Sci., **58**: 189–197.
TOLLENAAR, M., T. B. DAYNARD and R. B. HUNTER: 1979. Effect of temperature on rate of leaf appearance and flowering date in maize. Crop Sci., **19**: 363–366.
TOLLENAAR, M. and R. B. HUNTER: 1981. Quantification of the effects of temperature and photoperiod on maize development. Agronomy Abstracts 1981, Amer. Soc. of Agronomy, p. 14.
VAN SOEST, P. J.: 1965. Comparison of two different equations for the prediction of digestibility from cell contents, cell wall constituents and the lignin content of acid detergent fiber. Paper **118**, Ann. Meeting Amer. Dairy Sci. Ass., Lexington, Kentucky, 1965, pp. 1–7.
VAN SOEST, P. J.: 1967. Development of a comprehensive system of feed analyses and its application to forages. J. anim. Sci., **26**: 119–128.
VAN SOEST, P. J.: 1977. Modified procedure for determining plant cell wall by the neutral detergent procedure. Paper presented at the 69th Ann. Meeting Amer. Soc. of Animal Sci., Madison, Wisconsin, 1977.
VAN SOEST, P. J. and L. H. P. JONES: 1968. Effect of silica in forage upon digestibility. J. Dairy Sci., **51**: 1644–1648.

VAN SOEST, P. J., R. H. WINE and L. A. MOORE: 1966. Estimation of the true digestibility of forages by the in vitro digestion of cell walls. Proc. X Int. Grassl. Congress, Helsinki, Finland, (ed.) A.G.G. HILL, pp. 438–441.

VOS, J.: 1981. Effect of temperature and nitrogen supply on post floral growth of wheat: measurements and simulations. Centre for agricultural Publishing and Documentation PUDOC, Wageningen, pp. 1–164.

WALDO, D. R., L. W. SMITH and E. L. COX: 1972. Model of cellulose disappearance from the rumen. J. Dairy Sci., **55**: 125–129.

WHIGHAM, D. K. and D. G. WOOLLEY: 1974. Effect of leaf orientation, leaf area and plant densities on corn production. Agron. J., **66**: 482–486.

WIEGAND, C. L. and J. A. CUELLAR: 1981. Duration of grain filling and kernel weight of wheat as affected by temperature. Crop Sci., **21**: 95–101.

WILKINS, R. J.: 1969. The potential digestibility of cellulose in forage and faeces. J. agric. Sci., Camb., **73**: 57–64.

WILSON, J. R.: 1982. Environmental and nutritional factors affecting herbage quality. In: Nutritional limits to animal production from pastures. (ed.) J. B. HACKER. Farnham Royal, U.K., Commonwealth Agricultural Bureaux, pp. 111–131.

WILSON, J. R. and T. T. NG: 1975. Influence of water stress on parameters associated with herbage quality of *Panicum maximum* var. *trichoglume*. Austr. J. agric. Res., **26**: 127–136.

WILSON, J. R., A. O. TAYLOR and G. R. DOLBY: 1976. Temperature and atmospheric humidity effects on cell wall content and dry matter digestibility of some tropical and temperate grasses. N.Z. J. agric. Res., **19**: 41–46.

CHAPTER 3

Neth. J. agric. Sci. 30 (1982) 297-316

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

P. C. Struik and B. Deinum

Department of Field Crops and Grassland Science, Agricultural University, Wageningen, Netherlands

Accepted: 14 July 1982

Key-words: forage maize, digestibility, light intensity, sowing time, plant density, hybrid, grain-filling period

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

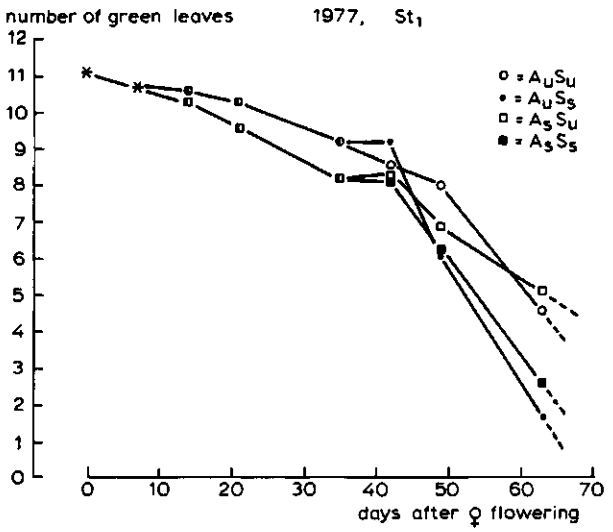


Fig. 1. Leaf-senescence pattern for four light treatments of early sowing in 1977.

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.

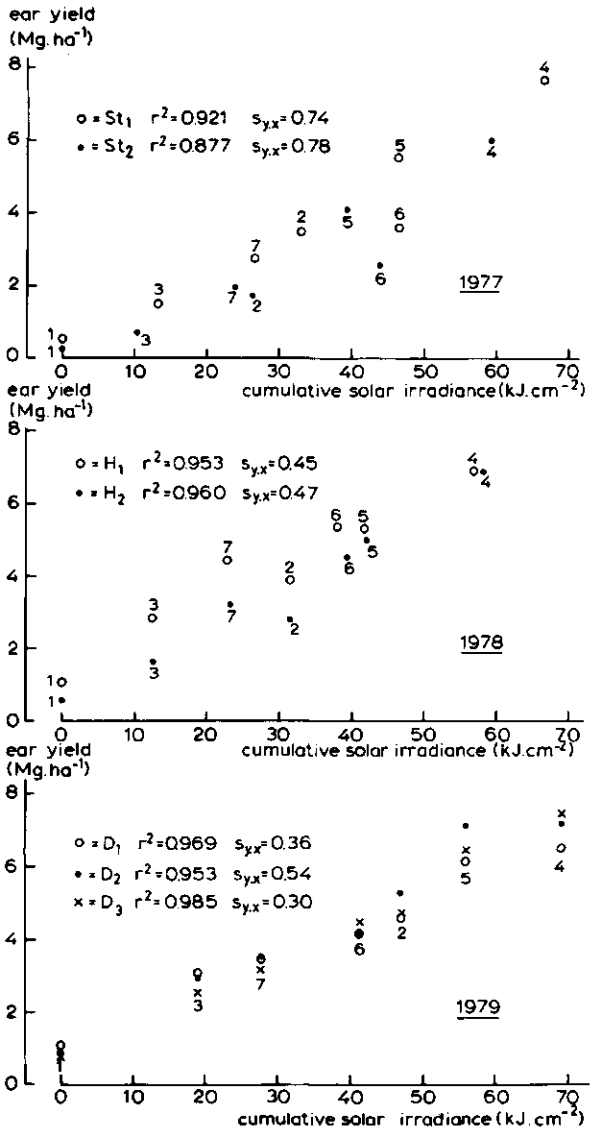


Fig. 2. Ear yields in relation to cumulative solar irradiance after start of A treatment.
1 = pre-treatment sampling, thus sampling at solar irradiance 0.
2 = A_u: second sampling; unshaded during A.
3 = A_s: second sampling; shaded during A.
4 = A_uS_u, 5 = A_uS_s, 6 = A_sS_u, 7 = A_sS_s: final samplings;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

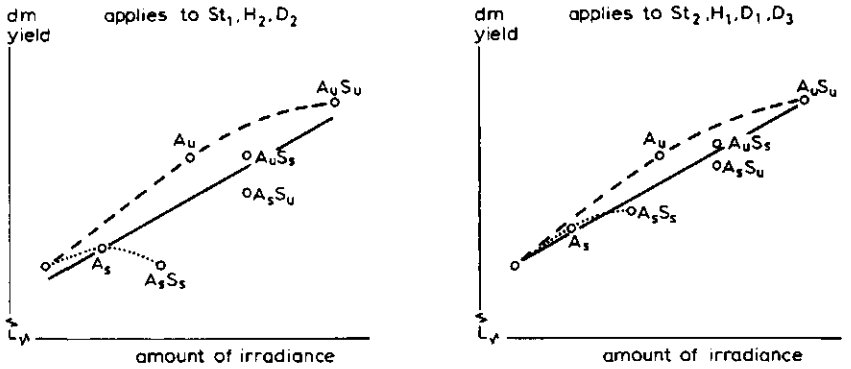


Fig. 3. Relation between dry-matter yield and amount of irradiance received (schematic). (—— = regression line, --- = control; . . . . = continuously shaded crops).

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.

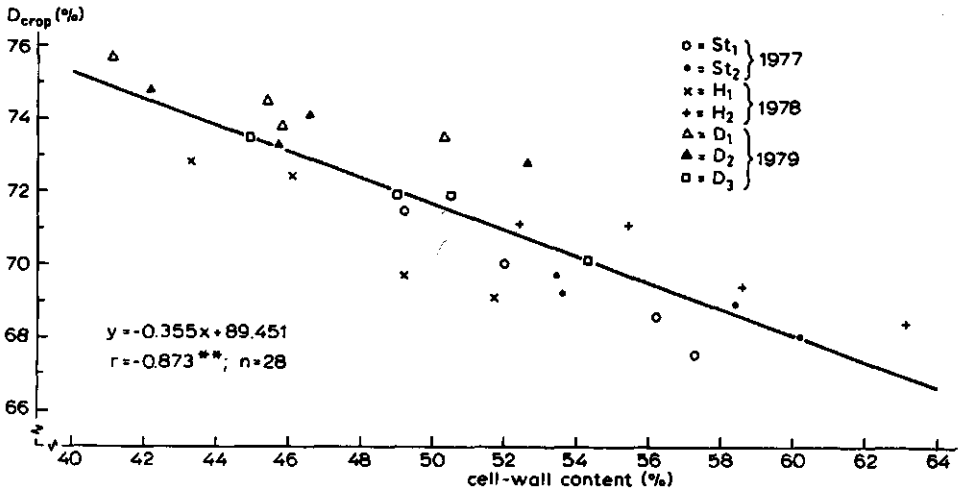


Fig. 4. The apparent digestibility of the whole-crop organic matter in relation to the cell-wall content of the whole crop (also as % of the organic matter) at final sampling.

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 if 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.

References

André, M., D. Massimino & A. Daguenet, 1978. Daily patterns under the life cycle of a maize crop. II. Mineral nutrition, root respiration and root excretion. *Physiologia Pl.* 44: 197-204.

Becker, W. R., 1976. Een handleiding voor de teelt van korrel- en snijmais. P.A. Publicatie No 21, pp. 1-84.

Behaeghe, T., E. Van Bockstaele & A. De Baets, 1981. Maïs als ruwvoederteelt. 4. Belang van de plantdichtheid, de zaaidatum, de oogstdatum en eventuele rijenbemesting bij maïsteelt. Samenvatting van recente proefresultaten. *Landbouwtijdschrift* 34: 573-587.

Bogers, R. J. & K. R. Libbenga, 1981. Molecular action mechanisms of plant growth regulators. In: B. Jeffcoat (Ed.), Aspects and prospects of plant growth regulators. Monograph No 6, British Plant Growth Regulator Group, Wantage, pp. 177-185.

Boote, K. J., 1977. Root: shoot relationships. *Proc. Soil Crop Sci. Soc. Florida* 36: 15-23.

Brouwer, R. & C. T. De Wit, 1968. A simulation model of plant growth with special attention to root growth and its consequences. In: W. J. Whittington (Ed.), Root growth. Butterworth, London, pp. 224-244.

Bunting, E. S., 1975. The question of grain content and forage quality in maize: comparison between isogenic fertile and sterile plants. *J. agric. Sci., Camb.* 85: 455-463.

Bunting, E. S., 1976. Effects of grain formation on dry matter distribution and forage quality in maize. *Expl Agric.* 12: 417-428.

Crapo, N. L. & H. J. Ketellapper, 1981. Metabolic priorities with respect to growth and mineral uptake in roots of *Hordeum, Triticum* and *Lycopersicon*. *Am. J. Bot.* 68: 10-16.

Deinum, B. & J. Knoppers, 1979. The growth of maize in the cool temperate climate of the Netherlands: Effects of grain filling on production of dry matter and on chemical composition and nutritive value. *Neth. J. agric. Sci.* 27: 116-130.

Early, E. B., W. O. McIlrath, R. D. Seif & R. H. Hageman, 1967. Effects of shade applied at different stages of development on corn (*Zea mays* L.) production. *Crop. Sci.* 7: 151-156.

Early, E. B., R. J. Miller, G. L. Reichert, R. H. Hageman & R. D. Seif, 1966. Effects of shade on maize production under field conditions. *Crop Sci.* 6: 1-7.

Fairey, N. A. & T. B. Daynard, 1978. Assimilate distribution and utilization in maize. *Can. J. Plant. Sci.* 58: 719-730.

Gerakis, P. A. & D. Papakosta-Tasopoulou, 1979. Growth dynamics of *Zea mays* L. populations differing in genotype and density and grown under illuminance stress. *Oecol. Plant.* 14: 13-26.

Hess, C. E., 1968. Internal and external factors regulating root initiation. In: W. J. Whittington (Ed.), Root growth. Butterworth, London, pp. 42-53.

Jenner, C. F., 1979. Grain-filling in wheat plants shaded for brief periods after anthesis. *Aust. J. Pl. Physiol.* 6: 629-641.

Knipmeyer, J. W., R. H. Hageman, E. B. Early & R. D. Seif, 1962. Effect of light intensity on certain metabolites of the corn plant (*Zea mays* L.). *Crop Sci.* 2: 1-5.

Koedjikov, H., 1967. The root system of maize. Bulgarian Academy of Sciences Press, Sofia, pp. 1-154.

Lupton, F. G. H., 1966. Translocation of photosynthetic assimilates. *Ann. appl. Biol.* 57: 355-364.

Major, D. J., 1980. Effect of simulated frost injury induced by paraquat on kernel growth and development in corn. *Can. J. Plant. Sci.* 60. 419-426.

Massimino, D., M. André, C. Richaud, A. Daguenet, J. Massimino & J. Vivoli, 1981. The effect of a day at low irradiance of a maize crop. I. Root respiration and uptake of N, P and K. *Physiologia Pl.* 51: 150-155.

Mengel, D. B. & S. A. Barber, 1974. Development and distribution of the corn root system under field conditions. *Agron. J.* 66: 341-344.

Michael, G., P. Allinger & E. Wilberg, 1970. Einige Aspekte zur hormonalen Regulation der Korngrösse bei Getreide. *Z. PflErnähr. Bodenkd.* 125: 24-35.

Montgomery, F. G., 1911. Correlation studies of corn. *Nebr. agric. Exp. Stn Ann. Rep.* 24: 108-159.

National Institute of Agricultural Botany, 1979. Recommended varieties of forage maize. Farmers leaflet No 7, pp. 1-5.

Noodén, L. D. & A. C. Leopold, 1978. Phytohormones and the endogenous regulation of senescence and abscission. In: D. S. Letham, P. B. Goodwin & T. J. V. Higgins (Ed.), Phytohormones and related compounds. A comprehensive treatise, Vol. 2. Elsevier/North-Holland, pp. 329-361.

Palmer, A. F. E., G. H. Heichel & R. B. Musgrave, 1973. Patterns of translocation, respiratory loss and redistribution of ^{14}C in maize labeled after flowering. *Crop Sci.* 13: 371-376.

Pendleton, J. W. & R. O. Weibel, 1965. Shading studies on winter wheat. *Agron. J.* 57: 292-293.

Penning de Vries, F. W. T., 1974. Substrate utilization and respiration in relation to growth and maintenance in higher plants. *Neth. J. agric. Sci.* 22: 40-44.

Struik, P. C., 1982. Production pattern, chemical composition and digestibility of forage maize (*Zea mays* L.). Mededeling No 64, Department of Field Crops and Grassland Science, Agricultural University, Wageningen, 28 pp.

Trewavas, A., 1981a. What is the function of growth substances in the intact growing plant? In: B. Jeffcoat (Ed.), Aspects and prospects of plant growth regulators. Monograph No 6, Bristish Plant Growth Regulator Group, Wantage, pp. 197-208.

Trewavas, A., 1981b. How do plant growth substances work? *Plant, Cell & Environment* 4: 203-228.

Tripathy, P. C., J. A. Eastin & L. E. Schrader, 1972. A comparison of ^{14}C-labeled photosynthate export from two leaf positions in a corn (*Zea mays* L.) canopy. *Crop Sci.* 12: 495-497.

Vaadia, Y. & C. Itai, 1968. Interrelationships of growth with reference to the distribution of growth substances. In: W. J. Whittington (Ed.), Root growth. Butterworth, London, pp. 65-79.

Van Soest, P. J., 1977. Modified procedure for determining plant cell wall by the neutral detergent procedure. Paper presented at the Annual Meeting of the American Society of Animal Science.

Van Soest, P. J., R. H. Wine & L. A. Moore, 1966. Estimation of the true digestibility of forages by the in vitro digestion of cell walls. *Proc. 10th int. Grassld Congr.* (Helsinki) 438-441.

CHAPTER 4

Neth. J. agric. Sci. 31 (1983) 101-124

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.)

P. C. Struik

Department of Field Crops and Grassland Science, Agricultural University, Wageningen, Netherlands

Received 11 November 1982; accepted 22 November 1982

Key-words: forage maize, light intensity, development, productivity, digestibility

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.

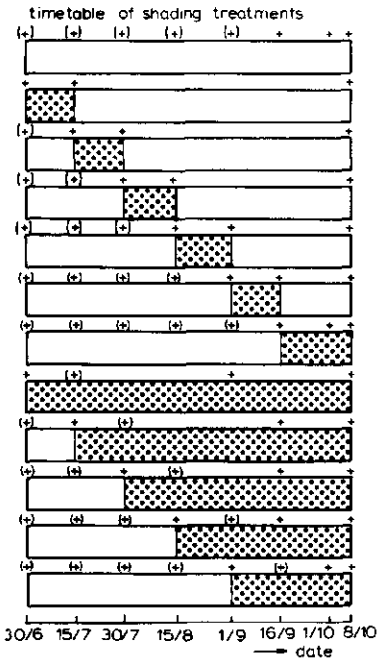
Treatments

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.

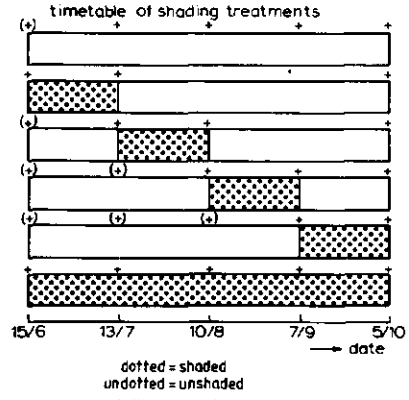
The 1981 experiment (henceforth called Experiment 2) contained four shading treatments, each lasting four weeks, and one continuously shaded treatment.

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}
$J_3s = J_3l$	37.6^{ab}	
J_1l	33.6^{a}	32.7^{a}
J_2l	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

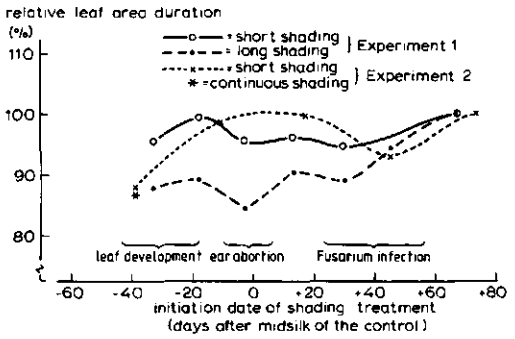


Fig. 2. Effect of date of initiation of short and long shading treatments on the relative duration of leaf area. Leaf-area duration of the controls = 100 %.

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.

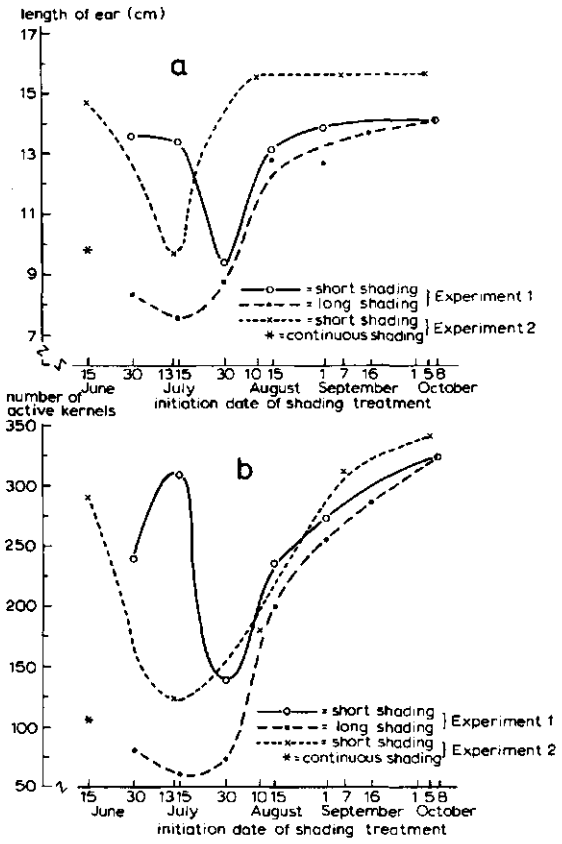


Fig. 3. Effect of date of initiation of shading (a) on length of the top ear and (b) on number of active kernels on the top ear.

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-

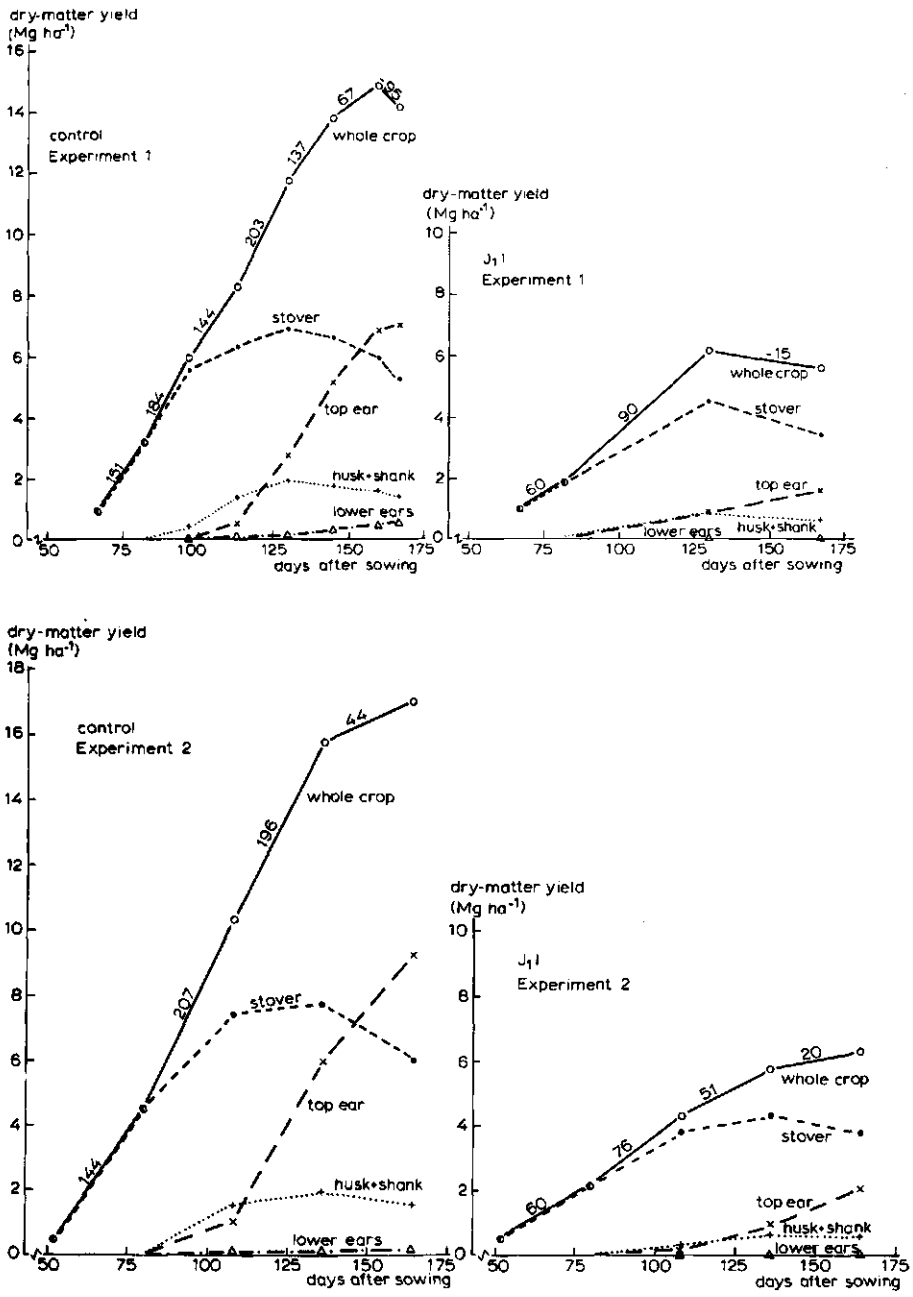


Fig. 4. Production pattern of unshaded and continuously shaded crops in both experiments. (— ○ — = whole crop; - - - ● - - - = stover; . . . + . . . = husk + shank; — × — = top ear; . — △ . — = lower ears; numbers indicate production rates in kg ha^{-1} day^{-1} for the periods involved).

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.

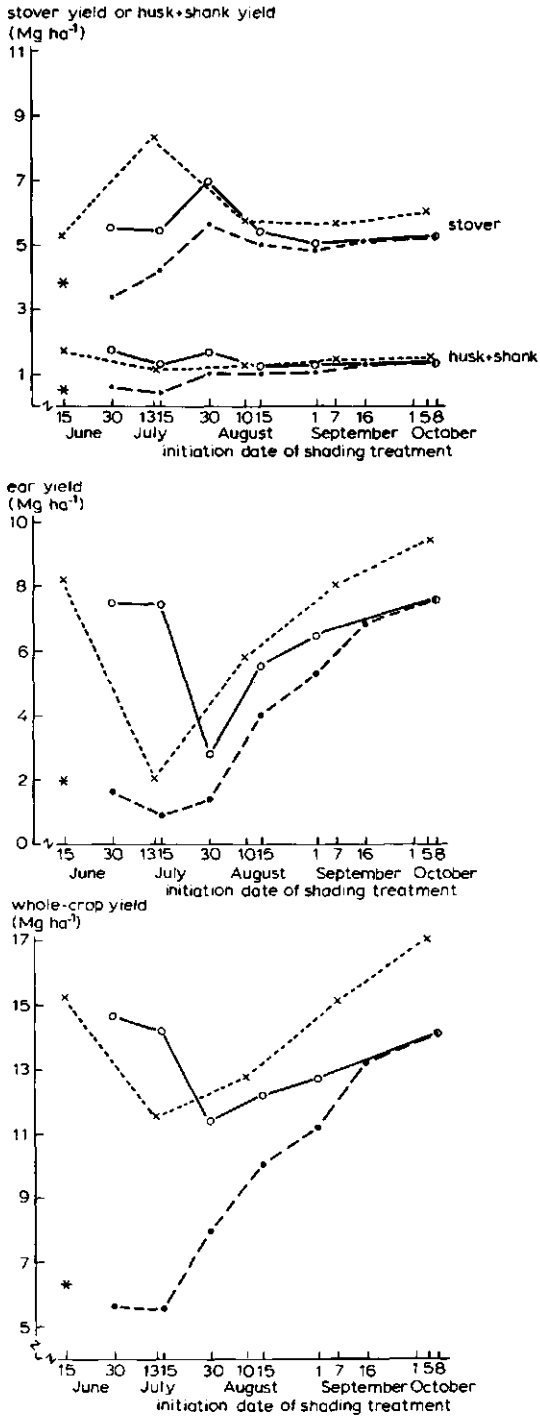


Fig. 5. Effects of shading on the yields of the various fractions and on whole-crop yield. (— ○ — = short shading, Experiment 1; - - ● - - = long shading, Experiment 1; - - - - × - - - - = short shading, Experiment 2; * = continuous shading, Experiment 2).

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):

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

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 (o——o 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):

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

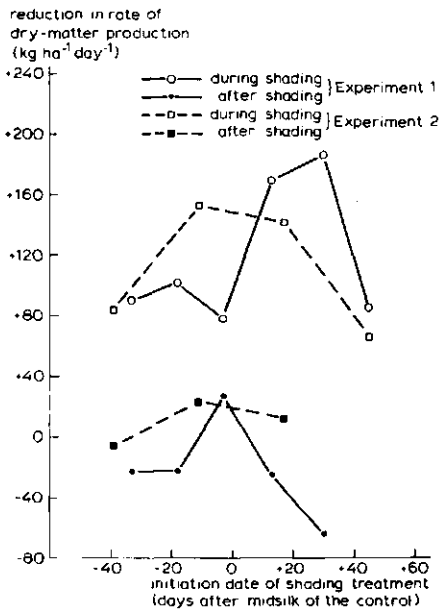


Fig. 6. Effect of date of initiation of short shading on the reduction in rate of dry-matter production during and after the treatment (including S_2 treatment).

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

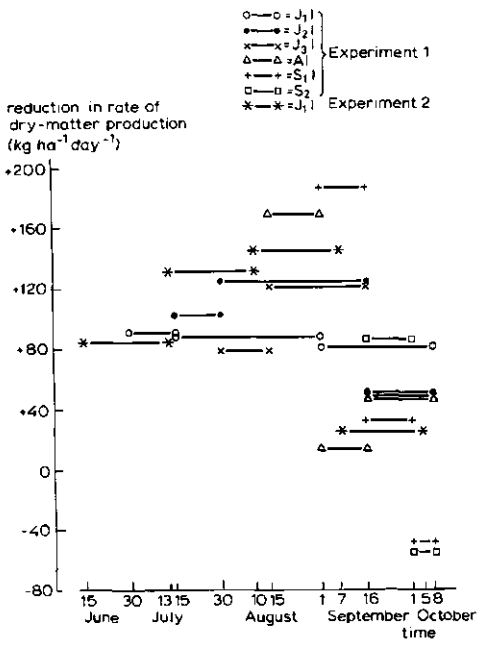


Fig. 7. Development over time of the reduction in rate of dry-matter production caused by long shading treatments initiated at different stages of growth.

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

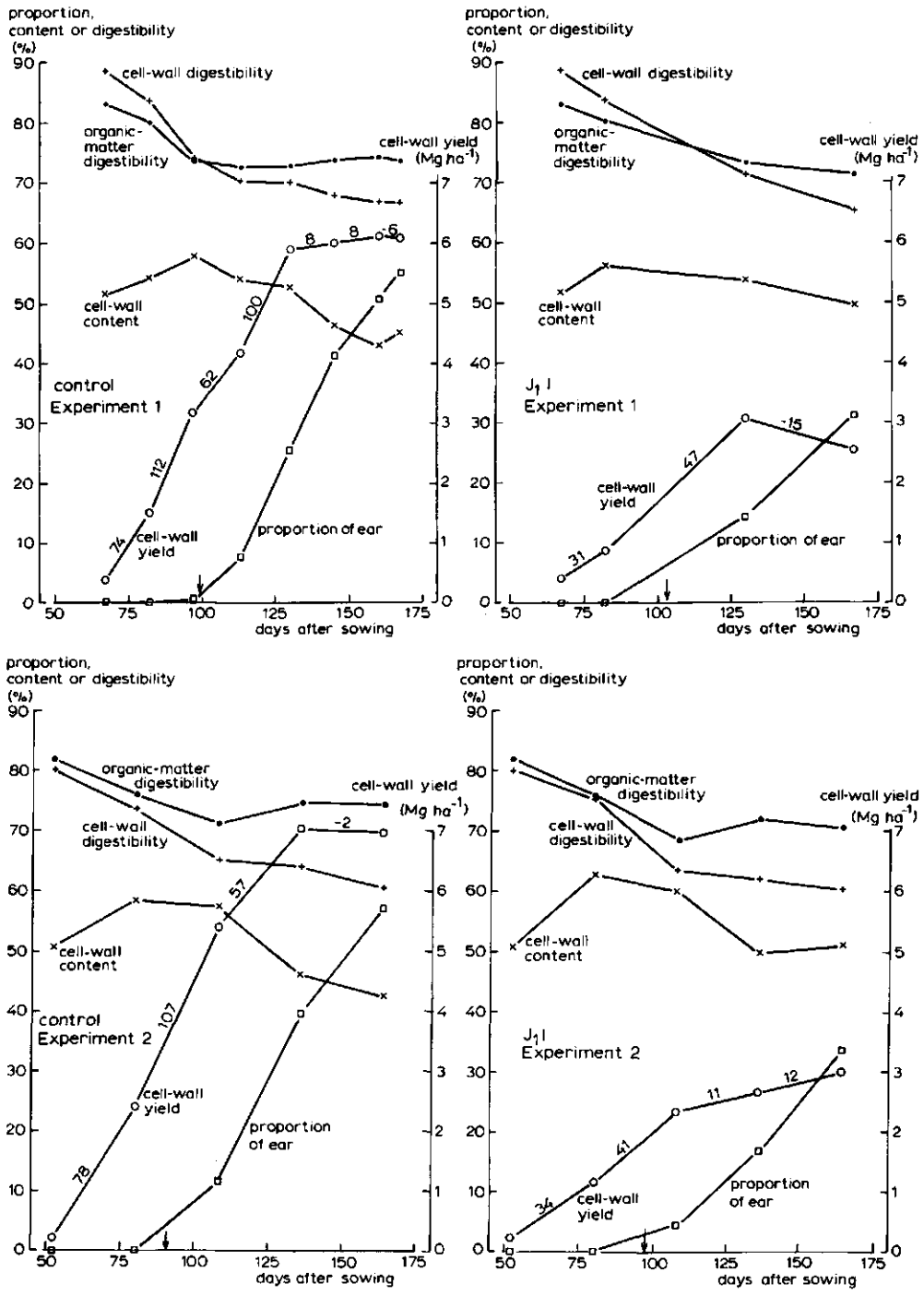


Fig. 8. Development over time of certain quality parameters in the control and J_1I treatments of both experiments. Numbers indicate rates of cell-wall production in kg ha^{-1} day^{-1}. Arrows indicate 50 % silking.

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.

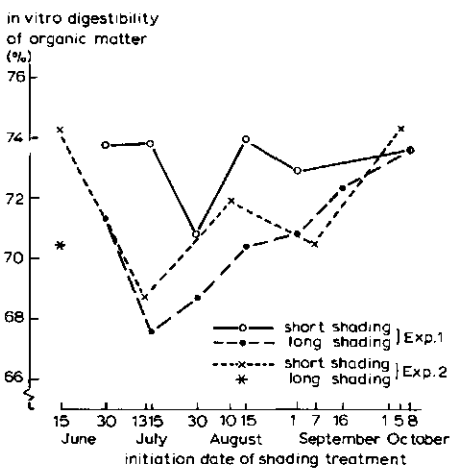


Fig. 9. Effect of date of initiation of long and short shading treatments on the digestibility in vitro of organic matter at final sampling.

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

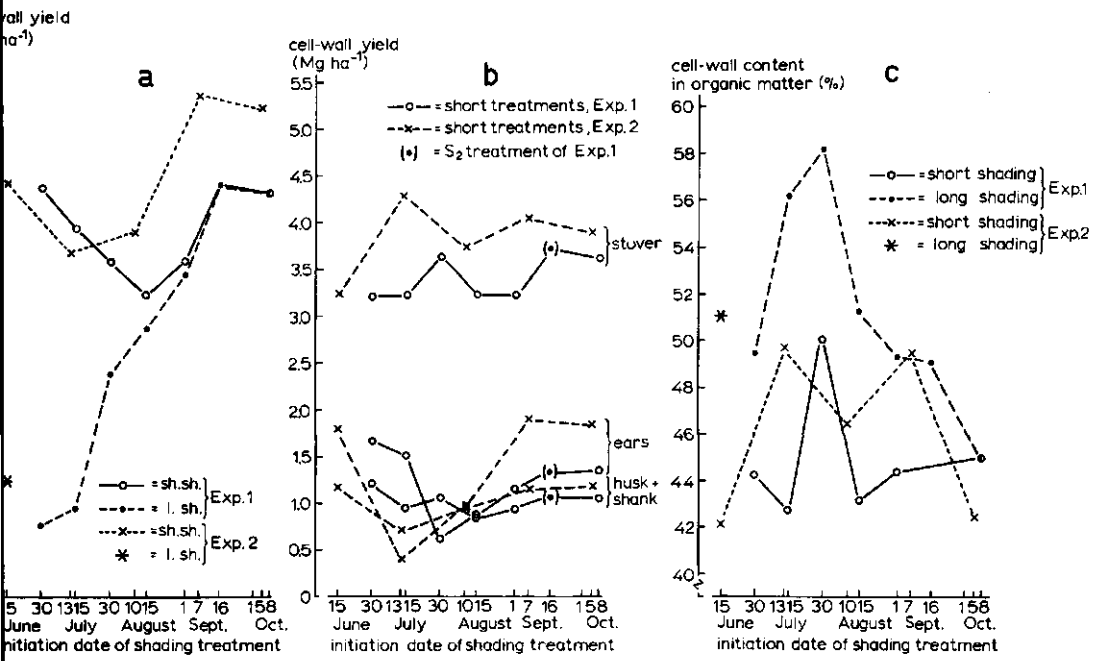


Fig. 10. The effects of shading (a) on the cell-wall yield of the whole crop, (b) on the cell-wall yield of the fractions (short shading only), and (c) on the content of cell walls in the organic matter at final sampling. In Fig. 10b the S_2 treatment has been added to show that the period during which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

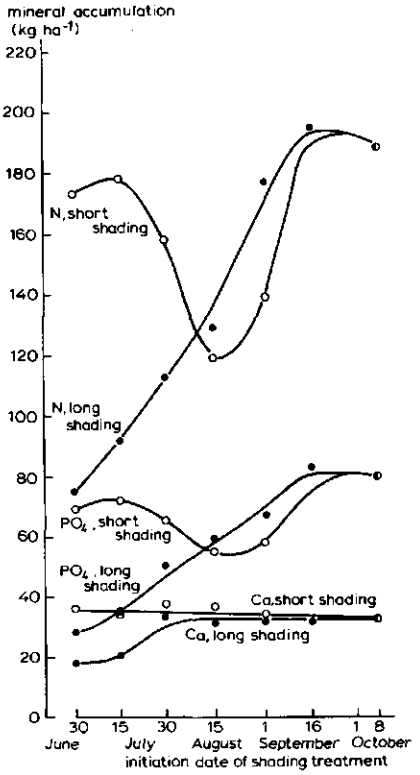


Fig. 11. Effects of shade on accumulation of Ca, N and PO_4.

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.

References

Allison, J. C. S. & H. Weinmann, 1970. Effect of absence of developing grain on carbohydrate content and senescence of maize leaves. *Plant Physiol.* 46: 435-436.

Bunting, E. S., 1975. The question of grain content and forage quality in maize: comparison between isogenic fertile and sterile plants. *J. agric. Sci., Camb.* 85: 455-463.

Dale, J. E., 1982. The growth of leaves. Studies in Biology No 137. Edward Arnold Publishers, London, pp. 1-60.

Deinum, B. & J. Knoppers, 1979. The growth of maize in the cool temperate climate of the Netherlands: Effect of grain filling on production of dry matter and on chemical composition and nutritive value. *Neth. J. agric. Sci.* 27: 116-130.

Early, E. B., W. O. McIlrath, R. D. Seif & R. H. Hageman, 1967. Effects of shade applied at different stages of plant development on corn (*Zea mays* L.) production. *Crop Sci.* 7: 151-156.

Early, E. B., J. C. Lyons, E. Inselberg, R. H. Maier & E. R. Leng, 1974. Earshoot development of Midwest dent corn (*Zea mays* L.). *Bull. Ill. Agric. Exp. Stn* 747, pp. 1-44.

Gmelig Meyling, H. D., 1973. Effect of light intensity, temperature and daylength on the rate of leaf appearance of maize. *Neth. J. agric. Sci.* 21: 68-76.

Phipps, R. H., 1980. A review of the carbohydrate content and digestibility value of forage maize grown in the cool climatic conditions of the UK and their relevance to animal production. In: W. G. Pollmer & R. H. Phipps (Eds), Improvement of quality traits of maize for grain and silage use. Martinus Nijhoff, The Hague/Boston/London, pp. 291-317.

Struik, P. C., 1983a. Effects of switches in photoperiod on crop morphology, production pattern and quality of forage maize (*Zea mays* L.) under field conditions. *Meded. Landbouwhogesch. Wageningen* 83-2:1-27.

Struik, P. C., 1983b. Effect of temperature on development, dry-matter production, dry-matter distribution and quality of forage maize (*Zea mays* L.). An analysis. *Meded. Landbouwhogesch. Wageningen* 83-3:1-41.

Struik, P. C. & B. Deinum, 1982. Effect of light intensity after flowering on the productivity and quality of silage maize. *Neth. J. agric. Sci.* 30: 297-316.

Wilkinson, J. M., 1976. Voluntary intake and efficiency of utilisation of whole-crop maize silage. *Anim. Feed Sci. Technol.* 1: 441-454.

CHAPTER 5

Neth. J. agric. Sci. 30 (1982) 69-83

Effect of a switch in photoperiod on the reproductive development of temperate hybrids of maize

P. C. Struik

Department of Field Crops and Grassland Science, Agricultural University, Wageningen, Netherlands

Accepted: 24 September 1981

Key-words: maize, photoperiod, day length, temperature, reproductive development, flowering, hybrid

Summary

In three phytotron experiments, the reaction of maize (*Zea mays* L.) to a switch in light phase was investigated. Number of leaves was increased by a long-day phase (20 h) before tassel initiation but was not affected thereafter. Reproductive development was delayed by long days before tassel initiation and slowed down by long days after tassel initiation, but ear development was affected more than tassel development. So the time lag between anthesis and silking increased when short days (12 h) were followed by long days. The opposite was true when long days were followed by short days. Direct responses to photoperiod, such as number of leaves and tassel branches, occurred over a rather short time. Indirect effects, such as area of leaves, height of plant and length of the ear shoot, however, were maximum when day length did not affect the number of leaves any more. One can therefore control vegetative and reproductive development separately to some extent by a day-length treatment and can desynchronize development of the male and female inflorescences, especially at higher temperature. The photoperiodic response of maize is clearly complex.

Introduction

Maize (*Zea mays* L.) is a monoecious plant with the staminate inflorescence on top (the tassel) and the pistillate ones in the axils of several lower leaves (the ears). The tassel terminates the main shoot and the ears terminate lateral branches, called shanks. There are mostly ten internodes on a shank, which normally do not elongate.

Maize is known as a (sub)tropical quantitative short-day plant, although qualitative short-day, day-neutral and long-day genotypes have been reported (Niopek, 1960; Francis et al., 1969; Francis et al., 1970; Hunter et al., 1974;

Teschemacher, 1974; Coligado & Brown, 1975; Blondon & Gallais, 1976; Aitken, 1980; Rood & Major, 1980). According to many authors (Francis et al., 1969; Rood & Major, 1980), the floral differentiation of maize can be evaluated by examining the developing tassel. In this view, the effects of photoperiod on plant development end with tassel differentiation. Because maize is determinate in growth, the rate of development is shown by the final number of leaves.

Under natural conditions, the ear is always initiated at a certain stage of tassel development, about two days after tassel initiation. The ear can only complete development if it does not lag too far behind the tassel (Fuchs, 1968).

However the female inflorescence has greater requirements for induction than the tassel (Niopek, 1960; Messiaen, 1963; Blondon & Gallais, 1976) and the gap between male and female flowering widens with a longer photoperiod (Messiaen, 1963; Moss & Heslop-Harrison, 1968; Faungfupong, 1975; Blondon & Gallais, 1976; Aitken, 1980). Because of a longer period to initiation, the number of leaves increases with longer days. The time of initiation is also longer; therefore the number of male and female florets can also be larger (Ragland et al., 1966; Moss & Heslop-Harrison, 1968; Hunter et al., 1977; Hunter, 1980).

Only a few people have worked on the effects of temporary changes in photoperiod. Faungfupong (1975) shortened the dark period after completion of tassel initiation and hardly found any effects on tassel development but a pronounced delay in silking. Scheffer (1978) accelerated reproductive development by shortening the photoperiod for some days. The moment of treatment was crucial: from the 1-leaf stage until the 9-leaf stage, there was a continuous increase in efficiency of the treatment. The effects also increased when the number of short days increased. Niopek (1960) and Kim et al. (1976) also found an acceleration of development when the photoperiod was shortened for a few days, and greater effects if the number of short photoperiods increased.

So one can influence vegetative development and the size of reproductive organs by photoperiod. However the ear and tassel differ in photoperiodic requirement for induction; they differ also in moment of initiation; the ear may develop poorly if it develops much slower than the tassel. These three aspects provide a way of uncoupling vegetative development, tassel development and ear development. Such an uncoupling by photoperiod could be useful in physiological and agricultural studies, for example on seed production or on the relevance of the ear for production pattern, productivity and quality of forage maize.

The purpose of the study was to find a method of changing the production pattern of maize without changing the rate of development of the main shoot.

Three trials were designed to influence initiation and development of the ear independently of the tassel by a different photoperiod at certain stages of growth. I used two hybrids from temperate regions (both described by Bundessortenamt, 1980), because they are almost day neutral. If these hybrids respond, photoperiod-sensitive strains will react in the same way or more sharply.

This article will be followed by a report on two trials in which some of the

main treatments were imposed on a normal maize crop. Special attention will be paid then to the consequences for yield and quality.

Materials and methods

Maize was grown in 6-litre pots (Trial 1) or 10-litre pots (Trial 2 and 3). Four seeds were sown in each pot. After emergence, the number of seedlings was reduced to two. Final plant density was about 6 m^{-2}. The pots contained a mixture of sandy soil and peat in equal volumes. Nutrient solution, adjusted to soil type, was provided adequately. Plants were watered once or twice a day. Relative humidity was kept at about 75 %. When the plants grew taller, the volume fraction of CO_2 in air was kept at 450×10^{-6}. The pots were placed on carts, which were moved around in each growth chamber three times per week until the plants were too tall and had to be put on the floor.

Photosynthetically active irradiance in the waveband 400-700 nm was 100 W/m^2 1.20 m above the floor for 12 h. Long-day treatment of 20 h was achieved by four incandescent bulbs (100 W) over 10 m^2, which burnt for 4 h before and 4 h after the basic light period. Minimum illuminance during the supplementary photoperiod was 100 lx corresponding to an irradiance in the waveband 400-700 nm of 0.4 W/m^2, which is more than the saturation point of the photosensitivity of maize (Francis et al., 1970; Francis, 1973; Teschemacher, 1974; Faungfupong, 1975).

In Trial 1, the plants that showed anther or silk extrusion were counted daily. In the other two trials, the dates of first visible extrusion of anthers and of silks were noted for each plant separately. The plants were checked daily at the same time of day.

Maximum leaf area was calculated at anthesis by the equation length × maximum width × 0.75 (Montgomery, 1911). The maximum diameter in the middle of the second internode above the soil was estimated with a marking gauge as a measure of stem thickness. Final plant height, tassel length (measured from the axil of the top leaf) and number of leaves were measured some time after the end of flowering. Ears were measured during grain filling.

Total number of visible kernels or florets was estimated for the top ear and for all the lower ears that arose from the axils. The area of the husk laminae (normally rudimentary, but for given treatments sometimes large) was estimated with an area meter. Dry-matter yields were of little relevance in these trials. They were correlated with leaf area, so far as estimated.

The treatments in each trial are tabulated and described with the results.

Results

Trial 1: effect of photoperiod and temperature after tassel initiation on development of hybrid Blizzard

Before treatment, all plants received a light phase of 12 h at 20 °C with an equal dark phase at 15 °C.

Table 1. Growth conditions after switch in photoperiod in Trials 1 and 2.

Temperature (°C)		Photoperiod (h)
day (12 h)	night (12 h)	
18	12	12
18	12	20
30	24	12
30	24	20

Treatments with 60 plants each as in Table 1 began at the 6.5-leaf stage (i.e. 6.5 visible leaves). Because the rate of leaf appearance is constant with a certain temperature regime, time and plant age are described linearly by means of a linear scale of visible leaves. In 16 dissected plants the shoot apex showed differentiation of the tassel branches and sometimes elongation of the basal branches (i.e. Stage D-E in Fig. 2 of Bonnett, 1966).

Photoperiod after tassel initiation influenced development rate. Male flowering was retarded by only about two days for both temperature regimes, when plants were exposed to long days. Female flowering, however, was retarded more, resulting in greater desynchronization. Variation in date of female flowering increased. Effects were greater at the high temperature; at the low temperature, protogyny was found with continuance of the 12-h photoperiod (Table 2).

Table 2. Some plant characteristics indicating vegetative and reproductive development in Trial 1 for hybrid Blizzard.

	Temperature after 6.5-leaf stage (°C)			
	day 18 / night 12		day 30 / night 24	
Photoperiod regime (h) →	12 → 12	12 → 20	12 → 12	12 → 20
Desynchronization of flowering (60 plants)				
50 % ♀ – 50 % ♂ (days)	–2	1	0	4
75 % ♀ – 75 % ♂ (days)	–2	3	2	7
95 % ♀ – 95 % ♂ (days)	–2	4	7	10
Reproductive development (24 plants)				
length of top ear (cm)	16.5	18.1	15.1	18.6
number of kernels in top ear	410	492	489	514
proportion of bisexual tassels (%)	15	7½	0	0
Vegetative development (24 plants)				
number of leaves	13.2	13.3	13.2	13.1
height of plant (cm)	234.9	243.0	231.7	250.7
height of plant/number of leaves (cm)	17.8	18.3	17.6	19.1
av. leaf area of a plant (dm^2)[1]	35.1	37.8	34.5	39.1
area of husk laminae (cm^2)	0.6	6.1	0.9	22.5
proportion of tillered plants (%)	54	29	0	0

[1] Especially the leaves above the top-ear node were larger for 12 → 20 h.

Differences in ear size reflect differences in duration of floret initiation and more pronounced elongation of the cob. Sex expression in the male inflorescence was influenced by temperature and photoperiod.

As treatment started when the number of leaf primordia was already fixed, there was no difference in final number of leaves. But there were some differences in vegetative development (Table 2), indicating that long day stimulated vegetative growth.

Long days after tassel initiation apparently caused an increase in apical dominance of the tassel and depressed development of the ear-shoot buds and the proportion of tillered plants. The main shoot showed a more pronounced vegetative growth. Although high temperatures normally cause a loss of sensitivity to photoperiod (Hunter et al., 1974; Coligado & Brown, 1975), there was a greater effect of photoperiod on the vegetative growth with a cycle of 30 and 24 °C.

Trial 2: effect of photoperiod before and after tassel initiation and of temperature on development of hybrid Nicco

The trial included 8 × 30 plants, in two photoperiod treatments of 12 and 20 h in early growth and the four combinations of temperature and photoperiod shown in Table 1 from the 5.2-leaf stage.

Double ridges could not yet be seen in most growing tips but the apex had started to elongate, indicating the real start of the reproductive phase (Niopek, 1960). Bonnett (1953) called this the 'transitional stage'.

As expected, earlier treatment (5.2-leaf stage) gave greater effects with photoperiods 12 → 20 h than in Trial 1, although the hybrid used in this trial also appeared to be more sensitive than Blizzard. Again effects of photoperiod were greater at the higher temperature (Table 3).

The photoperiod treatment 20 → 12 h, absent in Trial 1, acted in the opposite way to the treatment 12 → 20 h. For example, desynchronization was less than with the treatment 12 → 12 h and the plants had shorter internodes (plant height divided by number of leaves in Table 3). With the treatment 20 → 20 h, anthesis was much later than for 12 → 20 h, but silking date was about the same, with smaller standard deviations. So anthesis date was more influenced by photoperiod after the change than in Trial 1.

Low temperature after the photoperiod switch improved synchronization in all photoperiod treatments but especially with long photoperiod after tassel initiation. Reproductive development was also less affected by photoperiod at lower temperature.

Some abnormalities occurred. Shanks were enormous for 12 → 20 h treatment (compare length of the top-ear shoot with length of the top ear), especially with the cycle of 30 and 24 °C because of excessive elongation of the internodes. Sex expression of the ear shoots was sometimes disturbed, again especially with the temperature cycle of 30 and 24 °C, and the photoperiods 12 → 20 h. Once there was a plume 13.5 cm long on an ear. Such aberrations caused a severe reduction in the number of kernels. The hybrid Nicco tends to form more than one (flowering) ear per lateral branch, as happened in the trial, but its extent was not

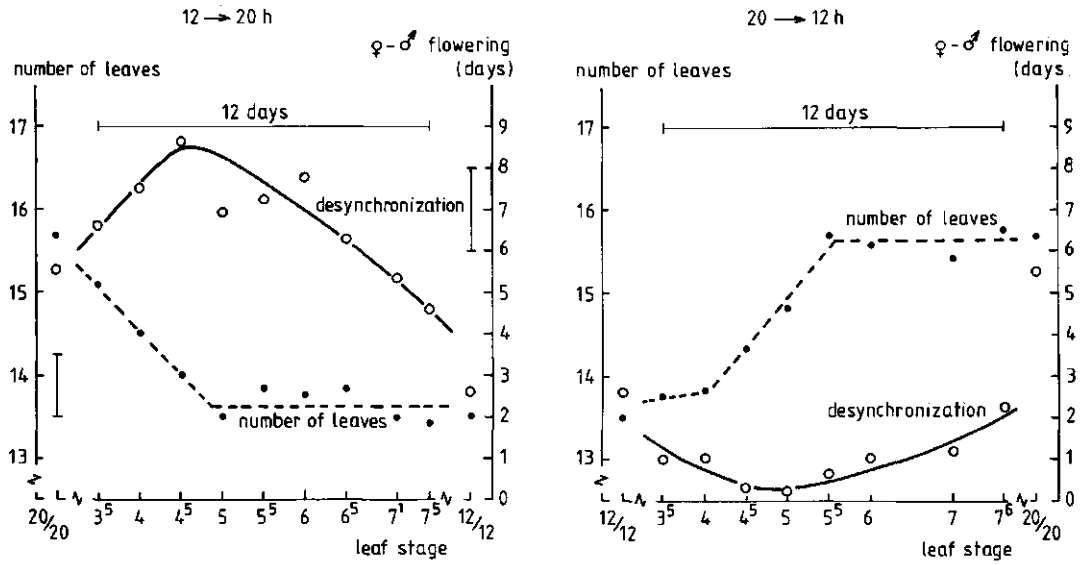


Fig. 1. Number of leaves (– – –●– – –) and desynchronization of silking and anthesis (——○——) in relation to leaf stage at time of photoperiodic switch.
Vertical bars in all figures indicate the least-significant difference for 19 treatments, according to Tukey's range test ($P < 0.10$).

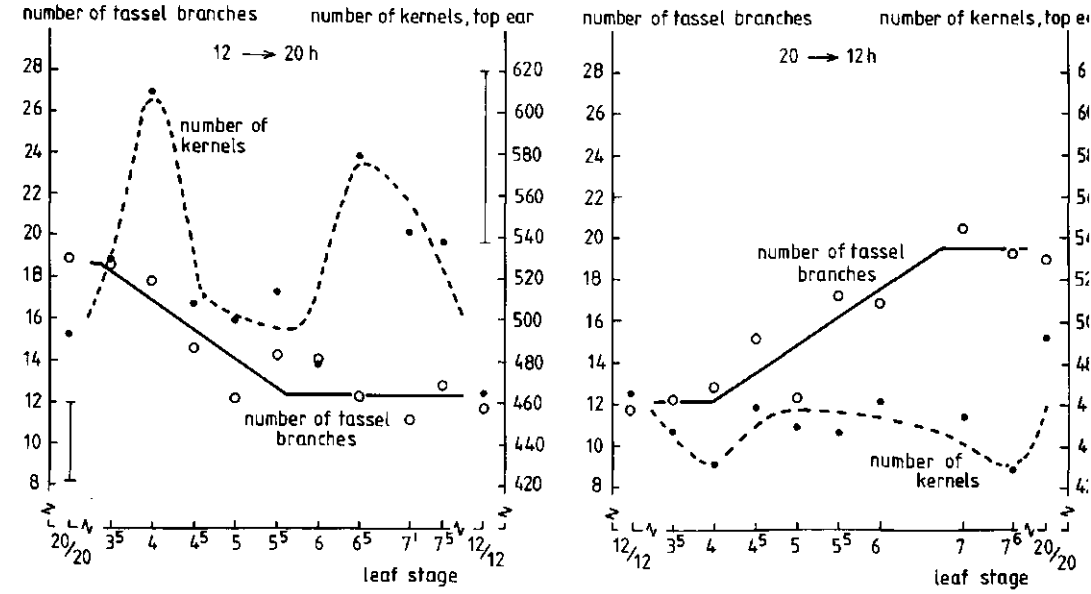


Fig. 2. Number of tassel branches (——○——) and number of kernels in the top ear (– – ●– –) in relation to leaf stage at time of photoperiodic switch.

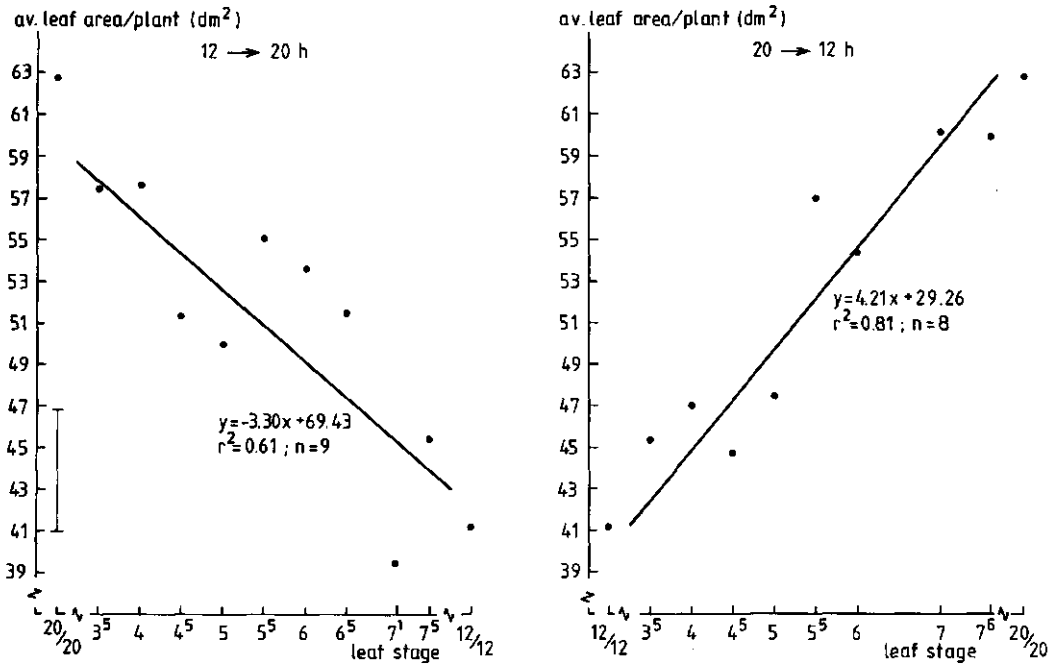


Fig. 3. Average leaf area per plant in relation to leaf stage at time of photoperiodic switch.

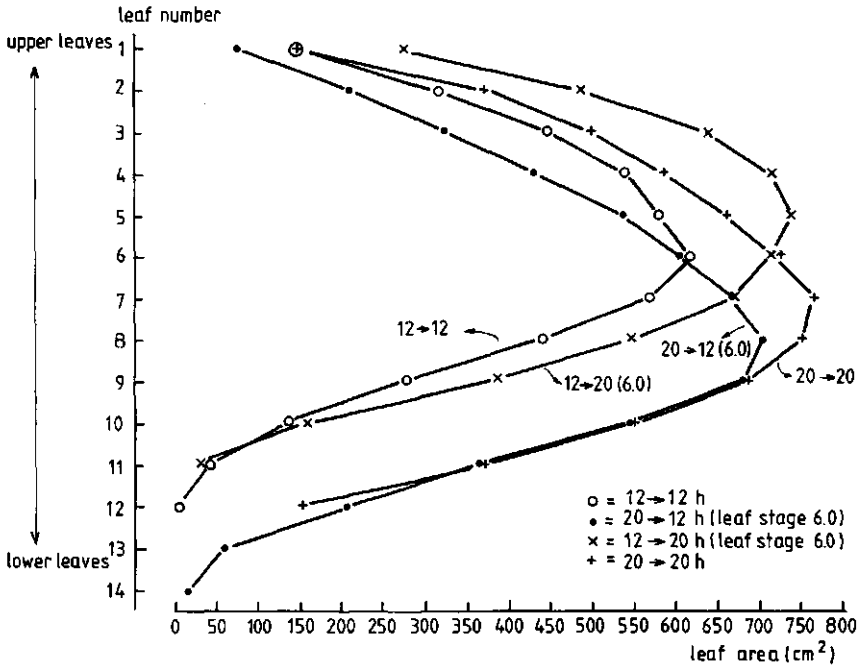


Fig. 4. Leaf area in relation to leaf number for four treatments.

Average leaf area per plant showed a linear relation with the moment of switch until the latest treatments (Fig. 3). This relation is hardly influenced by the number of leaves, but mainly by the area of the upper leaves.

In Fig. 4 the leaf areas for four treatments are given as an example. 12 → 20 h had larger upper leaves than 12 → 12 h, while 20 → 12 h had smaller ones than 20 → 20 h. The effect of a long photoperiod on leaf enlargement was dependent on the number of long days during the early development of the leaf.

In Fig. 5 the length of the tassel and of the complete top-ear shoot are related to the time of photoperiodic switch. These curves look like the desynchronization curves, but the minima or maxima are shifted to later stages. Similar curves can be drawn for stem thickness, length of the top ear, area of the husk laminae, height of the plant divided by number of leaves and individual leaf area if the leaves are counted form above; if leaves are counted from below, the relations are linear like for the total leaf area. For the ear shoot the correlation is not as high as for the tassel length, connected with the differences in number of kernels (compare Fig. 2 and 5).

Length of the top ear ranged from 16.4 cm for the 12 → 12 h control till 22.2 cm for 12 → 20 h, 6.5-leaf stage. The areas of the husk laminae were very small for 20 → 12 h (less than 20 cm^2/plant), but very large for 12 → 20 h (till almost 200 cm^2/plant), as in Trial 2.

From Trial 3, it is clear that different plant characteristics show different patterns of photoperiod response. With regard to number of leaves, for example, plants were only photosensitive during a short time but tassel length, among other things, was influenced during a long period and reached its extreme, when number of leaves was not changeable any more. Because of the

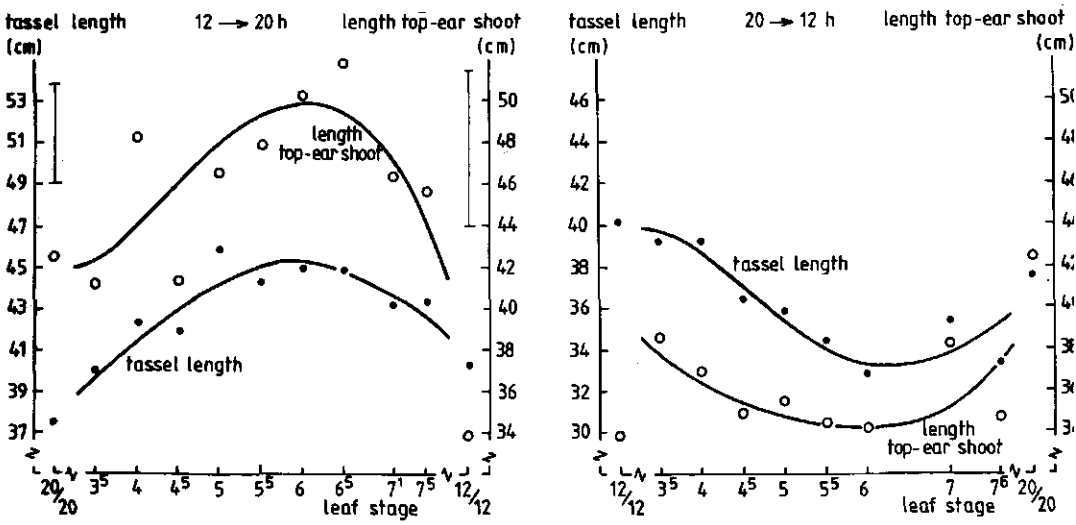


Fig. 5. Tassel length (——●——) and length of the top-ear shoot (——○——) in relation to leaf stage at time of photoperiodic switch.

complexity of the processes involved, even curves with more than one maximum or minimum can be obtained. In these trials, it has been demonstrated that photoperiod sensitivity in maize is not confined to the time from emergence to tassel initiation.

The results of the three trials are in agreement with each other, although there is an interaction with temperature and hybrid. The sexual abnormalities in Trial 2, however, caused some disturbance.

Discussion

Flowering. Rate of development of the reproductive organs of maize was retarded with long days but in the female inflorescence more than in the male one. Together with the time of initiation, this effect determined the course of desynchronization with a maximum for photoperiods 12 → 20 h and a minimum for 20 → 12 h (Fig. 6). The distance between the male and the female curve is influenced by temperature. At lower temperatures, protandry can even be reversed to protogyny.

Tassel development. Long days increased the number of leaf and tassel-branch primordia but only during the relatively short period before tassel initiation. The production of leaf primordia already stopped before the transition to the double-ridge stage. The tassel branches are the first parts of the tassel to differentiate (Bonnett, 1966). The effects of photoperiod and temperature on the

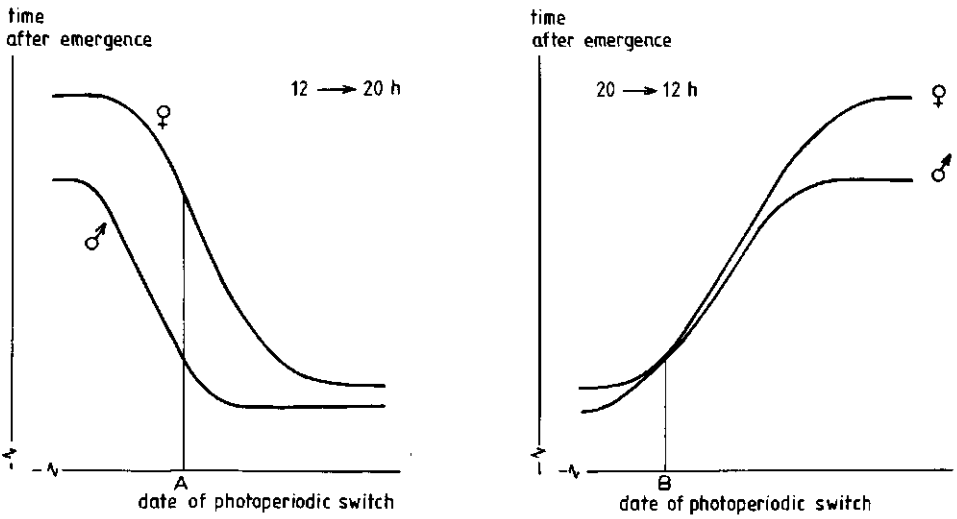


Fig. 6. Effects of photoperiodic switch on time to extrusion of anthers (♂) or silks (♀) (model). A gives the maximum desynchronization for 12 → 20 h. B gives the minimum desynchronization for 20 → 12 h.

number of tassel branches confirm those of Moss & Heslop-Harrison (1968) and Blondon & Gallais (1976). The development of the apex is very fast with short days: the larger the number of short days a plant undergoes during the sensitive stage, the fewer branches it will have. The minimum (number for treatment 12 → 12 h) was very soon reached. Development of the apex with long days took more time, so the maximum number of branches (number for 20 → 20 h) was reached much later.

Sex expression. Photoperiod caused mixing of ears and tassels in Trials 1 and 2. All flowers of a maize plant are originally bisexual and differentiation of the primordia proceeds acropetally (Bonnett, 1953). Sex reversal in the inflorescences would only be possible in the top of the ear or at the end of the tassel branches if it were caused by treatments after the 5.2-leaf stage. Moss & Heslop-Harrison (1968) found sex reversal in the tassel with very short days, and Galinat & Naylor (1951) even found proliferation of the tassel with short days. In Trial 2, female flowers reverted to male with high temperatures and a photoperiodic treatment of 12 → 20 h. In Trial 1, some sex reversal was found in the tassel at lower temperatures, especially for the photoperiods 12 → 12 h. These photoperiod and temperature effects on sex expression of a maize plant correspond to effects found in numerous other monoecious short-day plants (e.g. Heslop-Harrison, 1957).

Indirect responses. The effects on sex versatility, flowering dates and desynchronization, and number of leaf primordia and of tassel branches are the only specific reactions to the photoperiod stimulus, found in these trials (contrast Moss & Heslop-Harrison, 1968). Maximum reactions coincided with the period before and during the transition stage. These direct responses are 'qualitative' reactions to photoperiod, as they require a certain number of short days. Most other unspecific reactions are completely different, since they are consequences of effects on elongation of vegetative organs. They reached their maximum or minimum later, namely at about the first stage at which photoperiod no longer affected tassel-branch initiation. A later change in photoperiod changed no longer the rate of development of the main shoot, but reduced or augmented the number of long days during cell division or cell enlargement. So, most of the vegetative cells experienced the extreme number of long days available for growth at this point.

These indirect responses are due to 'quantitative' reactions to photoperiod: the effects depend on the number of long days after a certain stage, since the measure and duration of depression of the dominance of given reproductive organs is affected by this number.

Indirect responses with a different pattern. Two curves deviated from the general pattern. The relation for total leaf area was linear (Fig. 3), because the area of the individual leaves increased linearly with leaf stage. Under natural conditions, the transformation of the apex is responsible for a progressive decline in

initial fractional growth rate of the successive leaf primordia (Williams, 1966). If the initiation or development is retarded, the decline may be retarded or reduced, respectively. Effects of day length on rate of development or initiation were recorded for the entire range of time, at which the switch was made in Trial 3. A further extension of the range would have provided sigmoid curves.

Number of kernels in the top ear showed two clear peaks for 12 → 20 h, one at the beginning of the stage at which the plant is sensitive to photoperiod and one almost coinciding with the peak in elongation. It might be expected that number of kernels would give curves like the desynchronization curves, as they reflect the time available for initiation of floret primordia and as it is unlikely that rates of initiation differ (Allison & Daynard, 1979). The number of kernels, however, was much lower than expected when the change occurred at stages with 4.5, 5.0, 5.5 and 6.0 leaves, which probably form the trasition stage. The initiation rate of female florets could decline when the intensity of the flowering stimulus is drastically reduced during that stage, in which the ear apices are susceptible because of their backwardness.

Concluding remarks. Photoperiod treatments of maize should last until the female flowering; on no account should they be stopped after tassel initiation as requirements for induction, initiation and development are not the same for the two inflorescences. The sensitive stage for some direct effects is shorter than for the indirect effects.

Since conditions like temperature, radiation during the basic light period and drought influence the apical dominance of the tassel and the measure of protandry, there is an interaction with photoperiod.

The genotypic variation in photoperiodic sensitivity is enormous. But even accepted 'day-neutral' hybrids showed a large effect of switch in photoperiod. The induction, initiation and development of female organs are possibly still too photosensitive for West Europe. The developmental rate of the main-shoot apex is the main determinant of the vegetative growth; the rate of ear development influences the maturing process. Selection for a greater sensitivity to photoperiod of the main-shoot apex relative to ear-shoot apices and a smaller sensitivity of the lateral branches would provide plants with larger leaf area and better synchronization; if so, genotypes are created, in which the early-maturing characteristics of the treatment with photoperiods 20 → 12 h are combined with some of the positive effects on vegetative development of 20 → 20 h. So the positive effects of early and late genotypes are united.

Growing maize under unfavourable conditions (poor light, dense planting) often leads to a poor grain-set, partly by desynchronization of inflorescences. The trials suggest that this decrease in fertility can be partly overcome by long day before tassel initiation. The methods used offer a new line for plant physiology, since sink-source relation can be affected in an unusual way and as processes in male and female flowering can be separated.

CHAPTER 6

THE EFFECTS OF SWITCHES IN PHOTOPERIOD ON CROP MORPHOLOGY, PRODUCTION PATTERN AND QUALITY OF FORAGE MAIZE (*ZEA MAYS* L.) UNDER FIELD CONDITIONS

INTRODUCTION

Like all plants, maize consists of a variety of differentiated structures, each with its special form and function. These specialized organs and tissues are closely related via the distribution of photosynthates, nitrogenous compounds, nutrients and growth regulators. It is on these relations that the organization of the plant as a growing, developing and producing entity is based. The breeder and the grower, however, value certain plant parts more than others and will try to maximize their yield, even in the case of forage maize, where the whole plant is harvested.

The morphology of a forage-maize crop affects its quality as a roughage for ruminants. The digestibility of the plant parts varies greatly within a plant, because of differences in cell-wall content and in cell-wall digestibility (STRUIK, 1982a). The proportions of the various plant parts in the final crop can be affected by harvest date, cultural practice, genotype and climate, or can be artificially manipulated.

Effects stimulating the proportions of the most digestible parts of the plant in the organic matter will increase digestibility of the organic matter of the whole crop unless these stimulative effects simultaneously cause a decline in digestibility in other parts of the plant.

The most digestible part of the forage-maize plant is the kernel (BARNES et al., 1971; AERTS et al., 1978; WEAVER et al., 1978; HACKER and MINSON, 1981; STRUIK, 1982a). Numerous authors have reported that an increase in the proportion of grains or ears (grain + rachis) is accompanied by a decline in the digestibility of the non-ear parts (e.g. DEINUM and DIRVEN, 1971; DAYNARD and HUNTER, 1975; GALLAIS et al., 1976; PERRY and COMPTON, 1977; AERTS et al., 1978; WEAVER et al., 1978; PHIPPS and WELLER, 1979; GROSS and PESCHKE, 1980; HUNTER, 1981; STRUIK, 1982b). Continuous ageing of cell walls is one of the causes of this decline (STRUIK, 1982a). More important, however, is the fact that in most maize-growing regions part of the dry-matter accumulation in the grains is realized by the translocation of completely digestible cell solubles from vegetative parts to the ear. This material translocated includes minerals, nitrogenous compounds and carbohydrates (HANWAY, 1963; DAYNARD et al., 1969; BEAUCHAMP et al., 1976; STRUIK, 1982a, b); the intensity of the translocation greatly affects the final digestibility of the vegetative plant parts (STRUIK, 1982b; STRUIK and DEINUM, 1982).

The combined effects of cell-wall maturation, an increase in the proportion of ear in the crop and a decrease in stover quality mostly result in the whole-crop digestibility after grain set being approximately constant. The continuous de-

cline in quality that precedes flowering is halted in the case of maize. Because of the negative effect of grain filling on stover quality, it is questionable whether a high proportion of grain is needed to obtain a forage maize of good quality. Artificially preventing grain filling usually only induces slight decreases in whole-plant digestibility (CUMMINS and MCCULLOUGH, 1971; MARTEN and WESTERBERG, 1972; BUNTING, 1975, 1976; DEINUM and KNOPPERS, 1979), although STRUIK (1982b) has reported larger decreases. PHIPPS et al. (1982) even reported a considerable increase in whole-plant digestibility, caused by the improbably low digestibility of the ear fraction (grains + rachis + husks) of the fertile crops. Complete removal of ear shoots before pollination causes considerable declines in crop digestibility (STRUIK, unpublished data).

Since plant organs are mutually interdependent, the rate of post-silking production may depend on the success of grain set. Barrenness, artificial sterility and ear removal reduce photosynthesis (MOSS, 1962; RODE et al., 1979). BUNTING (1975, 1976), DEINUM and KNOPPERS (1979) and PHIPPS et al. (1982), however, reported that sterility hardly affected dry-matter yield in North-West Europe. In contrast, KIESSELBACH (1948) in Nebraska (U.S.A.), CAMPBELL (1964; Mississippi, U.S.A.), MARTEN and WESTERBERG (1972; Minnesota, U.S.A.) and STRUIK (1982b; Netherlands) found that the yield of sterile crops was considerably depressed. Removing the ears completely before pollination can depress yield by up to 50–60% (IREMIREN and MILBOURN, 1978; LESHEM and WERMKE, 1981; STRUIK, unpublished data). The repercussions of ear removal seem to be much greater than the repercussions of preventing grain set. In sterile plants that still bear intact husks, shanks and cobs, the storage capacity–though greatly reduced– is limited less than in plants whose ear shoots have been removed. The difference between the repercussions of removing the ears and of ear sterility is equivalent to the storage capacity of husks, shanks and cobs. Only when storage capacity in the stems, husks, shanks and cobs is insufficient (e.g. because of climate or weather conditions) grain filling is apparently required to maintain high productivity.

As well as the above-mentioned effects on digestibility, photosynthesis, production and storage capacity, grain filling has certain side effects:

- an increase in starch content. The starch content is important because starch tends to be inert during fermentation in the silage, in contrast with soluble carbohydrates, which are converted to organic acids (MCALLAN and PHIPPS, 1977).
- according to DEINUM and KNOPPERS (1979) more cell-wall material will be produced in the stover if grain filling is inhibited. The data obtained by KING et al. (1972), however, do not accord with this.
- the dry-matter content of a normal crop increases much faster than that of a grainless crop or that of a crop with a low proportion of the dry matter present in the ear. This effect of grain filling has been reported by BUNTING (1976), DEINUM and KNOPPERS (1979), PHIPPS et al. (1982), STRUIK and DEINUM (1982) and STRUIK (1983).
- leaf senescence may be affected by ear development; both delayed senescence

(MOSS, 1962) and advanced senescence (ALLISON and WEINMANN, 1970; CHRISTENSEN et al., 1981; THIAGARAJAH et al., 1981; STRUIK, unpublished data) may occur in sterile or earless crops. WILSON and ALLISON (1978) stated that an exceptionally large grain sink may cause the plant to die prematurely.

Removal of ears and prevention of pollination are rather drastic measures to take when investigating the effects of grain filling: these treatments are imposed at a physiological stage at which the plant is already fixed and 'programmed'. MCALLAN and PHIPPS (1977) and LESHEM and WERMKE (1981) used different plant densities to trace effects of grain filling and concluded that grain filling is not important for quality of the fresh crop. Other researchers (BEEREPOOT, 1981; DEINUM and BAKKER, 1981) have used genotypic variation to show that the proportion of ear in a crop is very positively correlated with crop digestibility, though it is not necessarily the most important factor. Earlier phytotron experiments done by the present author revealed that switches in photoperiod may alter vegetative and reproductive development after the duration of the vegetative phase has been fixed (STRUIK, 1982c). If these effects could be induced under field conditions, an elegant method would be available to measure the effects of crop structure on productivity, senescence, dry-matter content and digestibility. This report describes attempts to use this method.

MATERIALS AND METHODS

Background to the method

The method is based on the following physiological facts:

1. Initiation of the tassel (the terminal, staminate inflorescence) stops the initiation of leaf primordia.
2. Initiation of the ears (pistillate inflorescences) occurs some time after tassel initiation.
3. The photoperiodic requirements for the induction of the female inflorescence are greater than those of the male inflorescence. Ear *development* is also more sensitive to photoperiod than tassel development.
4. If the ear is made to lag behind the tassel more than normal during its early development, the gap between male and female flowering can widen greatly.
5. The rate at which the inflorescences develop partly determines the vegetative growth (e.g. stem elongation, leaf size) and the size of the reproductive organs.

Lengthening the photoperiod shortly after tassel initiation, but before the photoperiodic requirements of the ears have been completely fulfilled will induce the following reactions:

1. A short delay in anthesis but a pronounced delay in silking.
2. A considerable desynchronization of male and female flowering.
3. A larger leaf area.

It is possible to produce these effects without affecting the number of leaves

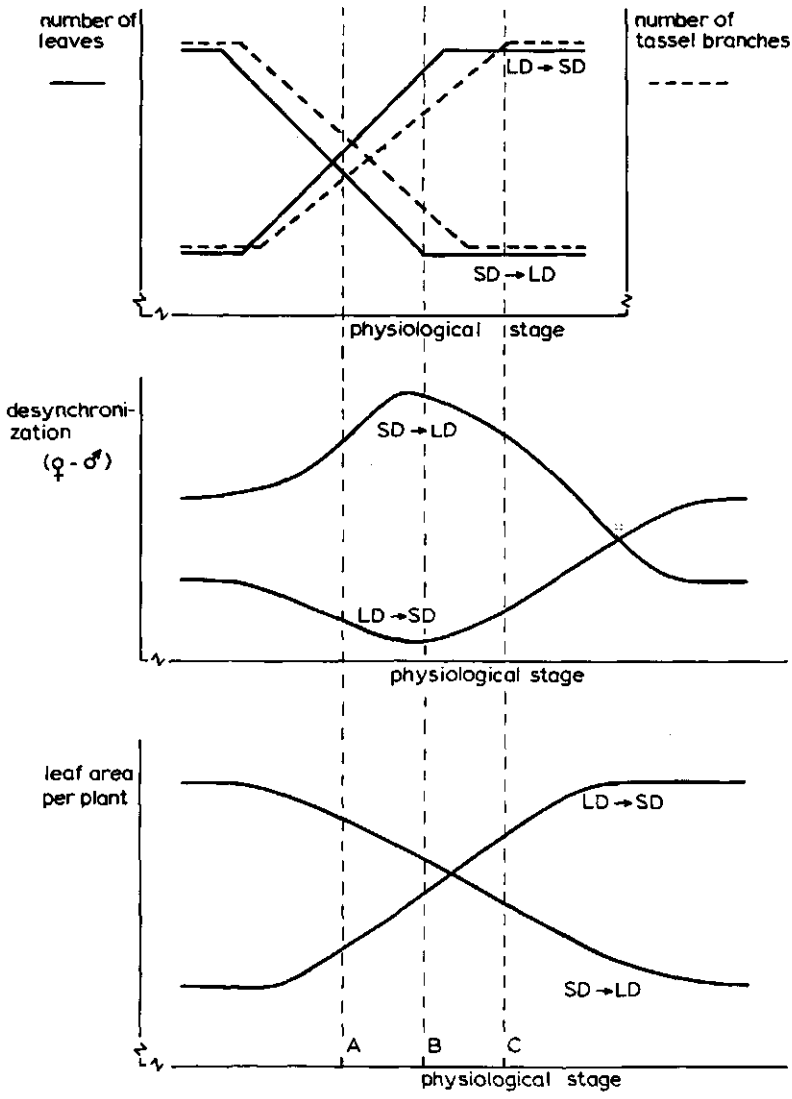


FIG. 1. Schematic representation of the effects of a photoperiod switch on number of leaves, number of tassel branches, desynchronization and leaf area as a function of the physiological stage at which the switch occurs. A, B and C indicate the stages at which 4.5, 5.5 and 6.5 leaves are visible. SD = short day; LD = long day; (based on STRUIK, 1982c).

(and thus the number of stem internodes) (Fig. 1). As well as the characteristics shown in Fig. 1, plant height, size of the reproductive organs and number of tillers may also be affected.

Shortening the photoperiod after tassel initiation will accelerate the fulfilment of the photoperiodic requirements of the ears and will therefore reduce the gap between silking and anthesis and will reduce the size of vegetative and reproductive organs.

The longer the lengthened photoperiod, the larger the effects will be.

Method of lengthening photoperiod under field conditions and treatments

In 1980 and 1981, field experiments were done in which the photoperiod was lengthened by suspending strings of incandescent bulbs (60 W) about 2.25 m above the soil level. The incandescent bulbs were distributed equally over each net plot and were capped with aluminium to increase illuminance and to decrease light dispersal to neighbouring plots. The equipment was checked daily.

Net plots were separated by large borders both between and within blocks. The average illuminance at soil level of plots receiving a lengthened photoperiod was 75.1 lx in 1980 and 77.0 lx in 1981; 95% of the measurements were above 50 lx, corresponding to an irradiance in the waveband 400–700 nm of 0.2 $W.m^{-2}$. The average illuminance at soil level of plots without photoperiod supplement was 0.2 (1980) and 0.4 (1981) lx; illuminance in these plots never exceeded values of 2.5 lx (0.01 $W.m^{-2}$), not even with considerable wind force. Saturation of the photosensitivity of maize is obtained at illuminances above 43–65 lx (FRANCIS et al., 1970; TESCHEMACHER, 1974; FAUNGFUPONG, 1975), while no photoperiod effects are observed with illuminance below 3 lx (FAUNGFUPONG, 1975).

In 1980 the photoperiods were switched at the 5.5-leaf stage; the photoperiod treatments were:

code	photoperiod before 5.5-leaf stage	photoperiod from 5.5-leaf stage until end of ♀ flowering
n → n	natural	natural
n → 20	natural	20 h
n → 24	natural	24 h
20 → n	20 h	natural
20 → 20	20 h	20 h
24 → n	24 h	natural
24 → 24	24 h	24 h

The 20 h treatment was obtained by lengthening the photoperiod both before and after the basic light period (night phase from 23.45 h to 3.45 h). In this paper the emphasis will be on the results of treatments n → n, n → 24, 24 → n and 24 → 24.

In the 1981 trial the photoperiods were switched at the 4.5-leaf stage and the 6.5-leaf stage. The following treatments were applied:

code	photoperiod before 4.5-leaf stage	photoperiod from 4.5-leaf stage until 6.5-leaf stage	photoperiod from 6.5-leaf stage until end of ♀ flowering
n → n	natural	natural	natural
n → 24a	natural	24 h	24 h
n → 24b	natural	natural	24 h
24 → n	24 h	24 h	natural
24 → 24	24 h	24 h	24 h

Cultural practice and technical details

The soils were amply fertilized. Rows were 75 cm wide. Herbicide had to be applied before emergence because of the installation of the equipment to lengthen the photoperiod. For optimum weed control an extra mechanical treatment was necessary in both years.

If necessary, drought was prevented by sprinkling.

In 1981 emergence was disappointing. To obtain uniform stands the density was therefore reduced to 4.4 plants per m^2.

The two experiments differed in year, treatments, location, choice of hybrid and density. Table 1 presents some general information about the methods.

Measurements of plant growth and development

Vegetative development

The data recorded weekly included number of visible leaves, number of green leaves and height of the plant. During early development these crop descriptions were done much more frequently (sometimes twice daily) to determine the exact date for the switch in photoperiod. At silking, the leaf area of the main shoot of 16 (1980) or 20 (1981) plants per treatment was estimated by multiplying the maximum length of each leaf by its maximum width by 0.75 (MONTGOMERY, 1911).

Shortly after flowering the number of leaves above the top ear was recorded for 16 (1980) or 20 (1981) plants per treatment.

The stem thickness of the main shoot was measured by estimating the maximum diameter in the centre of the second internode above the soil level. These observations were done after stem growth had ended and also involved 16 (1980) or 20 (1981) plants per treatment.

On each sampling date in 1981, the number of tillers per row harvested was also recorded.

Reproductive development

In 1980, the percentage of plants showing anther or silk extrusion was estimated every second day by observing 80 plants per treatment (i.e. 20 plants per plot). In 1981, 25 plants per plot (i.e. 100 per treatment) were screened daily

TABLE 1. Cultural practice and date of application of first photoperiod extension in 1980 and 1981.

Year	1980	1981
Location	Wageningen	Achterberg
Soil type	fine-textured clay	light and moist sand
Hybrid	LG 11 (FAO 260)	Nicco (FAO 300)
Final plant density ($pl.m^{-2}$)	10.05	4.36
Sowing date	24 April	24 April
Date of 50% emergence	16 May	12 May
First date of long-day treatment	14 May	7 May

during the main period and every second day at the start or at the end of the flowering period.

The number of tassel branches per plant was estimated on 20 plants per treatment in the 1981 experiment.

The length and number of kernels of the top ear were measured on 40 plants per treatment at the final sampling of both experiments. In 1981 maximum ear thickness was also measured.

The number of lower ears (i.e. all ears emerging from the axils of the leaves below the ear leaf of the main shoot) was measured on each sampling date. In 1981 the number of axillary ears (i.e. small ear shoots developed from the reproductive axillary buds in the axils of the husks of the top ear and large enough to extrude from the husks) was also recorded.

Plot size and sampling technique

The plots occupied an area of 10 × 9 m^2 (1980) or 10 × 7.5 m^2 (1981) with two border rows on either side of the plot and one row separating the rows intended for sampling. One extra net row was available for possible additional observations at final sampling. Both experiments were laid down as a completely randomized block design with four replicates. The plots were sampled 23 days after midsilk of the control (approximately at the onset of the rapid dry-matter accumulation in the kernels) and twice thereafter. In 1980 the dry-matter yields at the 5.5-leaf stage were estimated as well.

One row 6 m long (4.5 m^2) was harvested. The plants were cut off at soil level, counted and stored in a cold chamber during further processing. The plants were separated into stover (stem + leaves + tassel), husk + shank, top ear and lower ears. In 1981, tillers were treated as the fifth fraction. After recording the fresh weight, the fractions were chopped. Husk + shank and stover were chopped with a stationary 1-row FAHR MH 70 chopper. The chopped material was transported directly into an operating concrete mixer by means of a jet of air and a conveyor belt. Subsamples were taken from the stream of material while emptying the mixer. Top ears, lower ears and tillers were chopped with a vegetable cutter.

Subsamples were dried to constant weight in forced ventilated ovens at a maximum temperature of 70 °C.

After dry weighing, samples were bulked per plant part and per treatment, ground in hammer mills with sieves of 1 mm and subsampled again.

Chemical analyses

Although an extensive chemical analysis was carried out, only the results of the in vitro digestibility and cell-wall analysis will be presented, since these two criteria adequately describe quality dynamics. True digestibility in vitro of organic matter (D_{true}) was estimated according to the method of VAN SOEST et al. (1966). A series of standard maize samples of known in vivo digestibility for sheep, analysed in each run, made it possible to convert the data to apparent digestibility (D_{om}). The cell-wall content of dry matter (after dissolving the

starch) was estimated using the method described by VAN SOEST (1977). Cell-wall digestibility (D_{cwc}) was calculated from true digestibility (D_{true}), cell-wall content (cwc%) and ash content (ash%) by means of the formula

$$D_{cwc} = 100 - \frac{(100 - D_{true}) \times (100 - ash\%)}{cwc\%}$$

RESULTS AND DISCUSSION

1. Climatic data

Table 2 shows the mean temperature, amounts of radiation and precipitation for 1980 and 1981 at Wageningen. The most relevant differences in weather between these two years were:

a. May 1980 was cold, but sunny and dry; in contrast May 1981 was much warmer, with sufficient precipitation but less irradiance.
b. July was cool and extremely wet in 1980, especially in the first three weeks.
c. The period between 10% and 90% silking was much warmer in 1980 (mean temperature 19.6°C) than in 1981 (mean temperature 15.4°C).

These climatic patterns affected the way that the physiological effects induced

TABLE 2. Climatic data for Wageningen for 1980 and 1981.

Month	Average temperature (°C)		Solar irradiance ($MJ.m^{-2}$)		Rainfall (mm)	
Year	1980	1981	1980	1981	1980	1981
May	12.0	13.4	649	496	9.3	64.3
June	14.8	14.4	488	419	66.5	64.3
July	15.6	16.3	425	441	145.7	49.4
August	16.9	16.5	422	406	46.4	19.8[1])
September	15.2	14.7	333	311	27.4	57.9[1])
October	8.7	8.8	?	144	67.4	137.2

[1]) Drought prevented by sprinkling.

TABLE 3. Time required to reach specific developmental stages, expressed in days after sowing (24 April in 1980 and 1981).

	1980	1981
50% emergence	22	19
4.5-leaf stage	38	31*
5.5-leaf stage	43*	35
6.5-leaf stage	48	39*
50% ♂ flowering[1])	102	91
50% ♀ flowering[1])	100	92

[1]) of the control.
* time of change in photoperiod in some treatments.

by manipulating the photoperiod were manifested. The cool weather during early growth in 1980 delayed development and consequently the time of the photoperiod switch was later (Table 3). Therefore in 1980 the switch was done at a time when natural daylength was somewhat longer than in 1981. As well, dense cloud cover around the time of sunrise and sunset may shorten natural daylength considerably (FRANCIS, 1970). In 1980 the amounts of irradiance and the relative duration of sunshine during May and June were much higher than in 1981. The data on hourly recorded light intensity also suggest that photoperiods were longer in 1980. It must therefore be concluded that lengthening the photoperiod was less effective in 1980. Cool weather during the pre-silking period decreases apical dominance and will thus limit the effects of photoperiod on desynchronization (STRUIK, 1982c). Low temperatures also cause protandry to revert to protogyny (Table 3; cf. STRUIK, 1982c). High temperatures during the flowering period shorten the anthesis-to-silking interval of each individual plant and will therefore reduce the effects of photoperiod treatments.

2. *Vegetative development*

2.1. Leaf appearance

The rate of leaf appearance was not affected by photoperiod. This agrees with data presented by BROUWER et al. (1973), GMELIG MEYLING (1973) and HUNTER et al. (1977). Because of differences in the duration of leaf initiation, the numbers of leaves ultimately produced per plant differed (Table 4). The data fitted in the expected pattern shown in Fig. 1. Only the photoperiods before the photoperiod switch influenced the number of leaves, except in the case of treatment n → 24a, where the switch took place at the 4.5-leaf stage.

However, the differences between the number of leaves in the different treatments were small in both years.

2.2. Plant height and stem diameter

Photoperiod affects plant height by affecting the number of internodes and internode length (AITKEN, 1980; STRUIK, 1982c). Differences in plant height arose when differences in leaf number became apparent. Final plant heights are listed in Table 4 together with the mean internode length (estimated by dividing final plant height by final number of leaves) and stem diameter.

In 1980, the photoperiod before the switch affected plant height by means of its effect on the number of phytomeres. The photoperiod after the 5.5-leaf stage affected plant height through its effect on internode length, sometimes at the expense of the radial growth of the stem. Internode elongation correlated significantly with the anthesis-to-silking interval (simple linear correlation coefficient $r = 0.899$, $P < 0.01$) mentioned below. In 1981, differences were smaller than in 1980, and the internodes of plants grown under long days elongated less than in 1980. The linear correlation between desynchronization and internode elongation was again significant ($r = 0.936$, $P < 0.05$). Stem thickness was not affected in this experiment. Since the correlation between elongation and

desynchronization was significant in both years and since photoperiod itself is not the only factor determining internode elongation, these two correlated phenomena might have a common physiological basis. Perhaps the size of the tassel influences its production of auxins and gibberellins; these growth regulators are necessary for the suppression of axillary buds, cell elongation and cell division (cf. MESSIAEN, 1963; STRUIK, 1982c). The production of these growth regulators is probably not only affected by the duration of the light phase but also by the quality and intensity of the light during the extension of the photoperiod.

2.3. Leaf area and leaf senescence

Leaf area increases with longer photoperiods, not only because more leaves are produced but also because the individual leaves are larger (AITKEN, 1980; HUNTER, 1980; STRUIK, 1982c; see also Fig. 1). Leaf areas at silking are listed in Table 4. Data of individual plants suggest that 20 → 20 and 24 → 24 (1980) were somewhat underestimated. Otherwise the data agree with the trends anticipated in Fig. 1. Differences in light interception were not large enough to induce significant differences in dry-matter production.

The number of dead leaves in all photoperiod treatments showed a similar development over time. In 1980, however, 24 → n tended to senesce faster.

2.4. Other data on vegetative development

The number of above-ear leaves in 1980 was independent of photoperiod treatment. Thus, differences in final number of leaves were caused by differences in the number of leaves below the top ear. The ratio of leaf area above the ear to total leaf area was therefore smaller in treatments receiving longer photoperiods before the switch, especially when a long-day treatment was followed by a short-day treatment.

In the 1981 experiment, both the number of leaves below the ear and the number of leaves above the ear differed between treatments, resulting in relatively more leaf area above the ear in n → 24a and n → 24b than in the other treatments. These differences in distribution of leaf area might induce differences in dry-matter distribution.

The number of tillers will be discussed in section 3.2, together with other phenomena related to apical dominance.

Résumé:

The data on vegetative development agreed with those presented in an earlier paper (STRUIK, 1982c). *Differences between the treatments in these field experiments, however, were small. The main differences were in leaf area per plant and in plant height.*

TABLE 4. Data on vegetative development of all treatments in both experiments.

Treatment	Mean number of leaves/pl	Mean plant height (cm)	Mean internode length (cm)†	Mean stem diameter (cm)	Mean leaf area/pl (dm^2)
		1980			
n → n	14.1 a§	195 a	13.8	2.43 b	35.7 ab
n → 20	14.0 a	207 ab	14.8	2.22 ab	38.9 ab
n → 24	14.2 a	221 bc	15.5	2.02 a	41.6 b
20 → n	14.5 ab	207 ab	14.3	2.21 ab	36.5 ab
20 → 20	14.5 ab	204 ab	14.0	2.12 ab	35.2 a
24 → n	15.1 b	213 abc	14.1	2.10 ab	38.3 ab
24 → 24	15.2 b	231 c	15.2	2.32 ab	39.9 ab
		1981			
n → n	15.1 ab	212 a	14.0	3.21	65.3 a
n → 24a	15.6 bc	224 b	14.3	3.43	70.1 ab
n → 24b	14.9 a	222 b	14.9	3.30	71.0 abc
24 → n	16.3 d	219 ab	13.4	3.31	71.7 bc
24 → 24	16.2 cd	226 b	13.9	3.31	76.2 c

† Statistical analysis is not possible for this parameter.
§ Means with a letter in common are not significantly different at the 0.05 probability level, according to Tukey's studentized range test.

3. Reproductive development

3.1. Flowering dates and desynchronization

Fig. 2 illustrates the development over time of the proportion of plants showing pollen shed and silk extrusion for the n → n treatments of both experiments. The way of estimating desynchronization (i.e. number of days required to reach 50% silking minus number of days required to reach 50% pollen shed) is also illustrated.

Estimates of 50% flowering dates and desynchronization values are presented in Table 5. To simplify the discussion, the desynchronization data have been modified by subtracting the desynchronization value of the control. In this way the direct effect of temperature on desynchronization is neutralized.

The flowering dates differed in the same way in 1980 and in 1981. However, in 1981 the differences were much more pronounced. Long days before and after the photoperiod switch retarded both pollen shed and silking. However, the photoperiod before tassel initiation affected anthesis more than silking, whereas the opposite was true for photoperiod after tassel initiation. Each treatment therefore showed a characteristic desynchronization value.

Long photoperiods during the entire growing season increase the desynchronization because silking is delayed more than anthesis. This has already been

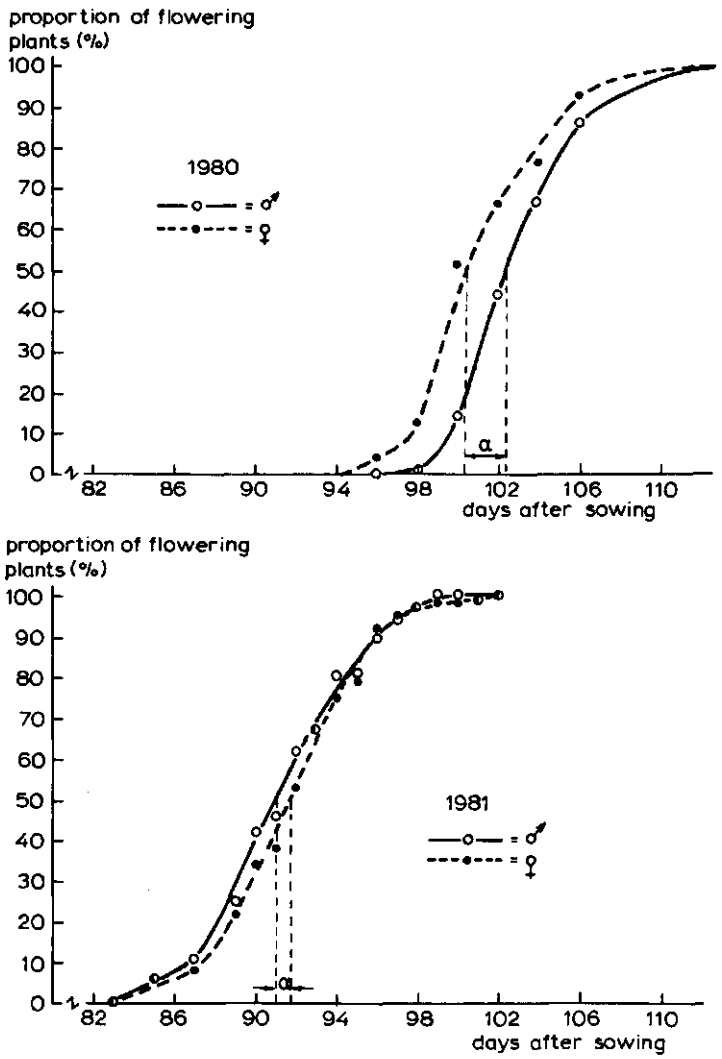


FIG. 2. Course of proportion of flowering plants in untreated plots of both experiments. *a* indicates the desynchronization (♀–♂).

reported by FAUNGFUPONG (1975), BLONDON and GALLAIS (1976), AITKEN (1980), STRUIK (1982c) and other researchers (see also Fig. 1). Although the difference between n → n and 24 → 24 was similar in both years, Nicco seems to react more sharply to photoperiod switches than LG 11, certainly if the later stage of the switch is taken into account.

Again, the differences between treatments were rather small but agreed with expectations based on phytotron experiments. Similar effects resulting from photoperiod switches were also obtained by FAUNGFUPONG (1975).

In all cases desynchronization was too short to affect the extent of pollination.

5. Dry-matter content

The proportions of dry matter in fresh material ('dry-matter content') are listed in Table 8 for certain fractions at final sampling. The dry-matter content of top ear, husk + shank and of the whole crop was significantly different at all samplings in both experiments. In all cases trends were similar: dry-matter content was approximately the same for n → n and 24 → n and much higher than for n → 24 and 24 → 24.

There were no clear differences in the dry-matter content of stover, or lower ears, or tillers, although the trends were often the same as those in the top ear, husk + shank and whole crop in 1981 (Table 8). Whole crop dry-matter content was calculated from the dry-matter content of the individual fractions and their proportions of fresh matter. During the grain-filling period the dry-matter content and the ear proportion both increase very rapidly; the proportion of husk + shank is small and the dry-matter content in the stover increases only slightly before complete senescence or frost damage. In these trials therefore, the dry-matter content of the whole crop was mainly determined by the proportion of ear in the fresh material and its dry-matter content (see Fig. 4). Any differences between treatments in the proportion of ears decreased during grain filling, whereas differences in the dry-matter content of the ears did not alter very much. Differences in the dry-matter content of the whole crop increased during the post-silking period because the fraction that exhibited the greatest differences

TABLE 8. Whole-crop yield and dry-matter content of stover, husk + shank, top ear and whole crop at final sampling.

	Dry-matter yield ($Mg.ha^{-1}$)	Proportion of dry matter in fresh material (%)			
	whole crop	stover	husk + shank	top ear	whole plant (incl. tillers)
		1980			
n → n	14.36	18.5	24.7	51.3	29.3
n → 24	14.79	18.7	23.0	47.9	27.3
24 → n	15.03	19.3	24.7	51.4	29.6
24 → 24	14.47	18.5	21.9	47.0	26.7
P	ns*	ns	0.051	0.011	0.005
		1981			
n → n	15.29	20.2	27.1	55.9	31.3
n → 24a	15.21	18.2	24.5	53.7	28.7
n → 24b	15.93	18.3	23.4	53.8	28.8
24 → n	15.45	19.5	27.9	55.5	30.6
24 → 24	15.39	18.9	24.2	53.6	29.1
P	ns	ns	0.013	0.004	0.039

* ns = not significant.

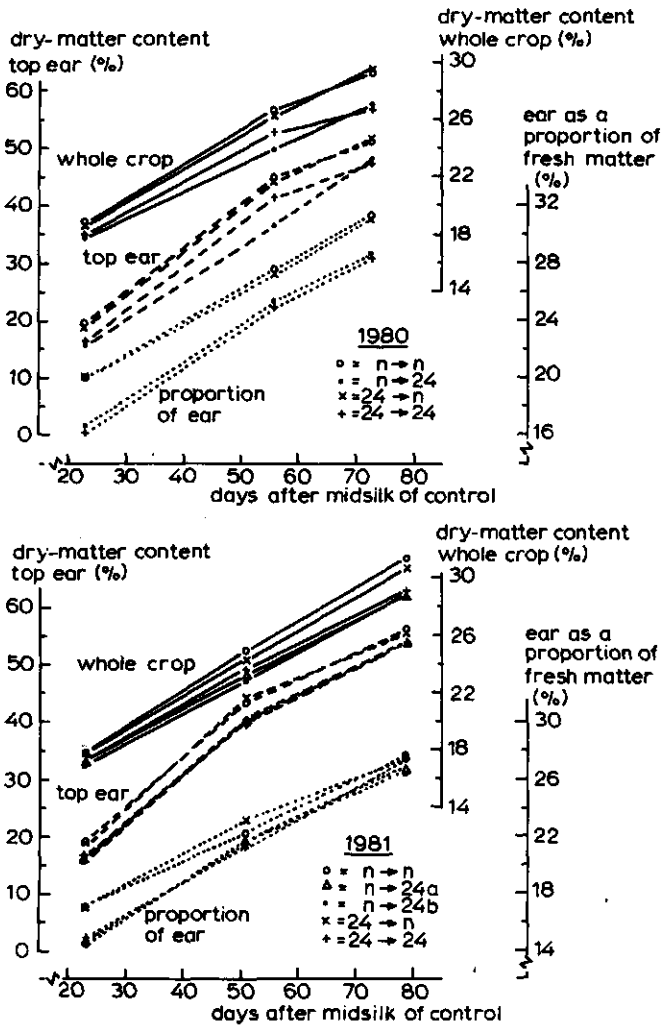


FIG. 4. Development over time of dry-matter content of the whole crop (——) and of the top ear (– – – –) together with the proportion of whole crop fresh material that is accounted for by the ears (....).

between treatments (i.e. the ear) became increasingly important. Since ear dry-matter content correlated with silking date, the dry-matter content of the whole crop also closely correlated with silking date. The linear correlation coefficients at final sampling were -0.943 ($P<0.01$; $n = 7$) and -0.998 ($P<0.01$; $n = 5$) for 1980 and 1981, respectively.

Thus the rate of the ear development and not the rate of development of the main shoot determined the course of the dry-matter content of the whole crop. At final sampling the dry-matter content of the whole crop decreased by 1.1% (1980) or 0.5% (1981) for every day the silking was delayed. These high regression coefficients emphasize the relevance of good ear development for the maturation of maize as a forage crop.

Résumé:
The dry-matter content of the whole crop was mainly affected by the dry-matter content of the ear and the proportion of ear in the fresh material. Dry-matter content was closely correlated with silking date.

6. Cell-wall content and in vitro digestibility

A plant is composed of cell walls and cell contents. Cell contents are almost completely digestible for ruminants but cell walls are only digestible to a certain–variable–extent. The digestibility of a forage-maize crop as roughage for ruminants is therefore determined by the cell-wall content and the digestibility of the cell walls. Vegetative parts contain a considerable amount of poorly digestible cell-wall constituents. By contrast, ear parts are mainly composed of cell contents and highly digestible cell walls.

Since whole-crop yields were fairly constant and dry-matter distribution was variable, the cell-wall content, cell-wall yield, cell-wall digestibility and in vitro digestibility of organic matter may vary. Table 9 presents the data from the most relevant treatments and fractions at final sampling.

The cell-wall yield at first post-anthesis sampling (23 days after midsilk of the control) showed only a small variation between treatments. The amounts of cell wall in the stover, however, were much greater if long days were applied after tassel initiation. In both years these differences were still present at final sampling (Table 9), although in 1980 the 20 h treatments did not conform to the pattern very well: at first the smaller amounts of cell wall in the stover were compensated for by larger amounts of cell wall present in the ear parts. At the first sampling after silking the ears in treatments n → n and 24 → n were more developed. Final ear size was stimulated by a photoperiod-induced deceleration of ear development, resulting in considerably high cell-wall production during September and high yields of cell wall in the ear (Table 9). No important differences were induced in cell-wall formation in husks + shanks. The combined effects of photoperiod treatment on cell-wall formation in different plant fractions resulted in final cell-wall yields of the whole crop shown in Table 9. Whole-crop data of the 1981 experiment were somewhat distorted by tiller development. Therefore data for the crops without tillers are given. Total cell-wall yield was affected by the extent of vegetative development, delay of reproductive development and ear size.

The effects of photoperiod switches on the cell-wall content in the stover were much greater in 1981 than in 1980, but cell-wall content in the ear differed considerably in both experiments because of differences in physiological stage and shelling percentage. In the 1981 experiment the cell-wall content of the top ear of 24 → 24 was lower than expected on the basis of data from other treatments and earlier samplings. Because of these effects on cell-wall content of the top ear and because of the effects of photoperiod mentioned above on the proportion of the ear, the cell-wall content of the whole crop showed clear differences between treatments, especially in the 1980 experiment. In this experiment, the cell-

wall content of the whole crop correlated significantly with silking date ($P < 0.05$).

Estimates of cell-wall digestibility are more inaccurate than estimates of cell-wall content or organic-matter digestibility, especially in ear samples where the cell-wall residue after in vitro digestion is only small. Differences in cell-wall digestibility were small and inconsistent; whole crop cell-wall digestibility at final sampling should therefore be regarded as being unaffected by photoperiod treatments. Thus the continuous decrease in cell-wall digestibility was similarly not affected by the physiological stage of the crop. Photoperiod treatments seemed to have disturbed the synchronization between crop maturity and cell-wall maturation.

In vitro digestibility of the fractions differed only slightly in both experiments (Table 9). Differences in whole-crop digestibility therefore depended mainly on differences in the proportions of the different fractions in the organic matter. Only in the 1980 experiment did these proportions still differ at final sampling.

Résumé:

Long days before and after tassel initiation stimulated cell-wall formation in vegetative parts. Long days after tassel initiation stimulated cell-well formation in the ears. Both cell-wall yield and cell-wall content were therefore affected by photoperiod treatment. The consequences of this on whole-crop digestibility were small.

Overview

The reaction of the plants to photoperiod switches, as expressed in the number of leaves, number of tassel branches, desynchronization and leaf area was as postulated in Fig. 1.

TABLE 9. Cell-wall yield (cwc yield), cell-wall content (cwc%), cell-wall digestibility (D_{cwc}) and in vitro digestibility organic matter (D_{om}) of stover, top ear and whole crop, excluding tillers, at final sampling.

	Stover				Top ear				Whole crop			
	cwc yield ($Mg.ha^{-1}$)	cwc% (%)	D_{cwc} (%)	D_{om} (%)	cwc yield ($Mg.ha^{-1}$)	cwc% (%)	D_{cwc} (%)	D_{om} (%)	cwc yield ($Mg.ha^{-1}$)	cwc% (%)	D_{cwc} (%)	D_{om} (%)
					1980							
→ n	3.19	60.5	62.0	61.2	1.18	15.4	73.1	83.6	5.33	37.1	65.6	74.0
→ 24	3.70	61.1	62.1	61.3	1.40	19.3	80.4	84.0	6.04	40.8	67.2	73.3
→ n	3.51	62.1	62.3	61.1	1.38	17.4	78.3	84.0	5.88	39.1	67.0	74.0
→ 24	3.70	61.3	62.5	61.7	1.52	21.6	76.4	82.5	6.16	42.6	67.1	72.7
					1981							
→ n	2.58	58.2	57.1	62.9	1.12	16.1	75.0	86.8	5.17	37.7	63.8	76.2
→ 24a	2.82	60.5	58.8	62.8	1.33	19.5	75.4	86.1	5.66	40.1	65.8	76.2
→ 24b	2.95	60.6	58.3	62.3	1.40	19.2	72.1	85.5	5.79	39.9	64.0	75.5
→ n	2.61	57.0	58.1	63.9	1.23	18.2	78.3	86.9	5.43	38.8	65.3	76.5
→ 24	2.91	59.7	58.6	63.0	1.29	18.1	74.6	85.6	5.61	39.1	64.1	75.9

CAMPBELL, C. M.: 1964. Influence of seed formation of corn on accumulation of vegetative dry matter and stalk strength. Crop Sci., **4**: 31–34.

CHRISTENSEN, L. E., F. E. BELOW and R. H. HAGEMAN: 1981. The effects of ear removal on senescence and metabolism of maize. Plant Physiol., **68**: 1180–1185.

CUMMINS, D. G. and M. E. MCCULLOUGH: 1971. Comparison of male sterile and male fertile corn for silage. Agron. J., **63**: 46–47.

DAYNARD, T. B. and R. B. HUNTER: 1975. Relationships among whole-plant moisture, grain moisture, dry matter yield and quality of whole-plant corn silage. Can. J. Plant Sci., **55**: 77–84.

DAYNARD, T. B., J. W. TANNER and D. J. HUME: 1969. Contribution of stalk soluble carbohydrates to grain yield in corn (*Zea mays* L.). Crop Sci., **9**: 831–834.

DEINUM, B. and J. J. BAKKER: 1981. Genetic differences in digestibility of forage maize hybrids. Neth. J. agric. Sci., **29**: 93–98.

DEINUM, B. and J. G. P. DIRVEN: 1971. Climate, nitrogen and grass. 4. The influence of age on chemical composition and in vitro digestibility of maize (*Zea mays* L.) and tall fescue (*Festuca arundinacea* Schreb.). Neth. J. agric. Sci., **19**: 264–272.

DEINUM, B. and J. KNOPPERS: 1979. The growth of maize in the cool temperate climate of the Netherlands: Effect of grain filling on production of dry matter and on chemical composition and nutritive value. Neth. J. agric. Sci., **27**: 116–130.

FAUNGFUPONG, S.: 1975. Effects of prolonged low light intensity and photoperiod on grain yield and some other agronomic characteristics of corn (*Zea mays* L.). Ph.D. thesis, Iowa State Univ., Ames, pp. 1–171.

FRANCIS, C. A.: 1970. Effective day lengths for the study of photoperiod sensitive reactions in plants. Agron. J., **62**: 790–792.

FRANCIS, C. A., D. SARRIA V., D. D. HARPSTEAD and C. CASSALETT D.: 1970. Identification of photoperiod insensitive strains of maize (*Zea mays* L.). II. Field tests in the tropics with artificial lights. Crop Sci., **10**: 465–468.

GALLAIS, A., M. POLLACSEK and L. HUGUET: 1976. Possibilités de sélection du maïs en tant que plante fourragère. Ann. Amélior. Plantes, **26**: 591–605.

GMELIG MEYLING, H. D.: 1973. Effect of light intensity, temperature and daylength on the rate of leaf appearance of maize. Neth. J. agric. Sci., **21**: 68–76.

GROSS, F. and W. PESCHKE: 1980. Nährstoffgehalt und Verdaulichkeit von Mais. 2. Mitteilung: Nährstoffgehalt und Verdaulichkeit von Maisstroh (Maispflanze ohne Kolben). Z. Das wirtschaftseigene Futter, **26**: 104–117.

HACKER, J. B. and D. J. MINSON: 1981. The digestibility of plant parts. Herbage Abstracts, **51**: 459–482.

HANWAY, J. J.: 1963. Growth stages of corn (*Zea mays* L.). Agron. J. **55**: 487–492.

HUNTER, R. B.: 1980. Increased leaf area (source) and yield of maize in short-season areas. Crop. Sci. **20**: 571–574.

HUNTER, R. B.: 1981. Silage - increasing grain content is not the answer. Highlights of agric. Res., **4**: 19–20.

HUNTER, R. B., M. TOLLENAAR and C. M. BREUER: 1977. Effects of photoperiod and temperature on vegetative and reproductive growth of a maize (*Zea mays*) hybrid. Can. J. Plant Sci., **57**: 1127–1133.

IREMIREN, G. O. and G. M. MILBOURN: 1978. The growth of maize. IV Dry-matter yields and quality components for silage. J. agric. Sci., Camb., **90**: 569–577.

KIESSELBACH, T. A.: 1948. Endosperm type as a physiological factor in corn yields. J. Amer. Soc. Agron., **40**: 216–236.

KIM, G. S., S. E. PARK, G. B. SUNG, S. G. HAN, M. H. HEU and Y. H. JUN: 1976. Effects of short-day length upon growth and tasseling in corn. Res. Rep. Off. rur. Dev. (Suwon), **18**: 193–198.

KING, C. C. JR, D. L. THOMPSON and J. C. BURNS: 1972. Plant component yield and cell contents of an adapted and a tropical corn, *Zea mays* L. Crop Sci., **12**: 446–449.

LESHEM, Y. and M. WERMKE: 1981. Effect of plant density and removal of ears on the quality and quantity of forage maize in a temperate climate. Grass and Forage Sci., **36**: 147–153.

MARTEN, G. C. and P. M. WESTERBERG: 1972. Maize fodder - influence of barrenness on yield and quality. Crop Sci., **12**: 367–369.

McAllan, A. B. and R. H. Phipps: 1977. The effect of sample date and plant density on the carbohydrate content of forage maize and the changes that occur on ensiling. J. agric. Sci., Camb., **89**: 589–597.

Messiaen, C.-M.: 1963. Physiologie du développement chez *Zea mays*. Annales des Épiphyties, **14**, no. Hors-série II, pp. 1–90.

Montgomery, F. G.: 1911. Correlation studies of corn. Nebr. agric. Exp. Stn Ann. Rep., **24**: 108–159.

Moss, D. N.: 1962. Photosynthesis and barrenness. Crop Sci., **2**: 366–367.

Perry, L. J. jr and W. A. Compton: 1977. Serial measures of dry matter accumulation and forage quality of leaves, stalks and ears of three corn hybrids. Agron. J., **69**: 751–755.

Phipps, R. H. and R. F. Weller: 1979. The development of plant components and their effects on the composition of fresh and ensiled forage maize. 1. The accumulation of dry matter, chemical composition and nutritive value of fresh maize. J. agric. Sci., Camb., **92**: 471–483.

Phipps, R. H., R. F. Weller and A. Cooper: 1982. A comparison between the accumulation of dry matter, chemical composition and nutritive value of isogenic sterile and fertile forage maize. Maydica, **27**: 27–40.

Ragland, J. L., A. L. Hatfield and G. R. Benoit: 1966. Photoperiod effects on the ear components of corn, *Zea mays* L. Agron. J., **58**: 455–456.

Rode, J. C., O. Berthenod and P. Chartier: 1979. Influence du degré de fécondation sur l'assimilation de la feuille de l'épi dans le cas du maïs. In: Inventaire des opérations de recherches 1973–1978. Département de bioclimatologie, INRA, p. 53.

Scheffer, K.: 1978. Kurzfassungen der Vorträge. 22. Jahrestagung der Gesellschaft für Pflanzenbauwissenschaften, Berlin, p. 12.

Scheffer, K.: 1982a. Pflanzversuche mit Mais. I. Ertrag und Wachstumsverlauf von mittelspätem Mais auf einem klimatischen Grenzstandort in Abhängigkeit vom Aussaattermin. Kali-Briefe (Büntehof), **16** (2): 111–122.

Scheffer, K.: 1982b. Pflanzversuche mit Mais. II. Der Anbau von späten Sorten unter dem Einfluss einer künstlich verlängerten Photoperiode. Kali-Briefe (Büntehof), **16** (3): 123–138.

Struik, P. C.: 1982a. Production pattern, chemical composition and digestibility of forage maize (*Zea mays* L.). Mededeling no. **64**, Vakgroep Landbouwplantenteelt en Graslandkunde, Agric. Univ., Wageningen, pp. 1–28.

Struik, P. C.: 1982b. Effect of temperature on development, dry-matter production, dry-matter distribution and quality of forage maize (*Zea mays* L.). An analysis. Mededelingen Landbouwhogeschool Wageningen, (in press).

Struik, P. C.: 1982c. Effect of a switch in photoperiod on the reproductive development of temperate hybrids of maize. Neth. J. agric. Sci., **30**: 69–83.

Struik, P. C.: 1983. 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.). Neth. J. agric. Sci., **31** (2), (in press).

Struik, P. C. and B. Deinum: 1982. Effects of light intensity after flowering on the productivity and quality of silage maize. Neth. J. agric. Sci., **30**: 297–316.

Teschemacher, H. R.: 1974. Untersuchungen zur quantitativen Bedeutung der photoperiodischen Abhängigkeit der Infloreszenzentwicklung verschiedener Maissorten. Inaugural Dissertation, Christian-Albrechts-Universität, Kiel, pp. 1–87.

Thiagarajah, M. R., L. A. Hunt and J. D. Mahon: 1981. Effects of position and age on leaf photosynthesis in corn (*Zea mays* L.). Can. J. Bot., **59**: 28–33.

Van Soest, P. J.: 1977. Modified procedure for determining plant cell wall by the neutral detergent procedure. Paper presented at the 69th Ann. Meeting Amer. Soc. of Animal Sci., Madison, Wisconsin, 1977.

Van Soest, P. J., R. H. Wine and L. A. Moore: 1966. Estimation of the true digestibility of forage by the in vitro digestion of cell walls. Proc. X. Int. Grassl. Congress, Helsinki, Finland, (ed.) A. G. G. Hill, pp. 438–441.

Weaver, D. E., C. E. Coppock, G. B. Lake and R. W. Everett: 1978. Effects of maturation on composition and in vitro dry matter digestibility of corn plant parts. J. Dairy Sci., **61**: 1782–1788.

WILSON, J. H. and J. C. S. ALLISON: 1978. Production and distribution of dry matter in maize following changes in plant population after flowering. Ann. appl. Biol., **90**: 121–126.

GENERAL DISCUSSION

The general discussion falls into two parts. First, the effects of climate and weather on yield and quality are discussed: this leads on into a description of the ideal weather conditions for growing forage maize in North-West Europe. The second section describes an ideotype of maize for the production of forage under the conditions normal in North-West Europe.

1. INFLUENCE OF CLIMATE AND WEATHER ON THE YIELD AND QUALITY OF FORAGE MAIZE IN THE NETHERLANDS

The influence of climate and weather on the yield and quality of forage maize is very complex and is complicated by the variation in production environment.

A sizeable amount of literature on the subject of the relationships between the maize crop and weather has accumulated during recent decades. Most of these studies, however, are only concerned with dry-matter yield of the whole crop or of the grains. In the previous chapters the effects of climatic conditions on the physiology, development, productivity, dry-matter allocation, and quality of forage maize were described and discussed. This part of the general discussion

- assesses the suitability of the Dutch climate for growing forage maize
- summarizes the effects of short periods of adverse or favourable weather conditions during different stages of growth
- describes the ideal weather for growing forage maize with the cultivation techniques current in The Netherlands.

1.1. *Evaluation of the suitability of the Dutch climate for growing forage maize*

Maize originates from subtropical regions and hence the maize plant is endowed with the following ecophysiological characteristics:

- its minimum temperature for germination and growth is high
- its optimum temperature for germination, photosynthesis, growth and developmer is high
- it is able to produce CH_2O via the C_4 pathway of photosynthesis and thus it shows a high rate of net photosynthesis at high temperature and high light

intensity
- it requires short days for the initiation of male and female inflorescences
- it makes economical use of available water; however, maize is very sensitive to drought, especially during reproductive development.

This suggests that the Dutch climate is not very suitable for growing maize. Indeed, The Netherlands are on the northern margins of the range of maize.

In Table 1, average climatic conditions at De Bilt (the central meteorological station) during the period 1931-1960 are compared with the range of these conditions at Wageningen (approx. 40 km east of De Bilt) during the period 1977-1981. It was this latter period that the field experiments reported in this thesis were carried out. Compared with normal values, these five years were cooler (especially during early spring and during summer), drier, and cloudier during June. Data on photoperiod are not presented: the pattern of this climatic factor hardly differs between years although some variation exists (Chapter 6). At the 6-leaf stage of field-grown maize, the natural photoperiod is 17-18 h. Breeding has satisfactorily overcome the constraint of sensitivity to photoperiod.

The prevailing weather conditions in The Netherlands deviate markedly from the optimum conditions for many processes in the plant, particularly because of the thermophilic nature of maize. Table 2 illustrates this nature by showing the optimum temperature or temperature ranges for plant processes occurring during early plant growth and for plant parameters determined in the same growth phase. The thermophilic nature is also an important constraint on the plant's productivity and development during late summer and autumn.

The minimum temperatures required for processes such as imbibition, germination, early seedling growth and photosynthesis range from 6-10 ^{o}C (e.g. Blacklow, 1972a,b; Miedema, 1982). The minimum temperatures for pollination, silking and fertilization are much higher. For example, during a certain number of consecutive days the maximum daily temperature must exceed 15-20 ^{o}C, depending on genotype, to enable silking.

The optimum temperatures for all processes are much higher than the normal temperatures in The Netherlands. Yield, however, is determined by both rate and duration of dry-matter production. The optimum temperature for final yield therefore depends on the duration of the period during which active leaves can be present. The duration of this period is, for example, affected by genotype and the occurrence of frost, pests and diseases. The number of days available for the growth of a forage-maize crop is large in The Netherlands (160-180 days). Te Velde (1983) has stated that years with

Table 1. Climatic conditions at De Bilt during the period 1931-1960 and their range at Wageningen during the period 1977-1981.

	Mean air temperature (°C)		Solar irradiance ($MJ.m^{-2}$)		Rainfall (mm)	
	average	range	average	range	average	range
	1931-1960	1977-1981	1931-1960	1977-1981	1931-1960	1977-1981
Month	(De Bilt)	(Wageningen)	(De Bilt)	(Wageningen)	(De Bilt)	(Wageningen)
April	8.5	6.2 - 8.4	388	350 - 453	49	15 - 51
May	12.4	11.7 - 13.4	518	472 - 649	52	9 - 76
June	15.5	14.4 - 15.1	531	419 - 507	57	62 - 148
July	17.0	15.3 - 16.7	478	425 - 484	78	31 - 146
August	16.8	15.1 - 16.9	415	388 - 422	89	20 - 134
September	14.3	13.2 - 15.2	304	251 - 333	71	6 - 69
October	10.0	8.7 - 11.2	177	144 - 194	72	37 - 137
Total/mean	13.5	12.7 - 13.2	2811	2574 - 2901[1)]	468	323 - 445

1) estimated for 1980; in this year some of the data on solar irradiance are lacking.

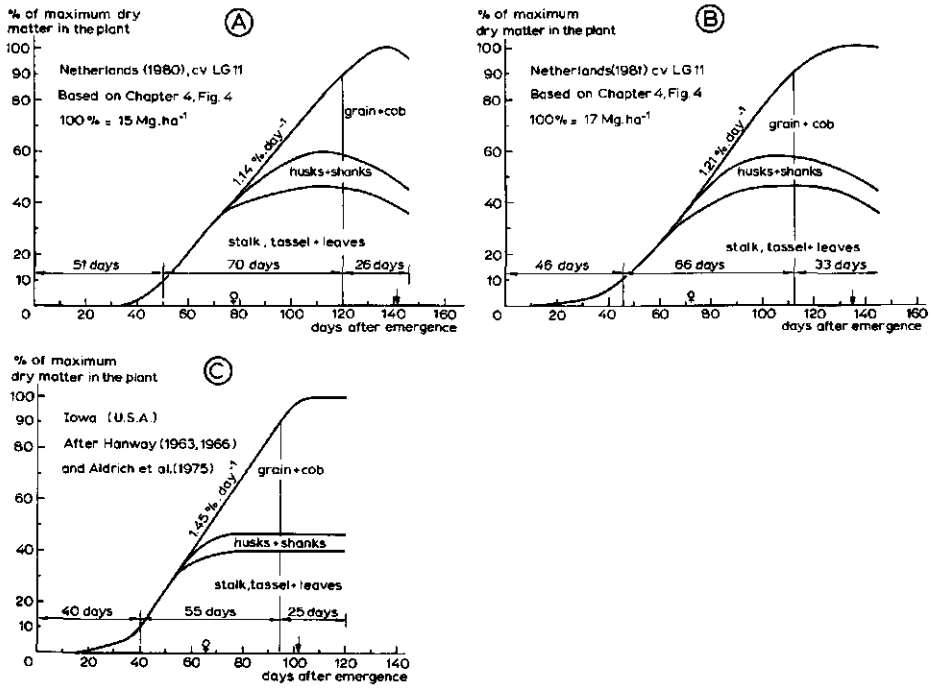


Fig. 1. Production and allocation of dry matter in a maize crop, grown under various conditions. The growing period is divided into the period from emergence until 10% of maximum dry matter, the period from 10% until 90% of maximum dry matter, and the period after 90% of the maximum dry matter has been reached. The duration of these periods is indicated, as well as the rate of increase in relative whole-plant yield during the period from 10% until 90% of maximum dry matter.

♀ signs indicate mid-silking.

Vertical arrows indicate 30% dry matter in the fresh crop.

- above-normal light intensity during July - September
- normal precipitation, equally distributed over the entire growing season
- absence of stresses such as frosts or periods of drought.

In The Netherlands digestibility is high and varies litlle between locations and years (Chapter 2; B. Deinum, personal communication; see Table 3).

Table 3. Apparent digestibility (D_{om}) ± standard deviation of several groups of samples obtained from farmer's lots. Data on the ensiled crops are from a random test of samples offered to the routine laboratory for feed evaluation. Data on the fresh crops are from the factor analyses, carried out by the Research Station for Arable Farming and Field Production of Vegetables (Lelystad), for a selected region of The Netherlands.

year	1981			1982	
	n	D_{om} (%)		n	D_{om} (%)
ensiled	25	73.5 ± 1.26	ensiled	50	73.5 ± 1.21
fresh	54	72.8 ± 1.39	fresh	54	73.3 ± 1.69

The variation in whole-crop digestibility shown above is mainly caused by genotype, sampling error, proportion of ear in the dry matter and cell-wall content. However, in the factor analysis of 1982, considerable variation in digestibility of the cell walls of the stover was observed between locations (range 55.1 - 65.8%). This variation contributed considerably to the differences in organic-matter digestibility of the whole crop but could not be ascribed to or explained by any of the over 200 plant and location characteristics measured (J. Boer, pers. comm.). This is surprising, since only temperature treatments during long periods of growth are known to affect cell-wall digestibility of the stover to this extent when harvesting date and genotype are not varied (Chapter 2). Thus, some unknown factor or factors not included in the research reported in this thesis is or are also relevant for crop quality.

After grain set, both cell-wall digestibility and cell-wall content decline (Chapters 1 and 4). The rate of decrease in cell-wall content, however, strongly depends on light intensity (Chapters 2, 3 and 4). Since light intensity becomes so low during October that net production becomes negative, digestibility peaks at the beginning of October (see Fig. 2; cf. Kilkenny, 1978). The optimum is most pronounced for hybrids showing a low cell-wall

digestibility. For these hybrids the year-to-year variation also will be greater.

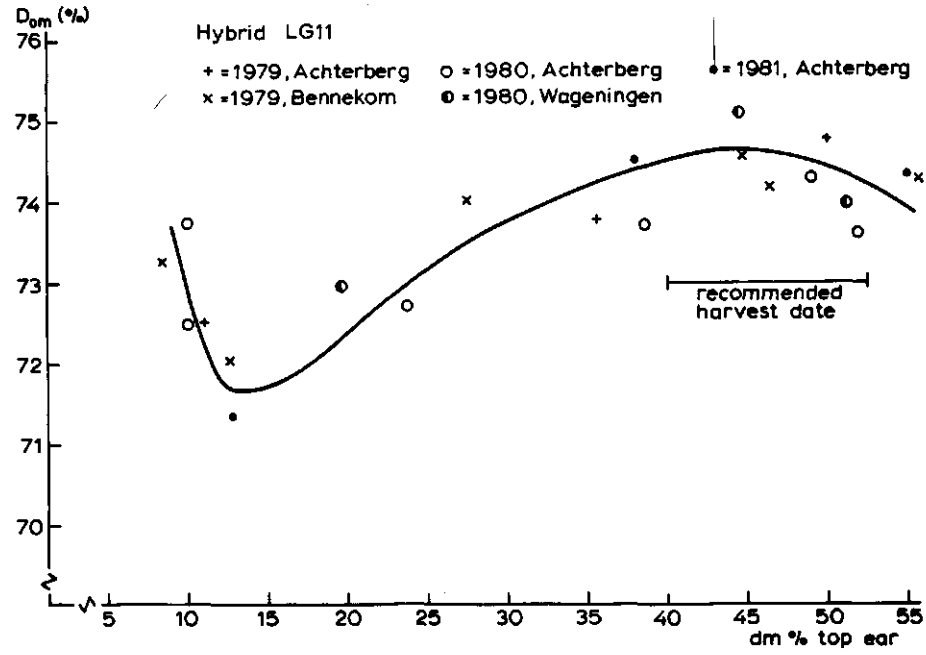


Fig. 2. Relation between ear maturity (dm% top ear) and organic-matter digestibility (D_{om}).

Variation between years is caused by the ratio of production of cell walls to production of cellular contents. This ratio depends on the weather conditions during specific growth stages and the physiological reactions of the plant that these conditions induce. Drought during silking, for example, has been one of the most important constraints on digestibility during recent years. The effects of weather conditions on specific physiological processes and their consequences for yield and digestibility are described in section 1.2.

Dry-matter content of the whole crop mainly correlates with the rate of the crop's development and thus with temperature; the proportion of ear in the fresh matter, the maturity of the ear and the redistribution of soluble dry matter from the stover to the ear mainly determine the dry-matter content of the whole crop (cf. Ideotype description). The rate of development of a certain genotype can be well predicted from the cumulative temperature

totals. This is especially true for the period after silking (e.g. Bloc et al., 1983a). However, it is more difficult to use cumulative temperature totals to predict the duration of the period from sowing until silking, because of the variation in number of leaves (Bloc et al., 1983b) and the effects on development of pre-emergence soil conditions (e.g. Coligado & Brown, 1975b). *Fusarium* infection might also play a role (Chapters 3 and 4), whereas frost may contribute to a rapid decline of the water content.

The weather conditions mentioned earlier as being necessary to optimize the dry-matter yield in The Netherlands also increase dry-matter content but have little effect on digestibility.

1.2. *Evaluation of the effects of weather on the development, productivity and quality of forage maize*

In addition to the more general effects of climatic conditions on yield, dry-matter content and digestibility of forage maize, weather conditions have specific effects on physiology and development during certain stages of the crop's development. These effects have repercussions on the subsequent productivity and dry-matter distribution of the crop and thus on yield, dry-matter content and digestibility. These effects and their repercussions will be described in detail in this section.

Sowing to emergence

Soil temperatures are seldom injurious to imbibed seeds or young seedlings if maize is sown at the end of April (Miedema, 1982). Soil temperatures and soil moisture do affect the rate of imbibition and germination and thus influence the interception of irradiance during the periods with high light intensity. These influences mainly affect yield. Because soil temperature affects the rate of extension of the mesocotyl more than the rate of shoot extension, high temperatures during this phase might stimulate lodging during later stages of growth (cf. Ideotype description). Soil conditions during germination are extremely important for subsequent growth and development (Coligado & Brown, 1975b; Miedema, 1982). This will be evident from the discussion below. This phenomenon stresses the importance of proper tillage in spring.

Emergence to tassel initiation

During this phase the growing point of a plant of one of the popular genotypes is still below the surface, but the leaves are partly above soil

level. The main factors affecting growth during this stage are soil temperature, soil moisture (directly or by its influence on soil temperature), air temperature and solar irradiance (directly or by its influence on temperature of leaves, shoot apex and soil). These factors affect the rates of the following processes:

- leaf initiation, i.e. the production of leaf primordia
- leaf appearance
- leaf extension
- growth and activity of roots
- photosynthesis
- tassel initiation

Since temperature has a greater effect on leaf initiation than on tassel initiation, more leaves are initiated at higher temperatures. The final number of leaves also depends on genotype and photoperiod and is determined during a short period prior to tassel initiation (Tollenaar & Hunter, 1981; Bonhomme, 1983; Derieux, 1983; Chapters 2, 5 and 6); leaf number increases by 0.1 - 0.35 leaves per ^{o}C increase in temperature (e.g. Duncan & Hesketh, 1968; Coligado & Brown, 1975a; Tollenaar et al., 1979; Derieux, 1983) but this increase may vary according to genotype, photoperiod and diurnal temperature range. The air and soil temperatures just prior to tassel initiation show considerable variation both between years and between locations within years. This short-term weather factor strongly influences the subsequent growth and development of the crop and therefore restricts the value of maturity-indexing systems based on temperature or heat units (Chapter 2; cf. Bloc et al., 1983b). Under field conditions, photoperiod is much less important than soil and air temperatures. The effects of sowing date on leaf number, for example, are probably entirely caused by differences in temperature. An increase in number of leaves will positively influence productivity because (cf. Ideotype description):

- total leaf area is slightly larger;
- leaf-area duration is longer;
- the presence of young (thus very active and more frost resistant) leaves in the top of the canopy is prolonged;
- the emergence of the tassel, which shades the leaves, is delayed.

However, an increase in number of leaves (or phytomeres) also prolongs cell-wall formation, raises the potential cell-wall yield, prolongs the pre-silking period, and boosts the water accumulation (see Chapter 2). Delayed maturity and reduced digestibility (especially when cell-wall digestibility of the stover is poor) are thus adverse side-effects of a larger number of leaves.

The temperature of the shoot apex is the primary factor influencing rate of leaf appearance (e.g. Brouwer et al., 1973; Gmelig Meyling, 1973; Tollenaar et al., 1979; Thiagarajah & Hunt, 1982; Bonhomme, 1983; Chapter 2). An increased rate of leaf appearance, irrespective of leaf number, is favourable, since it accelerates vegetative development and thereby advances the formation of a closed canopy (see section 1.1), reproductive development and maturity. Because of this acceleration, the climatic conditions during all subsequent stages of growth are more favourable for production and development, i.e. the crop is more able to profit from the favourable periods of the growing season (cf. Fig. 1). The effects of these favourable conditions on digestibility, however, are small and inconsistent, since both the production of cell wall and of cell solubles are favoured (Chapter 2).

Leaf extension greatly depends on temperature, light intensity, water availability and photoperiod. Temperature is the main limiting factor during early seedling growth as leaf extension is mainly affected by the temperature of the meristematic region of the shoot. Temperature also affects the ultimate size and shape of the leaves. High temperatures induce a more linear shape, thus increasing the proportion of the midrib. For small leaves this influence is of minor importance.

The very young seedling is also extremely sensitive to water shortage (Barloy, 1983). Water stress limits leaf extension particularly. According to Miedema (1982), low temperatures *per se* do not induce water stress, although leaf temperature and root temperature may differ greatly. There is an almost linear relationship between the growth of the primary root and temperature in the range of 10-25 ^{o}C (Blacklow, 1972b). Because the rate of growth of roots at low soil temperatures is slow, the availability of phosphate may become limiting, resulting in anthocyanin pigmentation of the leaves. According to Miedema (1982) mineral deficiencies are not caused by reduced root *activity* at lower temperatures.

Photosynthesis is very sensitive to temperature in the range prevailing during early growth. Blondon and co-workers, however, found that the optimum temperature for photosynthesis shifted towards a lower value when a cold treatment was given during early growth (Blondon et al., 1981, 1983). This shift of the optimum is an important adaptation of the plant to the cool conditions of temperate, maritime climates and is most pronounced in cold-resistant genotypes (Blondon et al., 1981, 1983).

The duration of the pre-tassel initiation period is less sensitive to temperature than most other processes. Thus the rate of differentiation of

1981, 1983), high temperature (Chapter 2) and low light intensity (Chapter 4): they may be very important, as they influence the late-season vigour of the maize crop. A cold spell, such as frequently occurs in June, might cause temporary chlorosis.

From the limited number of observations obtained during the present research, it appeared that maximum leaf area of the control crops (reached at or shortly after silking) closely correlated with the soil temperature at -5 cm during the first 10 days of May, i.e. *during germination*. This observation agrees with the results of Miedema et al. (1982) who found that early vigour of the seedling is affected by conditions during germination. Coligado & Brown (1975b) even incorporated a development potential factor in their bio-photo-thermal model: this factor depended on the number of days from sowing to emergence. This factor explains why the leaf area of the crops grown in glasshouses is much higher than the leaf area of field-grown plants (see Fig. 3). It also explains the large positive effects of plastic mulches in spring, and the effects of sowing date on leaf area and rate of development (see e.g. Chapters 1 and 2).

Yet, climatic factors after tassel initiation also affect leaf dimensions. Prolonged differences in temperature levels during the period from tassel initiation to anthesis are of minor importance for leaf area (Chapter 2). Low light intensity reduces leaf area considerably when plants are exposed to such conditions during the early growth of the leaves (i.e. before mid-July). Photoperiod only affected leaf area during the 3-8 leaf stage (Chapter 5). Low temperatures have a large negative effect on the rate of leaf extension, whereas drought also greatly reduces leaf extension. Under conditions prevailing in The Netherlands, variation in leaf area within one genotype from year to year is probably mainly caused by variation in soil temperatures before emergence, provided that all other conditions are optimum. This agrees with the finding that delaying the sowing time results in an increase in leaf area (see e.g. Fig. 3). The conclusion that soil temperatures during early growth are the main determinant for leaf area, however, needs further confirmation. Longevity of leaves and leaf activity are much more variable and more affected by conditions during later stages of growth.

b. The rate of floret initiation is constant under defined conditions, but affected by temperature (Allison & Daynard, 1979). The final number of floret primordia on the top ear is affected by temperature and photoperiod,

but only to some extent (e.g. Hunter et al., 1977; Allison & Daynard, 1979; Hunter, 1980; Chapters 2, 5 and 6). The optimum temperature for number of florets is low (Brooking, 1979) whereas the optimum photoperiod is long. Thus the temperate maritime conditions of North-West Europe are favourable for ear development. Because of low temperatures, the rates of floret initiation, grain set and grain filling are too slow for high-yielding hybrids to reach maturity before killing frosts occur; therefore the potentially large ear yields are not realized.
Shading dramatically limits the fecundity and fertility both in the tassel and in the ears (Chapter 4). Other stresses such as drought are also extremely harmful during this phase. The critical phase for successful pollen development is somewhat earlier than for successful ovule development and silk emergence. In The Netherlands, these sensitive phases are in July and early August. Solar irradiance during July is therefore the main climatic factor determining potential ear size of the commercially grown forage-maize crop in The Netherlands.
Factors affecting the size of the top ear influence the development of lower ears. These lower ears, however, are usually aborted.

c. Stem height is determined by the number of stem internodes (i.e. number of leaves) and the mean internode length. The number of stem internodes is determined by photoperiod and temperature prior to tassel initiation (see above). The length of the internodes is affected by photoperiod (see e.g. Blondon & Gallais, 1976; Aitken, 1980; Chapters 5 and 6), temperature (see e.g. Blondon & Gallais, 1976; Aitken, 1980; Chapters 2 and 5), water availability (unpublished data) and light intensity (see Blondon & Gallais, 1976; Chapter 4) both before and after tassel initiation. Soil conditions during early seedling growth may also affect stem-internode length.
Photoperiod is a fairly constant climatic phenomenon. Temperature did not prove to affect internode length to a great extent but had a dramatic effect on stem diameter (e.g. Chapter 2). Drought greatly reduces stem growth both longitudinally and radially (unpublished data). In The Netherlands, water availability is mostly sufficient for optimum stem elongation. Plants grown in glasshouses (with regular watering), however, are always taller than field-grown plants. These differences cannot be attributed merely to water accumulation. The favourable conditions before tassel initiation may also boost plant height. Light intensity affects plant height but the effects depend on the growth stage. Shading greatly reduces plant height

Résumé: Weather conditions during the period from tassel initiation until anthesis affect productivity, the rates of development and the dimensions of the leaves and the stem, the development of the inflorescences, and the amounts of poorly digestible cell-wall components and of water in the plant.
Since these processes and parameters are partly independently affected, weather conditions during this phase influence yield, digestibility and dry-matter content.

Anthesis until grain set

This period is crucial because:

- the stem, roots, tassel and ear shoots are growing simultaneously; during this stage both roots and ear shoots are weak competitors and thus react sharply to slight changes in weather conditions
- the reproductive potential of the plant must become operational; the development from unfertilized ovule to dry-matter accumulating kernel is a crucial but critical step in the plant's development
- the balance between sink and source is set during this period, although rapid adjustment to reduced source size remains possible during early grain filling. Productivity during grain filling depends on the success of ear development (e.g. Tollenaar & Daynard, 1982). Roots probably play an important role during grain set (Chapter 3).
- In addition to their effect on productivity, ear development and subsequent grain filling affect senescence, dry-matter content, digestibility, feed intake and feed efficiency, processes in the silo, etc. These effects will be discussed when describing the ideotype for North-West Europe. The ideal proportion of ear in the dry matter at harvest is approx. 50% for concomitant hybrids.

To enable the tassel, the ear shoots and the roots to develop and grow at their optimum rates, the net photosynthesis rate must be maximal, whereas temperature must be moderate. High light intensity and maximum daily temperatures of 20-25^{o}C, (combined with an absence of drought or low air humidity) are favourable for grain set and root growth. The optimum size of the top ear actually depends on the weather conditions during grain filling.

Grain filling, maturation and senescence

This developmental phase of the forage-maize crop is characterized by the start or continuation of the following processes:

- production of photosynthates
- grain filling
- maturation
- senescence

If large amounts of highly digestible organic matter that are easy to harvest and to preserve are to be obtained it is vital that these processes occur in harmony and at rates that are not detrimental for the continuation of the other processes (see also Ideotype description). A prerequisite is that the leaf apparatus remains maximally active as long as possible. This requires absence of drought, frost and infirmities of old age. In phytotron experiments it has often been observed that prolonged low light intensity initiated during grain set is favourable for the longevity of leaves, especially at lower temperatures (Chapter 2). In field experiments, short shading treatments applied at grain set also retarded leaf senescence to some extent (Chapter 4).

Long shading treatments initiated during or after grain set and short shading treatments initiated during grain filling boosted leaf senescence under field conditions (Chapter 4). A rise in temperature during September and October not only accelerates leaf senescence but also rate of photosynthesis. Because the duration of the growing season is limited by the low light intensity during October and the occurrence of frost, above-normal temperatures during autumn are beneficial in North-West Europe. The production of photosynthates during grain filling depends on the weather during this phase and also on conditions during previous phases (see above).

Photosynthates produced during grain filling are mainly used for the synthesis of starch in the kernels. The productivity during grain filling greatly affects the rate of redistribution, whereas it has smaller - though certainly relevant - effects on the rate of grain filling. This discrepancy and its consequences have been discussed extensively, e.g. by Deinum & Knoppers (1979), and in Chapters 2, 3 and 4.

Rate of grain filling is mainly determined by temperature provided the carbohydrate supply is adequate. The dry-matter content of the grains and the 1000-kernel weight can therefore easily be predicted by cumulative temperature totals after silking or after grain set (e.g. Bloc et al., 1983).

Rate of dry-matter production, however, is more dependent on light intensity, although temperatures during September are often too low for high photosynthetic rates. In addition, the maize crop proved to be very sensitive to temporary reductions in light intensity in the middle of its grain-filling

of increased light intensity on the yield of digestible organic matter increases after tassel initiation and is maximum during pollination, grain set and grain filling. The consequences of changes in climate during a certain period, however, affect the efficiency of the effects of changes in climate during earlier or later stages of growth.

1.4. *Implications*

On the basis of these and earlier considerations the digestibility of forage maize can be predicted with an accuracy that is similar to the one obtained by *chemical* analysis. A rough prediction model is described in Table 5. This model is based on contemporary hybrids. In the period from mid-September to mid-October the digestibility of a forage-maize crop hardly changes (Fig. 2). In normal years the organic-matter digestibility of ensiled maize grown as a standard farmer's crop, using contemporary hybrids and harvested during this period is approximately 73.5% (cf. Table 3). If the crop is harvested before or after this period, the digestibility will be approx. 1% lower for every 10 days the harvest is delayed or advanced. The digestibility will certainly be lower if the grain set is poor because of extremely low light intensity or drought during silking or because pollination has been prevented artificially (Chapters 2 and 4). Reductions in digestibility are small when the proportion of ear in the final dry matter exceeds 30-40%. Below this value, digestibility declines at approx. 1% unit per 10% unit decrease in ear proportion. Abundant vegetative development, caused by favourable conditions before tassel initiation and estimated from stem height and stem diameter, increases dry-matter yield but may reduce digestibility, since structural material is produced faster and for longer and thus more cell solubles must be produced to achieve a certain decline in cell-wall content. Moreover, the production of these cell solubles must occur later in the growing season and thus under less favourable conditions. Digestibility might be 1% lower in years with extensive vegetative growth and 1% higher in years in which vegetative development is poor but reproductive development is normal. Unfavourable weather conditions during grain filling (especially poor light intensity) will also lower digestibility by approx. 1%. In contrast, the digestibility of crops grown in years with favourable weather during September will be about 1% higher. The adverse effects of abundant vegetative development and poor light intensity during grain filling will not be found when ear proportion is low because of previous conditions. In that case, the decline in cell-wall content is limited by physiological reasons. This

Table 4. Ideal temperature and light conditions during several stages of crop development for yield and quality of forage maize under Dutch conditions.

weather factor	plant parameter	pre-emergence	emergence to tassel initiation	period just prior to tassel initiation	tassel initiation to silking	silking to grain set	grain set to maturity
temperature	high dry-matter yield	+++	++	+	± or -	±	± or +
	high dry-matter content	±	±	-	++	+	+++
	low cell-wall content	±	±	-	± or +	±	± or +
	high cell-wall digestibility	±	±	± or -	± or -	±	±
	high organic-matter digestibility	±	±	-	±	±	± or +
	high yield of digestible organic matter	+++	++	±	± or -	±	± or +
light intensity	high dry-matter yield	+	+	±	++	+++	++
	high dry-matter content	±	±	±	± or +	+++	++
	low cell-wall content	±	±	±	± or -	+++	++
	high cell-wall digestibility	±	±	±	±	± or +	±
	high organic-matter digestibility	±	±	±	± or -	+++	++
	high yield of digestible organic matter	+	+	±	++	+++	+++

- = ideal temperature or light intensity lower than normal conditions
± = ideal temperature or light intensity equivalent to normal conditions, or changes in weather factor cause inconsistent effects
+, ++, +++ = ideal temperature or light intensity somewhat, much or very much higher than normal conditions.

restriction is therefore not valid when hybrids are used showing extremely low ear proportion when grown in The Netherlands. The range of digestibility between years will be approx. 69-76%. B. Deinum (personal communication) found ranges in digestibility within years of 70.6-76.1% for 1981 and 68.3-77.0% for 1982. The range in digestibility of the forage-maize hybrids described in the latest Dutch national variety lists is only approx. 4 units wide (Deinum & Bakker, 1981; RIVRO, 1983).

As both the relative digestibility of the hybrid and the weather conditions during different stages of growth are known, the final digestibility can be roughly estimated. This estimate is good enough to give the farmer an inkling of the digestibility relative to the digestibility in former years.
Further research, however, is required to identify the effects of site on digestibility within one year. In addition, more precise and extensive research on the effects of cultivation techniques, weather and their interactions on digestibility of the ensiled product is required. With this additional information the model could be refined to such an extent that digestibility could be predicted so accurately that it would dispense with the need for the farmer to have the forage-maize silage analysed.

Table 5. Tentative model for determining the digestibility of forage maize, grown under the cultivation techniques recommended in The Netherlands and using concomitant hybrids. Estimated normal value: 73.5%.

	Correction factor
Cultivation	
hybrid	see relative values in variety list
harvest date	-1% per 10 days delay or advance of harvest date; normal date mid-September to mid-October, depending on year
Crop characteristics	
poor grain set	-1% per 10% decline in ear proportion below 30-40% ear in the final dry dry matter. If this correction is applied no correction should be made for weather conditions.
abundant vegetative development	-1%
poor vegetative development but normal reproductive development	+1%
Weather	
overcast periods during September	-1%
high light intensity during September	+1%

2. AN IDEOTYPE OF FORAGE MAIZE FOR NORTH-WEST EUROPE

An ideotype may be defined as the ideal genotype, in which the capacities necessary to maximize productivity and quality under the prevailing climatic conditions and under recommended cultural practice are combined (contrast Donald, 1968; Mock & Pearce, 1975; Gunn, 1978). This implies that the ideotype thus described is only valid for a defined production environment, in this case for the climate described in the preceding chapter and for the cultivation techniques current in The Netherlands. It also implies that the ideotype should be realistic; a description of an ideotype might be useful, but a description of an utopian type (or even idiotype) would certainly not be.

The ideotype of forage maize should:

- yield a maximum and stable amount of digestible organic matter
- be easy to harvest and to preserve
- be tasty, nutritious and allow a high dry-matter intake
- be efficiently utilized by the animal.

These demands can be translated into the following model characteristics, which will be discussed below:

1. high and stable dry-matter yield
2. optimum composition of cellular contents
3. low amount of poorly digestible cell-wall constituents
4. high potential cell-wall digestibility and a fast rate of cell-wall digestion
5. high dry-matter intake by ruminants
6. sufficiently high dry-matter content, especially in the stover
7. moderate level of water-soluble carbohydrates in the stover
8. a certain proportion of ear in the dry matter
9. a low susceptibility to pests and diseases
10. a stocky stem and a superior root system.

It will also be noted that some characteristics can be improved by modifying cultural practice. Some relevant data on the effects of weather conditions have also been added.

1. *High and stable dry-matter yield*

The productivity of a crop depends on the presence of enough efficient leaf area during periods with high irradiance and on the plant's capacity to store the dry matter produced. Maize is thermophilic; thus it must be sown late and it usually finishes developing its leaf apparatus in August. Therefore the leaf area is insufficient to intercept all the incoming light during the months

with the highest irradiance. Genotypes with a maximum early-season vigour are therefore advantageous. The early vigour is mainly determined by the genotype's cold tolerance, i.e. tolerating a low minimum temperature for germination and growth, and having a high rate of photosynthesis, vegetative growth (including root growth) and vegetative development at low temperatures. Early vigour shows a considerable genetic variation and the response to selection proves to be high (e.g. Duncan & Hesketh, 1968; Mock & Eberhart, 1972; Gunn, 1975; Mock & Bakri, 1976; Mock & Skrdla, 1978; Eagles & Hardacre, 1979; Miedema, 1979a,b; Mock & McNeill, 1979; Stamp, 1980; Eagles & Brooking, 1981; Fakorede & Ojo, 1981; Semuguruka et al., 1981; Landi & Crosbie, 1982; Miedema, 1982; O. Dolstra pers. comm.).

A slow early development requires plant density to be high. Therefore the ideotype must be a weak intraspecific competitor. Mutual shading during later stages of the crop's development must be minimized, whereas light interception must be maximized. This can be realized by selection for:

- a prostrate leaf orientation, especially of the long mid-leaves. Numerous authors have indicated the advantages of vertically oriented, stiff leaves above the top ear under high plant densities or with narrow row spacings (e.g. Pendleton et al., 1968; Duncan, 1971; Hicks & Strucker, 1972; Winter & Ohlrogge, 1973; Ariyanayagam et al., 1974; Vidovič, 1974; Whigham & Woolley, 1974; Mock & Pearce, 1975; Fakorede & Mock, 1977; Frölich et al., 1977; Pepper et al., 1977; Frölich & Pollmer, 1978; Lambert & Johnson, 1978). It has been suggested that this erect leaf habit may be even more important for forage maize than for the grain crop (Gunn, 1975). However, this canopy structure is not advantageous for whole-crop yield in North-West Europe. The minimum leaf-area index to profit from the lower light-extinction coefficient in the upper canopy layers is seldom realized (see Monteith, 1965; Duncan, 1971; Winter & Ohlrogge, 1973; Vidovič, 1974; Fakorede & Mock, 1977). On the contrary, the rigidity of leaves is an adverse characteristic since it is associated with a much lower digestibility of the cell walls of the leaf and probably of the whole crop. From the results reported in Struik (1982a) it appeared that genotypically determined differences in cell-wall digestibility are expressed in all plant parts (see below). In addition, lodging, transpiration, and wind and hail damage also depend on the structure of the leaf canopy.

  Leaf angle in itself probably does not affect digestibility.
- a more pronounced oblong shape of the leaves
- smaller tassels (Mock & Schuetz, 1974; Mock & Pearce, 1975; Paterniani, 1981).

Tassels may reduce yield by reducing the radiant flux to the upper canopy layers, especially at high plant densities (Grogan, 1956; Duncan et al., 1967; Hunter et al., 1969) and also by competing with developing ears for nutrients or photosynthates (Grogan, 1956; Duncan et al., 1967). Small tassel size is also associated with tolerance to high plant density (Mock & Buren, 1972; Buren et al., 1974). The success of pollination is probably not greatly affected by a reduction in tassel size (cf. Daynard, 1983).

Maximum light interception with minimal mutual shading can also be realized by cultural practice:

- by another plant arrangement: narrower inter-row spacings and more space between plants within the row (Hoff & Mederski, 1960; Woolley et al., 1962; Hepting & Zscheischler, 1975; Parks, 1977; Prine, 1977; Pommer et al., 1981)
- by north-south orientation of the rows
- by oriented positioning of the seed in the row, causing the plane of the two leaf orthostiches to be perpendicular to the direction of the plant row (see Peters & Woolley, 1959; Prine, 1977)
- by uniform distribution of plants within a row (Hoff & Mederski, 1960; Krall et al., 1977; Johnson & Mulvaney, 1980).

The effects of mutual shading on the reproductive development can be minimized by the use of density-tolerant (often prolific) hybrids (Stinson & Moss, 1960; Moss & Stinson, 1961; Collins et al., 1965; Knipmeyer et al., 1962; Early et al., 1966, 1967; Russel, 1968; Buren et al., 1974; Bertin et al., 1976; Phipps & Weller, 1979; Wilkinson & Phipps, 1979; Phipps, 1980). These hybrids are also less stress-sensitive and show more stable yields. Prolificacy and density tolerance are variable and heritable traits (e.g. Mock & Buren, 1972; Harris et al., 1976; Sorrells et al., 1979). Hybrids showing these characteristics show less pronounced dominance of the tassel over the ears and of the uppermost ear over lower ears (e.g. Bauman, 1960; Buren et al., 1974; Bertin et al., 1976).

Struik (1982b) suggested that selecting for the ear-shoot apexes to be less sensitive to photoperiod than the main-shoot apex would provide plants with larger leaf area, better synchronization of the inflorescences and therefore with a greater resistance to stress, especially during and prior to silking. Genotypes that are completely day neutral might also show these favourable characteristics because synchronization is associated with photoperiodic sensitivity and photoperiod (Struik, 1982b, 1983a). Selection for insensitivity to photoperiod is possible (Mock & Pearce, 1975; Rood & Major, 1981a), although heritability is low (Rood & Major, 1981a).

The leaf area present in the ideotype should have an optimum efficiency. This includes:

- maximum rate of photosynthesis, for which genetic variation and response to selection exist (Duncan & Hesketh, 1968; Heichel & Musgrave, 1969; Crosbie et al., 1977, 1978a,b; Crosbie & Mock, 1980; Crosbie et al., 1981a,b).
- longevity (slow leaf senescence, late-season vigour) with maintenance of a high activity. The rate of the apparent photosynthesis of each leaf declines during ageing, but the rate of decline depends on genotype (e.g. Vietor et al., 1977). The rate of senescence (relative to the rate of dry-down of the ear) also varies considerably among hybrids (Tollenaar & Daynard, 1978; Daynard et al., 1979; RIVRO, 1983). The 'stay-green index' is an important selection criterion in breeding programmes.
- resistance to frost
- minimum demand of resources per unit of photosynthates produced.

A maximum rate of photosynthesis throughout the growing season necessitates the use of reasonably late hybrids (cf. Daynard et al., 1979; Fairey, 1980) because of:

- their large leaf area (see e.g. Hunter, 1980)
- the prolonged presence at the top of the canopy of new leaves, which have higher rates of photosynthesis and which tolerate lower temperatures than older leaves.
- the delayed emergence of the tassel, which shades the upper leaves.

Late hybrids may also be desirable because of the large storage capacity of their vegetative parts. 'Late' here means late in flowering, late in maturation and late in senescence.

Furthermore, respiratory losses must be minimized and photosynthates should be used as efficiently as possible by reducing:

- the photosynthates wastefully employed for the formation of non-harvestable or undesired plant parts, such as tassels and small tillers
- maintenance costs, especially of storage organs
- energy needs for the transport of sucrose to storage organs (thus a minimum of transport against concentration gradients).

The latter two items indicate that the storage of non-structural carbohydrates is most efficient in the grains.

2. *Optimum composition of cellular contents*

- Minerals

Maize silage is deficient in many mineral elements such as Ca, Co, Cu, I,

Mg, Mn, Na, P and Zn (Demarquilly et al., 1971; Malterre, 1976; Kilkenny, 1978; Leaver, 1978; Phipps, 1978; Phipps & Weller, 1979). Genetic variation in the content or uptake of these minerals, irrespective of maturity stage, is small (Phipps, 1978),but both genotypic variation and inheritance have been reported for Ca (Gorsline et al., 1961; Naismith et al., 1974; Bruetsch & Estes, 1976), Cu (Gorsline et al., 1964), Mg (Gorsline et al., 1961, 1964; Bruetsch & Estes, 1976), Mn (Gorsline et al., 1964), P (Gorsline et al., 1964; Baker et al., 1970; Naismith et al., 1974; Bruetsch & Estes, 1976; Kovačević, 1982) and Zn (Gorsline et al., 1964; Bruetsch & Estes, 1976). Since mineral supplements are given, these deficiencies are not important.

- Crude-protein content (CP content)

CP content is insufficient to meet the protein requirements of young cattle, finishing beef cattle and lactating cows (e.g. Demarquilly et al., 1971; Gunn, 1975; Kilkenny, 1978; Leaver, 1978; Phipps, 1978; Vérité, 1979). Considerable genetic variation in CP content exists (Dudley & Lambert, 1969; Roth et al., 1970; Gallais et al., 1976; Dudley et al., 1977; Derieux & Montalant, 1978; Maggiore et al., 1980; Motto et al., 1980), whereas heritability proved to be high (Mann et al., 1980; Motto et al., 1980; Schmidt, 1980). Increases in the protein content of the maize plant, however, cannot be achieved without lowering the total yield of dry matter per hectare (e.g. Wilkinson & Osbourn, 1975; Dudley et al., 1977; Derieux & Montalant, 1978; Gallais & Vincourt, 1983; Landry, 1983).

- Quality of crude protein (CP quality)

In normal maize hybrids, the protein of the kernels (predominantly zein) is deficient in the essential amino acids lysine and tryptophan. The introduction of opaque-2 and other mutant strains of maize with a higher CP content and a higher content of lysine and tryptophan than in normal hybrids significantly improves the nutritional value and protein quality for monogastric animals (e.g. Mertz et al., 1965; Pollmer et al., 1974; Thomas et al., 1976; Barbosa & Glover, 1978; Rosa et al., 1977a,b). In the rumen substantial degradation of protein and resynthesis of microbial protein by the micro-organisms occur; therefore, high-lysine maize has not been proved to have a nutritional advantage when fed to ruminants (e.g. Wilkinson & Osbourn, 1975; Andrew et al., 1979). The introduction of these mutant strains also reduces the agronomic value of the crop (cf. bm mutant strains; e.g. Klein et al., 1980). Lysine content in normal strains, however, is also variable (Zuber et al.,

1975) and the response to selection can be considerable (Choe et al., 1973). The apparent digestibility of CP depends on its content (e.g. Demarquilly, 1969). During fermentation in the silo, a proportion of the CP is readily degraded to non-protein N (Bergen et al., 1974; Wilkinson, 1976, 1979). The utilization of protein can therefore be increased by reducing the fermentation in the silo (Wilkinson, 1976, 1979), e.g. by reducing the mass fraction of water-soluble carbohydrates. Since the micro-organisms of the rumen are the main protein source for the ruminant, it is much more important that sufficient substrate is available for their growth.

- Vitamins

Vitamin supplements must always be given, because maize is deficient in vitamins e.g. vitamin A, D and E (Demarquilly et al., 1971; Phipps, 1978). Vitamins of the B complex are provided by the microbes in the forestomachs. Nothing is known about the genetic variation in vitamin content of forage maize.

- Non-structural carbohydrates (NSC)

The importance of the mass fraction of water-soluble carbohydrates (WSC) is discussed below. High contents of WSC + starch (i.e. NSC) increase the efficiency of utilization of the feed (see below) but reduce cell-wall digestibility (D_{cwc}), especially at high levels of intake, by

- lowering the pH and increasing the osmotic pressure of the rumen liquor (e.g. de Visser, 1980)
- increasing the time lag between ingestion and digestion of cell walls and decreasing the potential extent of cell-wall digestion (Mertens & Loften, 1980), possibly because of competition for nutrients between cellulolytic and amylolytic groups of rumen bacteria (El-Shalzy et al., 1961; de Visser, 1980)
- shortening the retention time.

To eliminate the adverse effects of high NSC content in forage maize, the ration must be supplemented with some roughage. These effects of NSC content also conceal genetic differences in D_{cwc} at *ad libitum* intake (see below) but reinforce the effect of NSC content on intake. In practice, genetic differences in cell-wall content or content of NSC might be more important for the feeding value than genetic variability in D_{cwc}.

Endosperm mutants (see Introduction) which change the susceptibility of starch granules to attack by amylases, have no nutritional advantage for

ruminants (e.g. Thomas et al., 1976).

Forage maize is primarily used as an energy source for ruminants. In addition, the nutritional quality of the cellular contents (e.g. CP content) correlates negatively with dry-matter yield. Whereas the energy content is essential, the composition of the non-structural material should therefore be of minor importance as a breeding objective.

3. *Low amount of poorly digestible cell-wall constituents*

The indigestible fraction of the maize plant is located in the cell walls. Thus the amount of certain cell-wall constituents should be minimized to enable extensive dilution of poorly digestible cell walls with completely digestible cellular contents. Since the digestibility of the cell walls is lowest in stem parts, the production of these cell walls should be limited. A low cell-wall content is also advantageous for dry-matter intake: the content of total cell wall or of indigestible cell wall, the short-term digestibility of cell wall and the bulk volume of cell walls in the feed are the best predictors of voluntary intake (e.g. Van Soest, 1967; Mertens, 1973; Marten et al., 1976; Van Soest, 1976; Mertens & Ely, 1979; Collins et al., 1980; van der Aar et al., 1981; Waldo & Jorgensen, 1981). The content of total cell wall should not be too low: optimum functioning of the rumen necessitates a certain level of structural material. This structural material, however, should show a fast rate of digestion and a high potential digestibility (see below).

Cell-wall production in the stover stops shortly after the onset of grain filling, but only if pollination has been sufficiently successful. This means that selection for a low amount of cell walls in the stover will yield very early hybrids with a high proportion of ear. The demands for resistance to lodging (see 10) and the necessity of constructing a very productive and large leaf apparatus limit the possibilities of selecting against amount of cell wall in the stover. The ideotype should thus:

- show a reasonably early anthesis (i.e. should have a limited number of short phytomeres)
- show a high leaf: stem ratio
- show a slow decrease in the rate of carbon assimilation after each individual leaf has fully expanded
- have a large ear to provide a storage capacity large enough to compensate for the smaller stem and to stop cell-wall formation in the stover. Grain filling, however, should be slow (see section 8).

Maximum dry-matter production and minimum cell-wall production in the stover are contradictory demands and thus the earliness of flowering must be a compromise between them. Fortunately, other characteristics of lateness (slow senescence and maturation) are partly independent of flowering date.

4. *High potential cell-wall digestibility and a fast rate of cell-wall digestion*

Genetic variation in cell-wall digestibility exists and heritability proved to be high (Beerepoot, 1981; Deinum & Bakker, 1981; Deinum & Struik, 1982). In contrast with the amount of cell wall and most other quality characteristics, selection for a high digestibility of cell walls (D_{cwc}) is possible without affecting grain yield or whole-plant yield (Gallais et al., 1976; Deinum & Bakker, 1981). Selection for a high potential extent and rate of cell-wall digestion will result in a reduction in the proportion of lignin and silica in the cell walls, may change the cellulose: hemicellulose ratio, but will also include selection for certain physical-chemical characteristics of cellulose and hemicellulose and for the bonding of and linkages between all cell-wall components. Selection for high D_{cwc} may therefore have repercussions on resistance to lodging. Undersander et al. (1977), however, found that lodging resistance might be increased without greatly affecting cell-wall composition, whereas Gallais et al. (1980) suggested that the lower lodging resistance of brown-midrib hybrids might be overcome by modifying the genetic background and without affecting digestibility.

Selection for improved cell-wall digestibility will be easier than selection for increased organic-matter digestibility. There is a high correlation between the D_{cwc} of different plant parts, and the order in which hybrids are ranked according to their D_{cwc} does not change in time if rate of development is sufficiently uniform. Therefore selection is possible by analysing any plant part at any stage of development, providing all genotypes are sampled at the same time. It is probably most convenient to analyse the complete stover harvested prior to anthesis, because this avoids sampling problems.

Some progress can be made by reducing the proportion of certain plant parts with high cell-wall contents and poorly digestible cell walls, e.g. rind and midrib. Rind thickness e.g. shows great genetic variation and selection can be successful (Chang & Loesch, 1972; Thompson, 1972; Undersander et al., 1977; Zuber et al., 1980; Twusami-Afriyie & Hunter, 1982).

Much has been written on the effects on digestibility, intake and feed

efficiency of the forage crop of incorporating brown-midrib mutant alleles (mostly bm_3) into the most promising hybrids (e.g. Barnes et al., 1971; Lechtenberg et al., 1972; Muller et al., 1972; Colenbrander et al., 1973; Colenbrander et al., 1975; Rook et al., 1977; Keith et al., 1979; Sheldrick, 1979; Gallais et al., 1980; Block et al., 1982; Daccord & Vogel, 1982; Stallings et al., 1982; Struik, 1982a). Adverse effects of these mutants on other agronomic characteristics such as grain yield, whole-plant yield, earliness, dry-matter content and lodging resistance (Zuber et al., 1977; Sheldrick, 1979; Gallais et al., 1980; Daccord & Vogel, 1982) and susceptibility to water-stress (V.L. Lechtenberg, personal communication) have so far prevented the commercial use of bm_3 hybrids. However, the research cited has stressed the possibility and necessity of breeding special hybrids intended for forage production.

Genetic variation in normal material is large enough to create hybrids that are as digestible as the bm mutants but which have none of the latter's disadvantages (Gallais et al., 1980). Accurate laboratory techniques for determining the forage quality of crosses, however, are expensive and complicated. Laboratory tests should therefore be restricted to genotypes that are at an advanced stage in the selection process, and to inbreds. Rapid, simple and cheap methods for accurately estimating forage quality must be developed (see Introduction).

5. *High dry-matter intake by ruminants*

Dry-matter intake (dm intake) is important if maize is voluntarily fed as the main feed in the ration and also when the rate of substitution for other forages or feeds is important. Voluntary dm intake is affected by:

- cell-wall content (e.g. Van Soest, 1976; Waldo & Jorgensen, 1981) or cell-wall volume (Van der Aar et al., 1981)
- rate and extent of organic-matter digestion (e.g. Donefer et al., 1960; Van Soest, 1976; Van Soest et al., 1978; Waldo & Jorgensen, 1981)
- dry-matter content (Daynard & Hunter, 1975; Malterre, 1976; Wilkinson, 1976; see also below)
- changes in the composition of the cell solubles occurring during ensiling: conversion of WSC to short-chain organic acids (increasing the level of free acidity and the level of acetic acid) and the conversion of protein to non-protein nitrogenous compounds (increasing the content of ammonia N) (Wilkinson, 1976; Phipps, 1980; Gallasz, 1982)
- NSC%, through its effects on pH in the silage and in the rumen, protein

degradation and retention time in the rumen
- palatability or acceptability, partly influenced by the factors mentioned above.

At high levels of intake, the available energy is used less efficiently. The composition of the ideotype must minimize this decline. The depression of digestion is great for cell-wall constituents and almost absent for cell solubles (Waldo & Jorgensen, 1981). Cell-wall content should therefore be low, the cell-wall components should have a large proportion of potentially digestible cell-wall components and the rate of digestion of the potentially digestible cell wall should be rapid (see above). On the other hand, a high content of NSC (part of the cell solubles) may increase the depression by reducing the rate of cell-wall digestion.

The cell wall: NSC ratio in the diet should not be too low: plant fibre fed as long material (over approx. 0.5 - 1.0 cm) stimulates rumen motility and rumination (e.g. van Vuuren, 1979). Rumen motility stimulates digestion by intensifying the contact between micro-organisms and feed particles. Rumination results in a reduction of particle size and is coupled with the secretion of saliva. Saliva neutralizes the volatile fatty acids produced by the ruminal micro-organisms, thus buffering the rumen fluid against a low pH. A high content of readily available carbohydrates, however, might result in a low ruminal pH (see above). A high digestibility of cell walls may limit the positive effect of long roughage. The risks of feeding disturbances can be minimized by feeding a balanced ration: at least one third of the daily dm intake should consist of long roughage (van Vuuren, 1979).

Genotypes with high proportions of grain will have a very high nutritive value provided the conditions for optimum rumen fermentation are maintained; genotypically determined differences in potential cell-wall digestibility are of minor importance for these genotypes.

The plant characteristics affecting dm intake have a large genetic variation. Selection for some of these factors, however, is very difficult. Some plant measurements may be used as indicators of potential dm intake. For example, Gallais et al. (1976) reported that stem diameter correlated positively with intake of digestible organic matter.

6. *Sufficiently high dry-matter content, especially in the stover*

The dry-matter content (dm%) is relevant as a quality factor, because it affects:
- the suitability for ensiling which is severely limited at dm% < 30-35% for

tower silos and at dm% < 25% for low clamp silos

- the concentration of nutrients in the fresh material
- the dry-matter intake; dry-matter intake is consistently and largely limited by dm% if dm% is lower than 30% (e.g. Fisher et al., 1968; Daynard & Hunter, 1975; Malterre, 1976; Daynard, 1978; Fisher & Fairey, 1979). The positive effect of an increase in dm% on dry-matter intake is small or absent in the range of 30-35%. Above 35-40% a slight decrease in intake is observed with *increasing* dm% (e.g. Malterre, 1976). This decrease in intake may be caused by heating resulting from the low bulk density of dry forage in the silo or by secondary fermentation.

The dm% is influenced by:

a. the production environment (e.g. plant density, temperature)
b. the duration of the vegetative period (or earliness in flowering)
c. the size of the ear, the rate of grain filling and the rate of grain dry-down (i.e. earliness of grain maturation and proportion of grains in the dry matter)
d. rate of tissue senescence, affected by genotype, diseases and pests, or otherwise (i.e. earliness of senescence of vegetative parts).

a. Environmental factors that reduce or limit the proportion of ear also limit the rate at which the dm% of the whole crop increases. However, it should be noted that the relationships between ear and stover are also relevant for the development of dm%.
Over a wide range of dm% of the ear, the dm% of the stover is fairly constant (e.g. Hunter, 1978; Gross & Peschke, 1980a). Extensive remobilization of cell solubles from the stover to the ear caused by adverse conditions, may cause the dm% of the stover to decline. This decline is rarely visible, since it is compensated for by the contemporary senescence and obscured by weather conditions. Data from a glasshouse experiment with three temperatures and two light intensities after grain set (Struik, unpublished data) clearly revealed the effect of redistribution on dm% (Fig. 2).
At low light intensity, grain filling and increase in ear dm% are slowed down. But even at a given dm% in the ear, the dm% of the stover and of the whole plant is lower because the grains fill with dry matter that has been temporarily stored in the stover. The dm% of the stover is therefore affected by the mass fraction of redistributable cell solubles still present in the stover. This mass fraction strongly depends on the production

7. *Moderate level of water-soluble carbohydrates in the stover*

The mass fraction of WSC in the dry matter of the stover should not be too low because:

- WSC are necessary to obtain a good and stable silage, since WSC are the substrate for the microbes during fermentation
- a certain level of WSC reduces the plant's vulnerability to infirmities of old age such as *Fusarium* infection (Blanco & Blanco, 1960; Mortimore & Ward, 1964; Molot, 1969a,b,c; Cook, 1978a; Struik & Deinum, 1982)
- WSC increase the nutritive value of the feed at voluntary intake, although the cell-wall digestion can be reduced (see above).

The mass fraction of WSC in the dry matter of the stover should not be too high either, because:

- WSC are converted to short-chain organic acids and may thus reduce voluntary intake and protein utilization (see above; Wilkinson, 1976; Phipps, 1980; Gallasz, 1982)
- the proportion of volatile acids might become large (Gallasz, 1982)
- if a high proportion of the NSC is water-soluble, losses of digestible organic matter are proportionally large when seepage occurs
- gaseous losses during fermentation in the silo might become large (Wilkinson & Phipps, 1979; Phipps, 1980; Gallasz, 1982)
- losses are also large when the ensiled material is exposed to the air, if the WSC content in the fresh crop was high
- ensiling crops with high WSC contents might reduce digestibility, but digestibility is not altered by ensiling when WSC have primarily been converted to starch (McAllan & Phipps, 1977; Phipps et al., 1979; Phipps, 1980). This difference is caused by a difference in the extent of the losses mentioned above. Analytical errors may also play a part.

This means that the conversion of WSC to starch is favourable for preservation and for nutritive value as long as it does not affect the late-season vigour of the plant. This vigour, however, is often affected in North-West Europe by prolonged periods of low light intensity in late summer and autumn. A WSC content of 5% on the basis of the dry matter of the stover might be enough to prevent the negative effects of low levels of WSC.

8. *A certain proportion of ear in the dry matter*

Numerous reports have discussed the relevance of grain filling for the

nutritive value, crop-growth rate and suitability for ensiling of forage maize. A review is given by Struik (1983a) (see Chapter 6). Below, this review will be summarized and some other aspects and the most recent literature, not cited in Chapter 6 will be discussed.

Ear formation and grain filling are important because:

- they affect the rate of crop growth during the post-silking period (recently reported by Tollenaar & Daynard, 1982) by affecting the rate of photosynthesis. The effects of alterations in source: sink ratio on crop-growth rate depend on genotype (Tollenaar & Daynard, 1982).
- the grains provide capacity to store photosynthates. This storage capacity is always necessary but is especially important in years when plants are small and the weather during autumn is favourable (e.g. 1980 in The Netherlands).
- a high proportion of ear in the dry matter might be beneficial for whole-plant quality, although this effect is very limited in marginal growing regions (e.g. Fisher & Fairey, 1979; Fairey, 1982). The cob: grain ratio must be low, since the cob is less digestible than the grains (Struik, 1982a). Shelling percentage is a variable and heritable trait (e.g. Loesch et al., 1976).
- ear formation inhibits the ongoing of the production of poorly digestible cell-wall material in the stover (Struik, 1983a).
- grain filling limits the fermentation processes in the silo, and positively influences voluntary intake, apparent digestibility after ensiling and feed efficiency by inducing water-soluble carbohydrates to be converted to starch (see above; Wilkinson, 1976; McAllan & Phipps, 1977; Phipps et al., 1979; Phipps, 1980; Gallasz, 1982).
- the dry-matter content of a normal crop increases much faster than that of a grainless crop or that of a crop with a low proportion of the dry matter present in the ear (e.g. Deinum, 1982, unpublished data; Fairey, 1982; Phipps et al., 1982; Struik & Deinum, 1982; Struik, 1983a,b).
- grain filling increases the proportion of insoluble matter in the fraction that is completely digestible, thus reducing losses of digestible organic matter when seepage occurs.
- the sink: source ratio affects the longevity of leaves (Tollenaar & Daynard, 1982; Struik, 1983b); literature on this topic is not consistent, partly because the effects depend on genotype (Tollenaar & Daynard, 1982). In general, if the ear monopolizes the carbohydrates, nitrogenous compounds,

hormones and other substances this might be deleterious under conditions that cause large differences between crop-growth rate and ear-growth rate (e.g. defoliation, shading etc.; see also Struik & Deinum, 1982; Struik, 1983c). A drastic reduction in the number of active kernels might also reduce crop-growth rate, because high levels of carbohydrates in the leaves or changes in the production of hormones accelerate ageing processes and reduce photosynthetic activity. The genotypically determined balance between sink and source does not influence leaf senescence as delicately as Tollenaar & Daynard (1982) have suggested; in practice the tolerance for small changes in source: sink ratio is great (e.g. Struik, 1983a; see also Fig. 3).

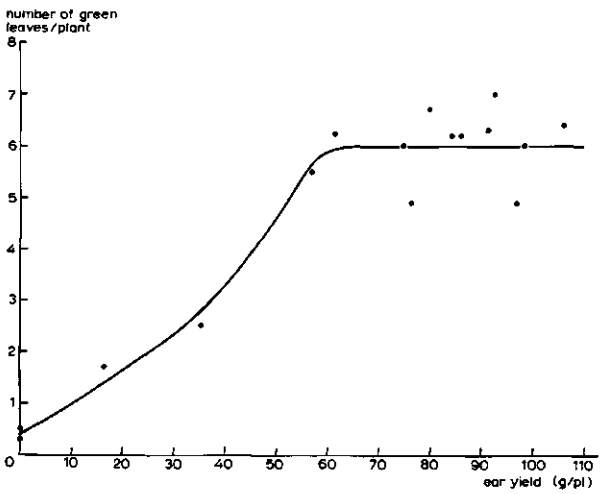


Fig. 5. Relation between ear yield (as measure of relative sink size) and number of green leaves at final harvest.
Ear yield was varied by removing ears or by artificially preventing pollination. (Plant density 8.9 m^{-2}; location: Wageningen; year 1980; harvest date: 13 October; Struik, unpublished data; see also Struik, 1983c, Fig. 8).

- rapid grain filling might affect late-season vigour by stimulating the susceptibility to *Fusarium* infection (see e.g. Barrière et al., 1981; Barrière & Gay, 1983), especially in years with relatively high night temperatures and low light intensities during September and October. Susceptibility to *Fusarium*, however, is not necessarily related to early maturity (e.g. Cook, 1978a; Barrière et al., 1981).

- high dm% in the grains caused by high rates of grain filling may induce insufficient utilization of the kernels. To ensure that starch digestion is not reduced, kernels should not have passed the hard-dough stage at maximum organic-matter yield (e.g. Honig & Rohr, 1982a,b; see also above).

On the basis of these considerations it may be concluded that the forage-maize ideotype should have an early silking date and should have a large ear, with a slow rate of grain filling. Selection for increased ear-size components reduces grain-filling rate (Ottaviano & Camussi, 1981), thus the monopolizing effect of the ear will not be increased (cf. Struik, 1982a). In this way the positive effects of grain formation and grain filling are ensured, whereas the negative effects are minimized. However, early silking is mostly associated with a small leaf area (see above) and thus with reduced productivity, unless the area and area duration of the individual leaves are very large. This association might be overcome by selecting for improved rate of leaf development (see Rood & Major, 1981b; Bonhomme, 1983; Vincourt et al., 1983). Rate of leaf appearance also correlates with final number of leaves, earliness and early vigour (Vincourt et al., 1983). The necessary variation and selection response of ear-size parameters (ear length and diameter, number of ovules and kernels, kernel size or depth, cob length and diameter and shelling percentage) are considerable (e.g. Loesch et al., 1976; Crosbie et al., 1978b; Cortez-Mendoza & Hallauer, 1979; Crosbie & Mock, 1980; Poneleit et al., 1980; Ottaviano & Camussi, 1981; Derieux et al., 1983).

9. *A low susceptibility to pests and diseases*

Climatic conditions in North-West Europe are unfavourable for the development of most of the important maize pests and diseases (Cook, 1978a). Those pests and diseases that are adapted to cool weather conditions are often less important for forage maize than they are for grain maize or CCM maize. Thus, to date, forage maize has been a healthy crop and damage of economic importance is infrequent. Yet it is evident that the forage-maize ideotype should have the minimum susceptibility to all pests and diseases that might occur in North-West Europe.

The most widespread diseases in N.W. Europe are root, ear and stalk rots, caused by, among others, *Fusarium* spp. such as *F. graminearum* Schw. (syn. *Gibberella zeae* (Schw.) Petch), *F. culmorum* (W.G. Sm.) Sacc., *F. moniliforme* Sheld, *F. avenaceum* (Fr.) Sacc. and many other species (see e.g. Mensah &

Zwatz, 1975; Cook, 1977, 1978a,b; Barrière, 1979). Damage due to *Fusarium* infection depends on the genotype of the maize plant, on cultural practice, stage of maturity, climatic conditions and sink-source relations during grain filling (e.g. Otto & Everett, 1956; Foley & Wernham, 1957; Michaelson, 1957; Mortimore & Wall, 1965; Krüger, 1970a,b; Krüger & Reiner, 1974; Krüger et al., 1975; Mensah & Zwatz, 1975a,b; Cook, 1977, 1978b; Krüger, 1978; Barrière, 1979; Krüger & Rogdaki-Papadaki, 1980; Barrière et al., 1981; Ebskamp, 1981). *Fusarium* infection might cause a small reduction in biological dry-matter yield of above-ground plant parts and in digestibility; it stimulates the dry-down of the crop but reduces lodging resistance. The relevance of lodging resistance is discussed below. Since the most productive hybrids show prolonged longevity and activity of leaves and/or flower late, selection for high-yielding ability will generally concomitantly limit *Fusarium* infection. The susceptibility to *Fusarium* irrespective of stage of maturity, however, also varies considerably (see e.g. Andrew, 1954; Krüger et al., 1975; Mensah & Zwatz, 1975a,b; Barrière, 1979; Barrière et al., 1981; Ebskamp, 1981; RIVRO, 1983). If the damage is to be kept at a low level, there must be a certain mass fraction of WSC in the pith (see above). The ideotype should be fairly late and have an active resistance in turgescent tissue (including roots), resistance in senescent or semi-senescent tissue, resistance to stresses (e.g. chilling, drought), a balanced sink: source ratio, an excellent stay-green index and a slow decline of photosynthesis after anthesis (Barrière, 1979; Barrière et al., 1981; Barrière & Gay, 1983). After reaching maximum dry-matter yield of the whole plant, the dry-down should be very fast.

Common smut (*Ustilago maydis* (DC) Corda) is more spectacular than *Fusarium* infection and is observed earlier in the season. The conditions that give rise to severe infection are still largely unknown. Genotypic differences in response to smut, however, are large (Ebskamp, 1981). Since the hybrids that are most popular in The Netherlands, are relatively resistant, no extensive build up of spores in the soil has occurred, even when maize has been grown continuously. The latest, high-yielding hybrids (e.g. Splenda), however, do show a greater susceptibility to smut infection (RIVRO, 1983; A.G. Ebskamp, personal communication) and this may lead to a build up of a damaging population density of *Ustilago maydis* spores (A.G. Ebskamp, personal communication). Therefore, the rotation of hybrids may have to be recommended in the future.

High levels of smut infection are still rare in The Netherlands (Ebskamp, 1981) but they might be toxic to animals unless the forage maize is ensiled (e.g. van der Beek, 1977; Burgstaller et al., 1977; Cook, 1978a; RIVRO, 1983). Fermentation processes in the silo destroy the spores. The quality of the ensiled product, however, is lower, as is the dry-matter yield, and the fermentation losses are higher when severe infection occurs (e.g. Burgstaller et al., 1977; Gross, 1977; Ebskamp, 1981).

Frit fly (*Oscinella frit* L.) and wireworms (*Agriotes* spp.) are the most important pests of maize in North-West Europe. Genotypes with great early vigour might be less sensitive. It is feared that the European corn borer (*Ostrinia nubilalis* Hbn.) may establish itself in North-West Europe.

Since breeders are well aware of the relevance of resistance to diseases and pests, this item does not need further emphasis.

10. *A stocky stem and a superior root system*

Lodging is a serious problem both in grain maize and forage maize. It causes a reduction in dry-matter yield, greater harvesting losses, a reduction in harvesting capacity and the contamination of the forage with soil. Resistance to lodging is therefore an important characteristic of genotypes, and selection for decreased lodging has been an important concern of all breeders.

Resistance to lodging is affected by or correlated with:

- susceptibility to pathogens (mainly *Fusarium* spp. see above)
- stem characteristics such as stem height, stem and rind thickness, rind: pith ratio, rind and pith strength (breaking force, crushing strength, resistance to puncture), stalk-section weight and stalk-lignin content (cf. Zuber et al., 1980; Twusami-Afriyie & Hunter, 1982)
- root-system characteristics, such as root number, root volume, root (clump) weight, amount of fibrous roots, root distribution through the soil profile, patterns of change in the root: shoot ratio through the growing season, and timing and extent of brace-root development (cf. Gunn, 1978; Jenison et al., 1981; Arihara & Crosbie, 1982)
- leaf characteristics (leaf orientation, leaf angle, stiffness, size and shape)
- ear characteristics (ear height, ear weight)
- other plant characteristics, such as early-season and late-season vigour,

cell-wall digestibility and earliness
- cultivation techniques (e.g. plant density, fertilization).

Stem characteristics are fairly easy to assess. In addition to plant height and stem thickness, numerous other screening techniques have been assessed for their usefulness as indicators of resistance to stalk lodging. Stem height (regardless of number of leaves) (Giesbrecht, 1961; Acosta & Crane, 1972; Josephson & Kincer, 1977), stem diameter (Twusami-Afriyie & Hunter, 1982), rind thickness (Chang & Loesch, 1972; Thompson, 1972; Twusami-Afriyie & Hunter, 1982), stem, rind and pith strength (Chang & Loesch, 1972; Thompson, 1972; Chang et al., 1976; Zuber et al., 1980; Twusami-Afriyie & Hunter, 1982), rind composition (Chang et al., 1976; Undersander et al., 1977; Zuber et al., 1980), stalk-lignin content (Undersander et al., 1977; Twusami-Afriyie & Hunter, 1982), and stalk-section weight (Chang & Loesch, 1972; Thompson, 1972; Chang et al., 1976; Twusami-Afriyie & Hunter, 1982) all show considerable genetic variation and inheritance. Stem diameter is probably the most interesting plant characteristic correlated with stalk strength. Diameter is fairly easy to measure and correlates positively with dry-matter yield (A. Gallais, personal communication), lodging resistance (Twusami-Afriyie & Hunter, 1982), early vigour (Beerepoot, 1981) and intake of digestible organic matter (Gallais et al., 1976). However, it correlates negatively with dry-matter content (Beerepoot, 1981) and digestibility (Gallais et al., 1976; Beerepoot, 1981).

Improvement of resistance to stalk lodging seems possible, without great repercussions on grain yield (Thompson, 1982; Twusami-Afriyie & Hunter, 1982) and probably also without repercussions on whole-plant yield. Stalk firmness often correlates negatively with digestibility or other quality factors (Chang et al., 1976; Undersander et al., 1977; Twusami-Afriyie & Hunter, 1982), since the morphology and anatomy of rind and pith change as a consequence of selection against the tendency for stalk lodging (Chang & Loesch, 1972; Chang et al., 1976). The negative correlation between resistance to stem lodging and digestibility, however, is highly significant but far from strict, whereas relative differences in lodging are often much greater than relative differences in digestibility (Undersander et al., 1977; Gallais et al., 1980; Beerepoot, 1981; Twusami-Afriyie & Hunter, 1982).

Zuber et al. (1980) found that an important part of the variation in stalk strength can be attributed to pith characteristics. The number of vascular bundles (with a high proportion of lignin) in the pith is not of

great importance for stalk strength (Chang & Loesch, 1972). Thus it would seem to be possible to select for improved stalk strength by improving pith strength, without greatly increasing lignin content in the pith. Since the pith is much more digestible than the rind (Struik, 1982a) and as the pith strength can be improved without greatly reducing pith digestibility, improving of pith strength (measured as described by Zuber et al., 1980) must be advocated. Improved pith strength might also reduce pith degradation by *Fusarium*.

A stocky stem with a low rind: pith ratio and a strong pith benefits intake, yield, and lodging resistance, and minimizes the adverse effects of thick stems.

Several effective, empirical methods for assessing genotypic differences in root anchorage have been developed. These techniques enable selection for superior root types and this reduces the risk of root lodging caused by root weakness or root pests. Genotypes differ very significantly in several root characteristics (Thompson, 1972; Jenison et al., 1981; Penny, 1981; Arihara & Crosbie, 1982; Peters et al., 1982) and root lodging is a heritable trait that can be improved through breeding (Thompson, 1972; Rogers et al., 1976; Penny, 1981; Arihara & Crosbie, 1982). Susceptibility to root lodging correlates positively with early vigour (Gunn, 1977, 1978), but selection for root characteristics is possible without reducing grain-yield potential (Peters et al., 1982). In some cases there might be a correlation between root: shoot ratio and kernel-growth rate (A. Gallais, personal communication). Selecting for superior root systems might result in a reduction in the whole-plant yield. Yet it seems worth paying attention to root-lodging tolerance in maize hybrids bred for forage production in North-West Europe. Genotypes also differ in root *activity* under stress conditions (Derieux, 1983).

Root lodging is most likely to occur from two weeks before silking to four weeks thereafter (Gunn, 1978). Wind and heavy rains foster both root and stalk lodging. Leaf characteristics, such as leaf orientation, leaf rigidity, leaf size and leaf shape affect the magnitude of the forces exerted on the plant, especially around silking.

This is another reason why the erect leaf habit is undesirable in The Netherlands (see also section 1).

The (physical) moment of the forces exerted on the plant also greatly depends on the ear weight and the ear height. Effective selection for lower ear height is possible (Giesbrecht, 1961; Vera & Crane, 1970; Acosta & Crane,

1972; Thompson, 1972; Josephson & Kincer, 1977; Harville et al., 1978; Paterniani, 1981) but for a balanced distribution of assimilates between above-ground plant parts and roots, a short distance between the monopolizing ear and the weak root sinks is not desirable (cf. Struik & Deinum, 1982). Vera & Crane (1970) and Josephson & Kincer (1977) have actually reported lower ear yields resulting from lowering the placement of the ear.

Of the other plant characteristics, vigour and cell-wall digestibility have already been discussed. Finally, lodging might be reduced by growing earlier hybrids or altering cultural practice. The consequences of these measures on yield, however, are so far-reaching that their application to minimize intermittent and unpredictably occurring lodging is not justifiable.

Conclusions

The above-described picture of an ideotype of forage maize for cultivation in the marginal regions of North-West Europe is not final. The qualifications of a forage-maize ideotype are so diverse and often even contradictory that it is not possible to combine them all in one genotype. The search for a forage-maize ideotype is therefore a search for the best compromise. In the opinion of the author, this compromise results in a genotype that has:

- good cold tolerance and early vigour
- early flowering combined with a fast rate of leaf development, approximately 15 leaves per plant, large and prostrate leaves, and a maximum longevity of leaves
- maximum rate of photosynthesis
- a small tassel
- tolerance to high plant densities
- a large ear with a slow rate of grain filling and placed in the axil of the sixth leaf from above
- a stocky stem with a high leaf: stalk ratio, a high pith: rind ratio and a very strong pith
- low susceptibility to pests and diseases
- a high potential extent and a fast rate of cell-wall digestion
- a moderate formation of brace roots.

If a hybrid with the above characteristics is produced, the resulting ideotype will have:

- an ability to give high yields
- a good tolerance to stress

- an excellent resistance to lodging and diseases

and will be:

- very suitable for ensiling
- very digestible, will allow a high dm intake and will have an excellent feed efficiency.

None of these qualities, however, will be maximized.

3. REFERENCES

Aar, P.J. van der, H. Boer, B. Deinum & G. Hof, 1981. Bulk volume: a parameter for measuring forage quality and its influence on voluntary intake. In: J.A. Smith & V.W. Hays (eds.), Proc. XIVth Int. Grassld Congr., Lexington, Ky, pp. 502-505.

Acosta, A.E. & P.L. Crane, 1972. Further selection for lower ear height in maize. Crop Sci. 12: 165-167.

Aitken, Y., 1980. The early maturing character in maize (*Zea mays* L.) in relation to temperature and photoperiod. Z. Acker- u. PflBau 149: 89-106.

Aldrich, S.R., W.O. Scott & E.R. Leng, 1975. Modern corn production (2nd edition), A & L Publications, Champaign, Illinois, U.S.A.

Allison, J.C.S. & T.B. Daynard, 1979. Effect of a change in time of flowering, induced by altering photoperiod or temperature on attributes related to yield in maize. Crop Sci. 19: 1-4.

Andrew, R.H., 1954. Breeding for stalk-rot resistance in maize. Euphytica 3: 43-48.

Andrew, S.M., J.H. Clark & C.L. Davis, 1979. Feeding value of opaque-2 corn grain and corn silage for lactating cows. J. Dairy Sci. 62: 1619-1625.

Arihara, J. & T.M. Crosbie, 1982. Relationships among seedling and mature root system traits of maize. Crop Sci. 22: 1197-1202.

Ariyanayagam, R.P., C.L. Moore & V.R. Carangal, 1974. Selection for leaf angle in maize and its effects on grain yield and other characters. Crop Sci. 14: 551-556.

Baker, D.E., A.E. Jarrell, L.E. Marshall & W.I. Thomas, 1970. Phosphorus uptake from soils by corn hybrids selected for high and low phosphorus accumulation. Agron. J. 62: 103-106.

Barbosa, H.M. & D.V. Glover, 1978. Genes and gene interactions affecting protein and lysine content in the endosperm of maize. Braz. J. Genetics 1: 29-39.

Barloy, J., 1983. Phase germination - levée et implantation. Colloque "Physiologie du maïs", Royan 15-17 Mars 1983.

Barnes, R.F., L.D. Muller, L.F. Bauman & V.F. Colenbrander, 1971. In vitro dry matter disappearance of brown midrib mutants of maize. J. Anim. Sci. 33: 881-884.

Baron, V.S. & T.B. Daynard, 1980. Comparison of European and Canadian corn hybrids for factors affecting field drying and harvestibility. Agron. Abstr., 1980 Ann. Meeting, Amer. Soc. Agron., Detroit, Michigan, p. 96.

Barrière, Y., 1979. Sélection du maïs pour la résistance à la pourriture de tiges. Etude de génotypes précoces. Ann. Amélior. Plantes 29: 289-304.

Barrière, Y. & J.-P. Gay, 1983. Approche physiologique de la sénescence du maïs. Colloque "Physiologie du maïs", Royan 15-17 Mars 1983.

Barrière, Y., A. Panouillé & R. Cassini, 1981. Relations source-puits et sélection du maïs pour la résistance à la pourriture des tiges. Agronomie 1 (8): 707-711.

Bauman, L.F., 1960. Relative yields of first (apical) and second ears of semi-prolific southern corn hybrids. Agron. J. 52: 220-222.

Beek, D. van der, 1977. Builenbrand in mais. Bedrijfsontwikkeling 8: 253-256.

Beerepoot, L.J., 1981. De genetische variatie in verteerbaarheid bij snijmais. LH, Vakgroep Landbouwplantenteelt en Graslandkunde, Doctoraalverslag, pp. 1-43.

Bergen, W.G., E.H. Cash & H.E. Henderson, 1974. Changes in nitrogenous compounds of the whole corn plant during ensiling and subsequent effects on dry matter intake by sheep. J. Anim. Sci. 39: 629-637.

Bertin, Ch., A. Panouillé & S. Rautou, 1976. Obtention de variétés de maïs "prolifiques en épis" productives en grain et à large adaptation écologique. Ann. Amélior. Plantes 26: 387-418.
Blacklow, W.M., 1972a. Mathematical description of the influence of temperature and seed quality on imbibition by seeds of corn (*Zea mays* L.). Crop Sci. 12: 643-646.
Blacklow, W.M., 1972b. Influence of temperature on germination and elongation of the radicle and shoot of corn (*Zea mays* L.). Crop Sci. 12: 647-650.
Blanco, M. & J.L. Blanco, 1960. Breeding for high sugar in the stalk at maturity and related subjects. Proc. Eucarpia 1st meeting of the Maize & Sorghum Section, Rome, 23-26 February, pp. 25-28.
Bloc, D., J.P. Gay & J.P. Gouet, 1983a. Evolution de la teneur en eau et du poids de 1000 grains pendant la maturation du maïs. Colloque "Physiologie du maïs", Royan 15-17 Mars 1983.
Bloc, D., J.P. Gay & J.P. Gouet, 1983b. Durée des phases végétatives et reproductives chez le maïs: influence de la température. Colloque "Physiologie du maïs", Royan 15-17 Mars 1983.
Block, E., L.D. Muller & L.H. Kilmer, 1982. Brown midrib-3 versus normal corn plants (*Zea mays* L.) harvested as whole plant or stover and frozen fresh or preserved as silage for sheep. Can. J. Anim. Sci. 62: 487-498.
Blondon, F., G. Clabault & M. Rainguez, 1981. Déplacement de l'optimum thermique de l'activité photosynthétique, sous l'action d'un traitement à temperature fraîche (10°C) chez le maïs: différenciation de deux variétés. C.R. Acad. Sci., série III, t. 292: 149-152.
Blondon, F., G. Clabault & M. Rainguez, 1983. Adaptation au froid et activité photosynthétique chez le maïs. Colloque "Physiologie du maïs", Royan 15-17 Mars 1983.
Blondon, F., & A. Gallais, 1976. Influence de la température, de la valeur de l'éclairement et de la photopériode sur le développement floral de quatre génotypes de maïs. Ann. Amélior. Plantes 26: 195-213.
Bonhomme, R., 1983. Mise en place des appareils foliaire et racinaire chez le maïs. Colloque "Physiologie du maïs", Royan 15-17 Mars 1983.
Brooking, I.R., 1979. Temperature effects on inflorescence development and grain filling of cereals. Proc. Agron. Soc. N. Zealand 9: 65-69.
Brouwer, R., A. Kleinendorst & J.Th. Locher, 1973. Growth responses of maize plants to temperature. In: Plant response to climatic factors. Proc. Uppsala Symp., 1970. UNESCO, Paris, pp. 169-174.
Bruetsch, T.F. & G.O. Estes, 1976. Genotype variation in nutrient uptake efficiency in corn. Agron. J. 68: 521-523.
Buren, L.L., J.J. Mock & I.C. Anderson, 1974. Morphological and physiological traits in maize associated with tolerance to high plant density. Crop Sci. 14: 426-429.
Burgstaller, G., B. Gedek, W. Gedek, D. Günzler, R. Hoffmann, W. Hollwich, W. Klee & P. Plank, 1977. Maisbeulenbrand (*Ustilago zeae*) -Einfluss auf Futterwert der Silage und Tiergesundheit. Z. Das wirtschaftseigene Futter 23: 60-76.
Campling, R.C., 1977. The feeding value of maize: a review. Ann. appl. Biol. 87: 284-290.
Carter, M.W. & C.G. Poneleit, 1973. Black layer maturity and filling period variation among inbred lines of corn (*Zea mays* L.). Crop Sci. 13: 436-439.
Chang, H.S. & P.J. Loesch, jr., 1972. Genetic variation of four anatomical traits and their association with stalk quality traits in maize (*Zea mays* L.). Crop Sci. 12: 271-274.
Chang, H.S., P.J. Loesch, jr. & M.S. Zuber, 1976. Effects of recurrent selection for crushing strength on morphological and anatomical stalk traits in corn. Crop Sci. 16: 621-625.

Choe, B.-H., M.S. Zuber, G.F. Krause & E.S. Hildebrand, 1976. Inheritance of high lysine in maize. Crop Sci. 16: 34-38.
Colenbrander, V.F., L.F. Bauman & V.L. Lechtenberg, 1973. Effect of brown midrib mutant genes on the nutritional quality of corn. Proc. 28th ann. Corn & Sorghum Res. Conf., Chicago, 1973. Amer. Seed Trade Ass. Publ. 28: 92-97.
Colenbrander, V.F., V.L. Lechtenberg & L.F. Bauman, 1975. Feeding value of low lignin corn silage. J. Anim. Sci. 41: 332-333 (Abstr.).
Coligado, M.C. & D.M. Brown, 1975a. Response of corn (*Zea mays* L.) in the pre-tassel initiation period to temperature and photoperiod. Agric. Meteorol. 14: 357-367.
Coligado, M.C. & D.M. Brown, 1975b. A bio-photo-thermal model to predict tassel-initiation time in corn (*Zea mays* L.). Agric. Meteorol. 15: 11-31.
Collins, M., A.M. Ferreira, D.A. Rohweder & N.A. Jorgensen, 1980. Laboratory analyses for predicting digestibility and intake of corn silage. Agron. J. 72: 889-892.
Collins, W.K., W.A. Russel & S.A. Eberhart, 1965. Performance of two-ear type of Corn Belt maize. Crop Sci. 15: 113-116.
Cook, R.J., 1977. The importance of stalk rot and smut in British maize. Ann. appl. Biol. 87: 266-270.
Cook, R.J., 1978a. Diseases and pests of maize. In: E.S. Bunting, B.F. Pain, R.H. Phipps, J.M. Wilkinson & R.E. Gunn (eds.), Forage maize, Agric. Res. Council, London, pp. 117-132.
Cook, R.J., 1978b. The incidence of stalk rot (*Fusarium* spp.) on maize hybrids and its effects on yield of maize in Britain. Ann. appl. Biol. 88: 23-30.
Cortez-Mendoza, H. & A.R. Hallauer, 1979. Divergent mass selection for ear length in maize. Crop Sci. 19: 175-178.
Cottyn, B.G., Ch.V. Boucqué, J.V. Aerts & F.X. Buysse, 1978. Verteerbaarheid en voederwaarde van droog of vochtig maïsgraan onder verschillende structuurvormen. Landbouwtijdschrift 31: 281-289.
Crosbie, T.M. & J.J. Mock, 1980. *Effects of recurrent selection for grain* yield on plant and ear traits of five maize populations. Euphytica 29: 57-64.
Crosbie, T.M., J.J. Mock & R.B. Pearce, 1977. Variability and selection advance for photosynthesis in Iowa Stiff Stalk Synthetic maize population. Crop Sci. 17: 511-514.
Crosbie, T.M., J.J. Mock & R.B. Pearce, 1978a. Inheritance of photosynthesis in a diallel among eight maize inbred lines from Iowa Stiff Stalk Synthetic. Euphytica 27: 657-664.
Crosbie, T.M., R.B. Pearce & J.J. Mock, 1978b. Relationships among CO_2-exchange rate and plant traits in Iowa Stiff Stalk Synthetic maize population. Crop Sci. 18: 87-90.
Crosbie, T.M., R.B. Pearce & J.J. Mock, 1981a. Selection for high CO_2-exchange rate among inbred lines of maize. Crop Sci. 21: 629-631.
Crosbie, T.M., R.B. Pearce & J.J. Mock, 1981b. Recurrent phenotypic selection for high and low photosynthesis in two maize populations. Crop Sci. 21: 736-740.
Cross, H.Z., 1975. Diallel analysis of duration and rate of grain filling of seven inbred lines of corn. Crop Sci. 15: 532-535.
Daccord, R. & R. Vogel, 1982. Feeding value of LG-11 maize and of its brown midrib mutant. In: H.J. Oslage & R. Daccord (eds.), Proc. Seminar on COST-PROJECT 82 "Maize as basic feed for beef production", Grangeneuve, Switzerland, pp. 17-29.
Daynard, T.B., 1978. Practices affecting quality and preservation of whole-plant corn silage. Can. J. Plant Sci. 58: 651-659.

Daynard, T.B., 1983. Possibilités d'amélioration de la productivité des maïs précoces. Colloque "Physiologie du maïs", Royan 15-17 Mars 1983.
Daynard, T.B., V. Baron, B. Andrews & P. Verdier, 1980. Evaluation of short-season Canadian and European corn hybrids grown in Ontario, Manitoba and France. Agron. Abstr., 1980 Ann. Meeting, Amer. Soc. Agron., Detroit, Michigan, p. 98.
Daynard, T.B., V.S. Baron & M. Tollenaar, 1979. Points of current interest in studies of the physiology of the maize plant. Paper presented at Euromais Congress, Cambridge, 1979.
Daynard, T.B. & R.B. Hunter, 1975. Relationships among whole-plant moisture, grain moisture, dry matter yield and quality of whole-plant corn silage. Can. J. Plant Sci. 55: 77-84.
Deinum, B., 1976. Effect of age, leaf number and temperature on cell wall and digestibility of maize. In: Carbohydrate research in plants and animals. Misc. Papers nr. 12, Agric. Univ. Wageningen, pp. 29-41.
Deinum, B. & J.J. Bakker, 1981. Genetic differences in digestibility of forage maize hybrids. Neth. J. agric. Sci. 29: 93-98.
Deinum, B. & J. Knoppers, 1979. The growth of maize in the cool temperate climate of the Netherlands: Effect of grain filling on production of dry matter and on chemical composition and nutritive value. Neth. J. agric. Sci. 27: 116-130.
Deinum, B., A. Steg & G. Hof, 1983. Measurement and prediction of digestibility of forage maize in the Netherlands. Anim. Feed Sci. Technol. 8 (in press).
Deinum, B. & P.C. Struik, 1982. Productivity and nutritive value of forage maize. In: H.J. Oslage & R. Daccord (eds.), Proc. Seminar on COST-PROJECT 82 "Maize as basic feed for beef production", Grangeneuve, Switzerland, pp. 8-16.
Demarquilly, C., 1969. Valeur alimentaire du maïs fourrage. Ann. Zootechnie 18: 17-32.
Demarquilly, C., Ph. Haurez, M. Journet, C. Lelong & C. Malterre, 1971. Le maïs plante entière: composition, valeur alimentaire, utilisation par les bovins. Bulletin Technique d'Information 264-265: 1-18.
Derieux, M., 1983. Sélection et adaptation. Colloque "Physiologie du maïs", Royan 15-17 Mars 1983.
Derieux, M., R. Bonhomme, F. Ruget & J.-B. Duburcq, 1983. Influence du génotype et du milieu sur le nombre d'ovules présents à la floraison. Colloque "Physiologie du maïs", Royan 15-17 Mars 1983.
Derieux, M. & Y. Montalant, 1978. Résultats d'un cycle de sélection généalogique pour la teneur en protéines du grain de maïs. Ann. Amélior. Plantes 28: 463-474.
Donald, C.M., 1968. The breeding of crop ideotypes. Euphytica 17: 385-403.
Donefer, E., E.W. Crampton & L.E. Lloyd, 1960. Prediction of the nutritive value index of a forage from in vitro rumen fermentation data. J. Anim. Sci. 19: 545-552.
Dudley, J.W. & R.J. Lambert, 1969. Genetic variability after 65 generations of selection in Illinois high oil, low oil, high protein and low protein strain of *Zea mays* L. Crop Sci. 9: 179-181.
Dudley, J.W., R.J. Lambert & I.A. de la Roche, 1977. Genetic analysis of crosses among corn strains divergently selected for percent oil and protein. Crop Sci. 17: 111-116.
Duncan, W.G., 1971. Leaf angles, leaf area and canopy photosynthesis. Crop Sci. 11: 482-485.
Duncan, W.G., 1975. Maize. In: L.T. Evans (ed.), Crop physiology. Some case studies. Cambridge University Press, London, pp. 23-50.

Duncan, W.G. & J.D. Hesketh, 1968. Net photosynthesis rates, relative growth rates, and leaf numbers of 22 races of maize grown at eight temperatures. Crop Sci. 8: 670-674.
Duncan, W.G., W.A. Williams & R.S. Loomis, 1967. Tassels and the productivity of maize. Crop Sci. 7: 37-39.
Eagles, H.A. & I.R. Brooking, 1981. Populations of maize with more rapid and reliable seedling emergence than Cornbelt dents at low temperatures. Euphytica 30: 755-763.
Eagles, H.A. & A.K. Hardacre, 1979. Genetic variation in maize (*Zea mays* L.) for germination and emergence at 10°C. Euphytica 28: 287-295.
Early, E.B., W.O. McIlrath, R.D. Seif & R.H. Hageman, 1967. Effects of shade applied at different stages of plant development on corn (*Zea mays* L.) production. Crop Sci. 7: 151-156.
Early, E.B., R.J. Miller, G.L. Reichert, R.H. Hageman & R.D. Seif, 1966. Effects of shade on maize production under field conditions. Crop Sci. 6: 1-7.
Ebskamp, A.G., 1981. Het cultuurwaardeonderzoek van snijmaisrassen in Nederland (II). Criteria bij de beoordeling van snijmaisrassen. Bedrijfsontwikkeling 12: 269-275.
El-Shalzy, K., B.A. Dehority & R.R. Johnson, 1961. Effect of starch on the digestion of cellulose in vitro and in vivo by rumen microorganisms. J. Anim. Sci. 20: 268-273.
Fairey, N.A., 1980. Hybrid maturity and the relative importance of grain and stover for the assessment of the forage potential of maize genotypes grown in marginal and non-marginal environments. Can. J. Plant Sci. 60: 539-545.
Fairey, N.A., 1982. Influence of population density and hybrid maturity on productivity and quality of forage maize. Can. J. Plant Sci. 62: 427-434.
Fakorede, M.A.B. & J.J. Mock, 1977. Leaf orientation and efficient utilization of solar energy by maize (*Zea mays* L.). In: Agrometeorology of the maize (corn) plant. World Meteorological Organization, no. 481, Geneva, pp. 207-230.
Fakorede, M.A.B. & D.K. Ojo, 1981. Variability for seedling vigour in maize. Expl Agric. 17: 195-201.
Fisher, L.J. & N.A. Fairey, 1979. Factors influencing the utilization by ruminants of corn silage in marginal growing areas. Can. J. Anim. Sci. 59: 427-439.
Fisher, L.J., V.S. Logan, L.S. Donovan & R.B. Carson, 1968. Factors influencing dry matter intake and utilization of corn silage by lactating cows. Can. J. Anim. Sci. 48: 207-214.
Foley, D.C. & C.C. Wernham, 1957. The effect of fertilizers on stalk rot of corn in Pennsylvania. Phytopathology 47: 11-12.
Frölich, W.G. & W.G. Pollmer, 1978. Die Blatthaltung bei Mais (*Zea mays* L.) als ertragsbeeinflussender Faktor. Kali-Briefe (Büntehof) 14: 345-354.
Frölich, W.G., W.G. Pollmer & D. Klein, 1977. Performance of isogenic liguleless-2 maize hybrids as influenced by irrigation, row width, plant density and nitrogen fertilizer. Z. Acker- u. PflBau 145: 207-223.
Gallais, A., L. Huguet, H. Berthet, G. Bertin, B. Broqua, A. Mourguet & R. Traineau, 1980. Preliminary evaluation of brown midrib maize hybrids for their feeding and agronomic value in France. In: W.G. Pollmer & R.H. Phipps (eds.), Improvement of quality traits of maize for grain and silage use. Martinus Nijhoff, The Hague, pp. 319-339.
Gallais, A., M. Pollacsek & L. Huguet, 1976. Possibilités de sélection du maïs en tant que plante fourragère. Ann. Amélior. Plantes 26: 591-605.

Gallais, A. & P. Vincourt, 1983. Possibilités d'amélioration du rendement en matière sèche du maïs ensilage. Colloque "Physiologie du maïs", Royan 15-17 Mars 1983.
Gallasz, E., 1982. Silierversuch von 6 verschiedenen high-sugar-maize Hybriden im Vergleich zu zwei bekannten Maissorten (ohne und mit ausgebildeten Kolben). Versuchsbericht Eidgenössische Forschungsanstalt für viehwirtschaftliche Produktion, Grangeneuve, Switzerland, pp. 1-5.
Giesbrecht, J., 1961. The inheritance of ear height in *Zea mays*. Can. J. Genet. Cytol. 3: 26-33.
Gmelig Meyling, H.D., 1973. Effect of light intensity, temperature and day-length on the rate of leaf appearance of maize. Neth. J. agric. Sci. 21: 68-76.
Gorsline, G.W., J.L. Ragland & W.I. Thomas, 1961. Evidence for inheritance of differential accumulation of calcium, magnesium and potassium by maize. Crop Sci. 1: 155-156.
Gorsline, G.W., W.I. Thomas & D.E. Baker, 1964. Inheritance of P, K, Mg, Cu, B, Zn, Mn, Al and Fe concentrations by corn (*Zea mays* L.) leaves and grain. Crop Sci. 4: 207-210.
Grogan, C.O., 1956. Detasseling responses in corn. Agron. J. 48: 247-249.
Gross, F., 1977. Einfluss von Maisbeulenbrand (*Ustilago zeae*) auf die Silagegärung. Z. Das wirtschaftseigene Futter 23: 77-82.
Gross, F., 1979. Nährstoffgehalt und Verdaulichkeit von Silomais. 1. Mitteilung: Bewertung von Silomais. Z. Das wirtschaftseigene Futter 25: 215-225.
Gross, F. & W. Peschke, 1980a. Nährstoffgehalt und Verdaulichkeit von Silomais. 2. Mitteilung: Nährstoffgehalt und Verdaulichkeit von Maisstroh (Maispflanze ohne Kolben). Z. Das wirtschaftseigene Futter 26: 104-117.
Gross, F. & W. Peschke, 1980b. Nährstoffgehalt und Verdaulichkeit von Silomais. 4. Mitteilung: Einfluss der Kolbenbildung auf Nährstoffgehalt und Verdaulichkeit von Silomais. Z. Das wirtschaftseigene Futter 26: 193-206.
Gunn, R.E., 1975. Breeding maize for forage production. Compte rendu intégral de 8me Congrès international de la section Maïs-Sorgho, Eucarpia, Paris-Versailles, pp. 563-575.
Gunn, R.E., 1977. Breeding forage maize varieties for Britain. Ann. appl. Biol. 87: 254-258.
Gunn, R.E., 1978. Forage breeding and seed production. In: E.S. Bunting, B.F. Pain, R.H. Phipps, J.M. Wilkinson & R.E. Gunn (eds.), Forage maize. Agric. Res. Council, London, pp. 133-151.
Hall, A.J., H.D. Ginzo, J.H. Lemcoff & A. Soriano, 1980. Influence of drought during pollen-shedding on flowering, growth and yield of maize. Z. Acker- u. PflBau 149: 287-298.
Hall, A.J., J.H. Lemcoff & N. Trapani, 1981. Water stress before and during flowering in maize and its effects on yield, its components, and their determinants. Maydica 26: 19-38.
Hanway, J.J., 1963. Growth stages of corn (*Zea mays* L.). Agron. J. 55: 487-492.
Hanway, J.J., 1966. How a corn plant develops. Special report no. 48, Iowa State Univ., Ames, Iowa, U.S.A., pp. 1-18.
Harris, R.E., R.H. Moll & C.W. Stuber, 1976. Control and inheritance of prolificacy in maize. Crop Sci. 16:843-850.
Harville, B.G., L.M. Josephson & H.C. Kincer, 1978. Diallel analysis of ear height and associated characters in corn. Crop Sci. 18: 273-275.
Heichel, G.H. & R.B. Musgrave, 1969. Varietal differences in net photosynthesis of *Zea mays* L. Crop Sci. 9: 483-486.
Hepting, L. & J. Zscheischler, 1975. The effect of between-row spacing and plant density on grain yield and dry-matter content in grain maize. Z. Acker- u. PflBau 141: 178-186.

Hicks, D.R. & R.E. Strucker, 1972. Plant density effect on grain yield of corn hybrids diverse in leaf orientation. Agron. J. 64: 484-486.
Hoff, D.J. & H.J. Mederski, 1960. Effect of equidistant corn plant spacing on yield. Agron. J. 52: 295-297.
Honig, H. & K. Rohr, 1982a. The influence of chopping on losses by undigested kernels and kernel fragments of maize, when feeding ruminants. In: H.J. Oslage & R. Daccord (eds.), Proc. Seminar on COST-PROJECT 82 "Maize as basic feed for beef production", Grangeneuve, Switzerland, pp. 32-41.
Honig, H. & K. Rohr, 1982b. Zur Bedeutung des Zerkleinerungsgrades von Silomais. 1. Mitteilung: Einfluss des Zerkleinerungsgrades auf die Verluste durch unverdaut ausgeschiedene Körner. Z. Das wirtschaftseigene Futter 28: 183-192.
Hunter, R.B., 1978. Selection and evaluation procedures for whole-plant corn silage. Can. J. Plant Sci. 58: 661-678.
Hunter, R.B., 1980. Increased leaf area (source) and yield of maize in short-season areas. Crop Sci. 20: 571-574.
Hunter, R.B., T.B. Daynard, D.J. Hume, J.W. Tanner, J.D. Curtis & L.W. Kannenberg, 1969. Effect of tassel removal on grain yield of corn (*Zea mays* L.). Crop Sci. 9: 405-406.
Hunter, R.B., M. Tollenaar & C.M. Breuer, 1977. Effects of photoperiod and temperature on vegetative and reproductive growth of a maize (*Zea mays*) hybrid. Can. J. Plant Sci.57: 1127-1133.
Jenison, J.R., D.B. Shank & L.H. Penny, 1981. Root characteristics of 44 maize inbreds evaluated in four environments. Crop Sci. 21: 233-237.
Johnson, R.R. & D.L. Mulvaney, 1980. Development of a model for use in maize replant decisions. Agron. J. 72: 459-464.
Johnson, D.R. & J.W. Tanner, 1972. Calculation of the rate and duration of grain filling in corn (*Zea mays* L.). Crop Sci. 12: 485-486.
Josephson, L.M. & H.C. Kincer, 1977. Selection for lower ear placement in two synthetic populations of maize. Crop Sci. 17: 499-502.
Keith, E.A., V.F. Colenbrander, T.V. Perry & L.F. Bauman, 1979. Nutritional value of brown midrib corn silage for lactating cows. J. Dairy Sci. 62: 788-792.
Kilkenny, J.B., 1978. Utilisation of maize silage for beef production. In: E.S. Bunting, B.F. Pain, R.H. Phipps, J.M. Wilkinson & R.E. Gunn (eds.), Forage maize. Agric. Res. Council, London, pp. 239-261.
Klein, D., W.G. Frölich, W.G. Pollmer & D. Eberhard, 1980. Performance of high-lysine maize hybrids under western European conditions. In: W.G. Pollmer & R.H. Phipps (eds.), Improvement of quality traits of maize for grain and silage use. Martinus Nijhoff, The Hague, pp. 75-90.
Knipmeyer, J.W., R.H. Hageman, E.B. Early & R.D. Seif, 1962. Effect of light intensity on certain metabolites of the corn plant (*Zea mays* L.). Crop Sci. 2: 1-5.
Kovačević, V., 1982. The ear-leaf percentage of nitrogen, phosphorus and potassium in the corn (*Zea mays* L.) inbred lines and their diallel progeny. Proc. 1st int. Symp. on Genetic specificity of mineral nutrition of plants, Belgrade, Yugoslavia, 30 VIII - 4 IX 1982, pp. 371-375.
Krall, J.M., H.A. Eseschie, R.J. Raney, S. Clark, G. TenEyck, M. Lundquist, N.E. Humburg, L.S. Axthelm, A.D. Dayton & R.L. Vanderlip, 1977. Influence of within-row variability in plant spacing on corn grain yield. Agron. J. 69: 797-799.
Krüger, W., 1970a. Wurzel- und Stammfäule bei Mais III. Die Wirkung von Bodenbearbeitungsmassnahmen auf Stammfäule. Phytopath. Z. 68: 1-8.
Krüger, W., 1970b. Wurzel- und Stammfäule bei Mais IV. Die Wirkung von Dünger auf das Auftreten der Wurzel- und Stammfäule. Phytopath. Z. 68: 334-345.

Krüger, W., 1978. Einfluss von Düngung und Bestandesdichte auf Stengelfäule, Stengelbruch und Ertrag des Maises. Z. Acker- u. PflBau 147: 190-203.
Krüger, W. & L. Reiner, 1974. Einfluss von Saattermin, Bestandesdichte und Sorten auf die Stengelfäule des Maises. Z. Acker- u. PflBau 139: 172-185.
Krüger, W., L. Reiner & H. Hoffmann, 1975. Zum Auftreten der Stengelfäule des Maises in Abhängigkeit von Reihenabstand und Anfälligkeit der Hybriden. Z. Acker- u. PflBau 141: 160-164.
Krüger, W. & C. Rogdaki-Papadaki, 1980. Über die Wirkung von Temperatur, Bodenart, Bodenverdichtung und Düngung auf die Wurzelfäule und das Pilzspektrum des Maises. Z. PflKrankh., PflSchutz 87: 298-316.
Lambert, R.J. & R.R. Johnson, 1978. Leaf angle, tassel morphology, and the performance of maize hybrids. Crop Sci. 18: 499-502.
Landi, P. & T.M. Crosbie, 1982. Response of maize to cold stress during vegetative growth. Agron. J. 74: 765-768.
Landry, J., 1983. Accumulation des protéines dans le grain de maïs. Colloque "Physiologie du maïs", Royan 15-17 Mars 1983.
Leaver, J.D., 1978. Utilisation of maize silage by dairy herd replacement. In: E.S. Bunting, B.F. Pain, R.H. Phipps, J.M. Wilkinson & R.E. Gunn (eds.), Forage maize. Agric. Res. Council, London, pp. 297-307.
Lechtenberg, V.L., L.D. Muller, L.F. Bauman, C.L. Rhykerd & R.F. Barnes, 1972. Laboratory and in vitro evaluation of inbred and F_2 populations of brown midrib mutants of *Zea mays* L. Agron. J. 64: 657-660.
Loesch, P.J., jr., C.F. Stark & M.S. Zuber, 1976. Effect of plant density on the quality of cobs used for corn cob pipes. Crop Sci. 16: 706-709.
Maggiore, T., E. Gentinetta, M. Motto, M. Perenzin, F. Salamini & C. Lorenzoni, 1980. Variability for protein and fibre content in three diallels of maize for silage production. In: W.G. Pollmer & R.H. Phipps (eds.), Improvement of quality traits of maize for grain and silage use. Martinus Nijhoff, The Hague, pp. 135-153.
Malterre, C., 1976. Different ways of utilising the maize crop for beef production. In: J.C. Tayler & J.M. Wilkinson (eds.), Improving the nutritional efficiency of beef production. Publ. EUR 5488e, Commission of the Eur. Committees, Brussels, pp. 104-164.
Mann, Ch.E., W.G. Pollmer & D. Klein, 1980. Parent-offspring correlations in maize materials diverse for protein content. In: W.G. Pollmer & R.H. Phipps (eds.), Improvement of quality traits of maize for grain and silage use. Martinus Nijhoff, The Hague, pp. 155-170.
Marten, G.C., R.D. Goodrich, R.M. Jordan, A.R. Schmid & J.C. Meiske, 1976. Evaluation of laboratory methods for determining quality of corn and sorghum silages: III. Biological and chemical methods for predicting animal intake. Agron. J. 68: 289-291.
McAllan, A.B. & R.H. Phipps, 1977. The effect of sample date and plant density on the carbohydrate content of forage maize and the changes that occur on ensiling. J. agric. Sci. Camb. 89: 589-597.
Mensah, R.A. & B.G. Zwatz, 1975a. Studie über die Stengelbruchkrankheit des Maises (*Zea mays* L.), Krankheitskomplex mit besonderer Berücksichtigung der Möglichkeiten einer künstlichen Infektion. Pflanzenschutz-Berichte XLIV: 161-194.
Mensah, R.A. & B.G. Zwatz, 1975b. Studie über die Stengelbruchkrankheit des Maises (*Zea mays* L.) mit besonderer Berücksichtigung der Ertragsbeeinflussung sowie der Anfälligkeit der Sorten. Die Bodenkultur 26: 175-197.
Mertens, D.R., 1973. Application of theoretical mathematical models to cell wall digestion and forage intake in ruminants. Ph.D. Thesis Cornell Univ., Ithaca, NY.

Mertens, D.R. & L.O. Ely, 1979. A dynamic model of fiber digestion and passage in the ruminant for evaluating forage quality. J. Anim. Sci. 49: 1085-1095.
Mertens, D.R. & J.R. Loften, 1980. The effects of starch on forage fiber digestion kinetics in vitro. J. Dairy Sci. 63: 1437-1446.
Mertz, E.T., L.S. Bates & O.E. Nelson, 1965. Growth of rats fed on opaque-2 maize. Science 148: 1741-1742.
Michaelson, M.E., 1957. Factors affecting development of stalk rot of corn caused by *Diplodia zeae* and *Gibberella zeae*. Phytopathology 47: 499-503.
Miedema, P., 1979a. Veredeling op koudetolerantie bij warmteminnende veldgewassen. Zaadbelangen 33: 198-200.
Miedema, P., 1979b. Potential use of CIMMYT gene pool material for improving low-temperature adaptation in *Zea mays*. Euphytica 28: 661-664.
Miedema, P., 1982. The effects of low temperature on *Zea mays*. Advances in Agronomy 35: 93-128.
Miedema, P., J. Post & P.J. Groot, 1982. The effects of low temperature on seedling growth of maize genotypes. PUDOC, Wageningen.
Mock, J.J. & A.A. Bakri, 1976. Recurrent selection for cold tolerance in maize. Crop Sci. 16: 230-233.
Mock, J.J. & L.L. Buren, 1972. Classification of maize (*Zea mays* L.) inbreds for population tolerance by general combining ability. Iowa State J. Sci. 46: 395-404.
Mock, J.J. & S.A. Eberhart, 1972. Cold tolerance in adapted maize populations. Crop Sci. 12: 466-469.
Mock, J.J. & M.J. McNeill, 1979. Cold tolerance of maize inbred lines adapted to various latitudes in North America. Crop Sci. 19: 239-242.
Mock, J.J. & R.B. Pearce, 1975. An ideotype of maize. Euphytica 24: 613-623.
Mock, J.J. & S.H. Schuetz, 1974. Inheritance of tassel branch number in maize. Crop Sci. 14: 885-888.
Mock, J.J. & W.H. Skrdla, 1978. Evaluation of maize plant introductions for cold tolerance. Euphytica 27: 27-32.
Molot, P.-M., 1969a. Recherches sur la résistance du maïs à l'Helminthosporiose et aux Fusarioses. I. Rôle de la composition chimique de la plante. Annales de Phytopathologie 1: 55-74.
Molot, P.-M., 1969b. Recherches sur la résistance du maïs à l'Helminthosporiose et aux Fusarioses. II. Facteurs de résistance. Annales de Phytopathologie 1: 353-366.
Molot, P.-M., 1969c. Recherches sur la résistance du maïs à l'Helminthosporiose et aux Fusarioses. III. Mode d'action des composés phénologiques. Annales de Phytopathologie 1: 367-383.
Monteith, J.L., 1965. Light distribution and photosynthesis in field crops. Ann. Bot. 29: 17-37.
Morizet, J., M. Pollacsek & D. Togola, 1983. Tolérance à la sécheresse de 4 variétés de maïs. Essai de mise en evidence des mécanismes impliqués. Colloque "Physiologie du maïs", Royan 15-17 Mars 1983.
Mortimore, C.G. & R.E. Wall, 1965. Stalk rot of corn in relation to plant population and grain yield. Can. J. Plant Sci. 45: 487-492.
Mortimore, C.G. & G.M. Ward, 1964. Root and stalk rot of corn in southwestern Ontario. III. Sugar levels as a measure of plant vigor and resistance. Can. J. Plant Sci. 44: 451-457.
Moss, G.I. & L.A. Downey, 1971. Influence of drought stress on female gametophyte development in corn and subsequent grain yield. Crop Sci. 11: 368-372.
Moss, D.N. & H.T. Stinson, 1961. Differential response of corn hybrids to shade. Crop Sci. 1: 416-418.

Motto, M., N. Difanzo, M. Perenzin, E. Gentinetta, T. Maggiore, F. Salamini & C. Lorenzoni, 1980. Genetic control of protein percentage in a diallel involving high-protein inbreds. In: W.G. Pollmer & R.H. Phipps (eds.), Improvement of quality traits of maize for grain and silage use, Martinus Nijhoff, The Hague, pp. 117-134.

Muller, L.D., V.L. Lechtenberg, L.F. Bauman, R.F. Barnes & C.L. Rhykerd, 1972. In vivo evaluation of a brown midrib mutant of *Zea mays* L. J. Anim. Sci. 35: 883-889.

Naismith, R.W., M.W. Johnson & W.I. Thomas, 1974. Genetic control of relative calcium, phosphorus and manganese accumulation on chromosome 9 in maize. Crop Sci. 14: 845-849.

Ottaviano, E. & A. Camussi, 1981. Phenotypic and genetic relationships between yield components in maize. Euphytica 30: 601-609.

Otto, H.J. & H.L. Everett, 1956. Influence of nitrogen and potassium fertilization on the incidence of stalk rot of corn. Agron. J. 48: 301-305.

Parks, W.L., 1977. Row spacing affects corn yield. Better Crops with Plant Food 61: 24-27.

Paterniani, E., 1981. Influence of tassel size on ear placement in maize (*Zea mays* L.). Maydica 26: 85-91.

Pendleton, J.W., G.E. Smith, S.R. Winter & T.J. Johnston, 1968. Field investigations of the relationships of leaf angle in corn (*Zea mays* L.) to grain yield and apparent photosynthesis. Agron. J. 60: 422-424.

Penny, L.H., 1981. Vertical-pull resistance of maize inbreds and their testcrosses. Crop Sci. 21: 237-240.

Pepper, G.E., R.B. Pearce & J.J. Mock, 1977. Leaf orientation and yield of maize. Crop Sci. 17: 883-886.

Peters, D.W., D.B. Shank & W.E. Nyquist, 1982. Root-pulling resistance and its relationship to grain yield in F_1 hybrids of maize. Crop Sci. 22: 1112-1114.

Peters & Woolley, 1959. News Release U.S.D.A., Washington, Feb. 25, 1959, cited by Hoff & Mederski (1960).

Phipps, R.H., 1978. Utilisation of maize silage for milk production. In: E.S. Bunting, B.F. Pain, R.H. Phipps, J.M. Wilkinson & R.E. Gunn (eds.), Forage maize. Agric. Res. Council, London, pp. 263-295.

Phipps, R.H., 1980. A review of the carbohydrate content and digestibility value of forage maize grown in the cool climatic conditions of the UK and their relevance to animal production. In: W.G. Pollmer & R.H. Phipps (eds.), Improvement of quality traits of maize for grain and silage use. Martinus Nijhoff, The Hague, pp. 291-317.

Phipps, R.H. & R.F. Weller, 1979. The development of plant components and their effects on the composition of fresh and ensiled forage maize. 1. The accumulation of dry matter, chemical composition and nutritive value of fresh maize. J. agric. Sci. Camb. 92: 471-483.

Phipps, R.H., R.F. Weller & A. Cooper, 1982. A comparison between the accumulation of dry matter, chemical composition and nutritive value of isogenic sterile and fertile forage maize. Maydica 27: 27-40.

Phipps, R.H., R.F. Weller & R.J. Fulford, 1979. The development of plant components and their effects on the composition of fresh and ensiled forage maize. 3. The effect of grain content on milk production. J. agric. Sci. Camb. 92: 493-498.

Pollmer, W.G., D. Klein, M. Bjarnason & D. Eberhard, 1974. Die Verbesserung der Proteinqualität und Proteinquantität bei Mais als Züchtungsaufgabe. Z. Acker- u. PflBau 140: 241-257.

Pommer, G., W. Sanchez & H. Häckel, 1981. Auswirkungen verschiedener Reihenweiten und Bestandesdichten auf den Ertrag von Maissorten mit waagrechter und aufrechter Blatthaltung. Z. Acker- u. PflBau 150: 113-128.

Poneleit, C.G. & D.B. Egli, 1979. Kernel growth rate and duration in maize as affected by plant density and genotype. Crop Sci. 19: 385-388.
Poneleit, C.G., D.B. Egli, P.L. Cornelius & D.A. Reicosky, 1980. Variation and associations of kernel growth characteristics in maize populations. Crop Sci. 20: 766-770.
Prine, G.M., 1977. Plant population, row width and kernel orientation effects on grain yield of early and medium-maturing corn. Proc. Soil Crop Sci. Soc. Flor. 36: 157-160.
Purdy, J.L. & P.L. Crane, 1967. Inheritance of drying rate in 'mature' corn (*Zea mays* L.). Crop Sci. 7: 294-297.
Rijksinstituut voor het Rassenonderzoek van Cultuurgewassen (RIVRO), 1983. 58e Beschrijvende rassenlijst voor landbouwgewassen 1983, Leiter-Nypels, Maastricht.
Robelin, M., 1983. Fonctionnement hydrique et adaptation à la sécheresse. Colloque "Physiologie du maïs", Royan 15-17 Mars 1983.
Rogers, R.R., W.A. Russell & J.C. Owens, 1976. Evaluation of a vertical-pull technique in population improvement of maize for corn rootworm tolerance. Crop Sci. 16: 591-594.
Rohr, K., H. Honig & R. Daenicke, 1982. Effect of altering the physical form of maize silage on rumination, rumen fermentation and digestibility of nutrients. In: H.J. Oslage & R. Daccord (eds.), Proc. Seminar on COST-PROJECT 82 'Maize as basic feed for beef production', Grangeneuve, Switzerland, pp. 42-52.
Rohr, K., H. Honig & R. Daenicke, 1983. Zur Bedeutung des Zerkleinerungsgrades von Silomais. 2. Mitteilung: Einfluss des Zerkleinerungsgrades auf die Wiederkauaktivität, die Pansenfermentation und die Verdaulichkeit der Rohnährstoffe. Z. Das wirtschaftseigene Futter 29 (in press).
Rood, S.B. & D.J. Major, 1981a. Diallel analysis of the photoperiodic response of maize. Crop Sci. 21: 875-878.
Rood, S.B. & D.J. Major, 1981b. Diallel analysis of leaf number, leaf development rate, and plant height of early maturing maize. Crop Sci. 21: 867-873.
Rook, J.A., L.D. Muller & D.B. Shank, 1977. Intake and digestibility of brown midrib corn silage by lactating dairy cows. J. Dairy Sci. 60: 1894-1904.
Rosa, J.G., D.M. Forsyth, D.V. Glover & T.R. Cline, 1977a. Normal, opaque-2, waxy, waxy opaque-2, sugary-2 and sugary-2 opaque-2 corn (*Zea mays* L.) endosperm types for rats and pigs. Studies on energy utilization J. Anim. Sci. 44: 1004-1010.
Rosa, J.G., D.M. Forsyth, D.V. Glover & T.R. Cline, 1977b. Normal, opaque-2, waxy, waxy opaque-2, sugary-2 and sugary-2 opaque-2 corn (*Zea mays* L.) endosperm types for rats and pigs. Studies on protein quality. J. Anim. Sci. 44: 1011-1020.
Roth, L.S., G.C. Marten, W.A. Compton & D.D. Stuthman, 1970. Genetic variation of quality traits in maize (*Zea mays* L.) forage. Crop Sci. 10: 365-367.
Russell, W.A., 1968. Testcrosses of one- and two-ear types of Corn Belt maize inbreds: I. Performance at four plant densities. Crop Sci. 8: 244-247.
Schmidt, W., 1980. Proteingehalt und Proteinqualität bei Mais. Chancen und Möglichkeiten der Züchtung. Mais-Kolloquium 1980, Einbeck, pp. 27-45.
Semuguruka, G.H., W.A. Compton, C.Y. Sullivan & M.A. Thomas, 1981. Some measures of temperature response in corn (*Zea mays* L.). Maydica 26: 209-218.
Sheldrick, R.D., 1979. The quality of 'brown-midrib-3' mutant maize grown for forage under field conditions in southern England. Grass & Forage Sci. 34: 283-291.
Sibma, L., 1977. Maximization of arable crop yields in the Netherlands. Neth. J. agric. Sci. 25: 278-287.

Sorrells, M.E., J.H. Lonnquist & R.E. Harris, 1979. Inheritance of prolificacy in maize. Crop Sci. 19: 301-306.
Stallings, C.C., B.M. Donaldson, J.W. Thomas & E.C. Rossman, 1982. In vivo evaluation of brown-midrib corn silage by sheep and lactating cows. J. Dairy Sci. 65: 1945-1949.
Stamp, P., 1980. Variabilität von Spross- und Wurzelmerkmalen junger Maispflanzen in Abhängigkeit von Genotyp und Temperatur. Z. Pflanzenzüchtg. 84: 226-239.
Stinson, H.T. & D.N. Moss, 1960. Some effects of shade upon corn hybrids tolerant and intolerant of dense planting. Agron. J. 52: 482-484.
Struik, P.C., 1982a. Production pattern, chemical composition and digestibility of forage maize (*Zea mays* L.). Mededeling no. 64, LH, Vakgroep Landbouwplantenteelt & Graslandkunde, Wageningen, Netherlands, pp. 1-28.
Struik, P.C., 1982b. Effect of a switch in photoperiod on the reproductive development of temperate hybrids of maize. Neth. J. agric. Sci. 30: 69-83.
Struik, P.C., 1983a. The effects of switches in photoperiod on crop morphology, production pattern and quality of forage maize (*Zea mays* L.) under field conditions. Mededelingen Landbouwhogeschool 83-2, Wageningen, pp. 1-27.
Struik, P.C., 1983b. 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.). Neth. J. agric. Sci. 31: 101-124.
Struik, P.C., 1983c. Effect of temperature on development, dry-matter production, dry-matter distribution and quality of forage maize (*Zea mays* L.). An analysis. Mededelingen Landbouwhogeschool, 83-3, Wageningen, pp. 1-41.
Struik, P.C. & B. Deinum, 1982. Effect of light intensity after flowering on the productivity and quality of silage maize. Neth. J. agric. Sci. 30: 297-316.
Thiagarajah, M.R. & L.A. Hunt, 1982. Effects of temperature on leaf growth in corn (*Zea mays*). Can. J. Bot. 60: 1647-1652.
Thomas, V.M., D.V. Glover & W.M. Beeson, 1976. Nitrogen and energy utilization of new endosperm types of corn with growing steers. J. Anim. Sci. 42: 529-534.
Thompson, D.L., 1972. Recurrent selection for lodging susceptibility and resistance in corn. Crop Sci. 12: 631-634.
Thompson, D.L., 1982. Grain yield of two synthetics of corn after seven cycles of selection for lodging resistance. Crop Sci. 22: 1207-1210.
Tollenaar, M. & T.B. Daynard, 1978. Leaf senescence in short-season maize hybrids. Can. J. Plant Sci. 58: 869-874.
Tollenaar, M. & T.B. Daynard, 1982. Effect of source-sink ratio on dry matter accumulation and leaf senescence of maize. Can. J. Plant Sci. 62: 855-860.
Tollenaar, M., T.B. Daynard & R.B. Hunter, 1979. Effect of temperature on rate of leaf appearance and flowering date in maize. Crop Sci. 19: 363-366.
Tollenaar, M. & R.B. Hunter, 1981. Quantification of the effects of temperature and photoperiod on maize development. Agron. Abstr. 1981, Amer. Soc. Agron., p. 14.
Twusami-Afriyie, S. & R.B. Hunter, 1982. Evaluation of quantitative methods for determining stalk quality in short season corn genotypes. Can. J. Plant Sci. 62: 55-60.
Undersander, D.J., L.F. Bauman, V.L. Lechtenberg & M.S. Zuber, 1977. Effect of cyclic selection for high and low crushing strength on rind, pith and whole-stalk composition in corn. Crop Sci. 17: 732-734.
Van Soest, P.J., 1967. Development of a comprehensive system of feed analyses and its application to forages. J. Anim. Sci. 26: 119-128.

Van Soest, P.J., 1976. The estimation of digestibility from chemical composition. In: Carbohydrate research in plants and animals, Misc. papers 12, Agric. Univ., Wageningen, pp. 137-145.

or at the beginning of August. The digestibility of the cell-wall material produced during subsequent ear development is still high at harvest. This cell-wall formation ends during early grain filling. If pollination and grain set are successful, the endosperm cells in the kernels are filled with completely digestible starch. Some of the sucrose necessary to synthesize the starch is produced during grain filling. The remainder comes from the stalk, shank, cob and husks. These plant parts contain considerable pools of previously stored soluble carbohydrates and other compounds. Depending on the rate of photosynthesis, these metabolites are redistributed and used for dry-matter accumulation in the grains. If photosynthesis during grain filling is sufficiently high, the mass fraction of cellular contents in the whole crop increases at such a rate that the decline in cell-wall digestibility is overcompensated. This results in a small increase in digestibility of the whole crop until the rate of photosynthesis becomes so low (because of low light intensity and ageing of leaves) that this increase reverses and becomes a small decrease.

Thus the production of poorly digestible cell-wall components, of very digestible cell-wall components and of wholly digestible cellular contents occurs at different, partly overlapping, stages. Therefore the amounts and nature of these components can be affected separately. The crop's digestibility depends on the cell-wall digestibility and the ratio between cell-wall yield and dry-matter yield. The results of experiments reported in this thesis suggest that the cell-wall digestibility of the whole plant mainly depends on the plant's genotype and physiological age, and on temperature. The mean seasonal temperature does not vary sufficiently to induce year-to-year variation in cell-wall digestibility. Within one hybrid and with normal sowing and harvest dates, digestibility only depends on the ratio of cell wall to cellular contents. This means that digestibility is a rough indicator of the favourableness of the environmental conditions after grain set vis-à-vis the conditions before grain set.

The duration of these two periods is determined by the crop's rate of development. In turn, this rate is affected by environmental conditions and by genotype. Development is often affected by short-lived weather conditions, because certain developmental stages only last a few days or because some transitions in the plant's development are drastic.

In addition to digestibility, dry-matter content is an important quality characteristic, since it influences the processes in the silo and in the ruminant. Development influences the ultimate dry-matter content more

than the ultimate digestibility. Until grain set the amount of water in the crop increases, although the water content slowly decreases. During grain filling the amount of dry matter continues to increase but the crop loses water, especially if the ears are large. The rates of vegetative and reproductive development, the size of the stem and of the ear, and the rates of grain filling, of maturation and of senescence determine the dry-matter content at harvest. The proportion of insoluble dry matter in the fresh stover is probably more important for conservation losses than the dry-matter content of the whole crop. Therefore the intensity of redistribution also plays a role.

The general pattern of production and quality outlined above is based on the results of field and phytotron experiments in which the effects of levels of and of changes in temperature, light intensity and photoperiod on the development, dry-matter production, allocation of dry matter, digestibility and dry-matter content were investigated. In some experiments, genotype and cultivation technique were also varied. The experiments not only increased the understanding about the general pattern of production and quality and the factors influencing this pattern but also yielded information on specific ecophysiological reactions of the maize crop to short-lived changes in weather.

Effects of climatic factors

Temperatures higher than normal during the period before tassel initiation increase forage-maize yields in The Netherlands, since they accelerate the growth of the seedling and therefore boost the productivity later on. High temperatures just before the tassel initiation result in more leaves per plant. A large number of leaves may increase productivity but negatively influences digestibility and dry-matter content. After the initiation of tassel and ears, a rise in temperature causes a rise in the rates of production and of development. As the temperature coefficient of the photosynthetic rate is much lower than that of the rate of development, the ultimate effect on yield is negative, unless the growing season is curtailed, e.g. by frost or low light intensity. Continuously higher temperatures also lower the cell-wall digestibility as a result of increased lignin content and altered physical/chemical structure. The effects of temperature on cell-wall digestibility are much less pronounced if the rises in temperature are only temporary. During certain phases after tassel initiation high temperatures may also have some adverse effects on ear development.

Short periods with low light intensity early in the growing period strongly reduce the dimensions of the stem without reducing ultimate yield or quality. Low light intensity during critical stages of reproductive development undoubtedly has far-reaching repercussions on yield, digestibility and dry-matter content. During grain filling, the reactions of maize to low light can also be dramatic. However,the experiments suggested that after a while adaptation or even recovery is possible. Low light intensity at the end of the season can make the crop more susceptible to *Fusarium*.

Long periods of low light intensity result in large yield depressions. If such periods do not start too early in the growing season, low light intensity also reduces digestibility and retards the dry-down of the crop.

By means of switches in photoperiod applied during early development it appeared to be possible to synchronize or desynchronize vegetative and reproductive development of the main stem and of the ear shoots. Simultaneously, the size of the vegetative and reproductive organs was also affected. Research into the consequences of such effects may be useful to improve the description of an ideotype of forage maize.

Ideal weather conditions in The Netherlands for growing forage maize

The Dutch climate is suitable for the production of high-quality forage maize. However, productivity is severely limited by the low soil and air temperatures in spring and to a smaller extent by the low air temperatures during September and October. During these months, light intensity is more limiting. Because of the prolonged absence of killing frosts, however, yields of forage maize in temperate regions are fairly high. The ideal weather for growing maize in The Netherlands is characterized by sufficient, frequent rainfall (but not too much), high temperatures from sowing to just before tassel initiation and during grain filling, and much irradiance, especially after tassel initiation until harvest.

It seems possible to predict the digestibility of forage-maize crops fairly accurately on the basis of the genotype, crop characteristics and weather.

Ideotype of forage maize for North-West Europe

The ideotype of maize for forage production in North-West Europe shows the following characteristics:

- a good cold tolerance and early vigour and also a good tolerance of high plant densities

- a fast rate of leaf appearance, an excellent stay-green index and the highest possible rate of photosynthesis
- early flowering, a small tassel and a large ear with a slow grain filling
- a stocky stem, with a high proportion of strong pith
- low susceptibility to pests and diseases
- a high potential cell-wall digestibility and a fast rate of cell-wall digestion
- a moderate formation of brace roots.

SAMENVATTING

De opbrengstpotenties van snijmais in Noordwest-Europa zijn gedurende de laatste decennia aanzienlijk gestegen dank zij de introductie van produktievere rassen en door verbetering van teelttechniek. Het kolfaandeel en het gehalte aan droge stof werden voornamelijk verhoogd door wijzigingen in teelttechniek. Nieuw geïntroduceerde rassen bleken daarentegen iets minder goed verteerbaar.

Fundamenteel inzicht in het produktiepatroon en het verloop van de verteerbaarheid en van het droge-stofgehalte bij snijmais en in de factoren, die daarbij een rol spelen, ontbreekt echter nog goeddeels. In dit proefschrift wordt onderzoek besproken dat tot doel had dit inzicht te vergroten.

Produktiviteit in het algemeen

Mais heeft een aantal ecofysiologische eigenschappen, die er de oorzaak van zijn, dat het gewas zich in het in Noordwest-Europa heersende klimaat niet optimaal kan ontwikkelen. Van deze eigenschappen is vooral het thermofiele karakter van de plant van belang. Bodem- en luchttemperaturen gedurende de eerste weken na inzaai zijn van doorslaggevende betekenis voor de uiteindelijke opbrengst. Nadien is de produktie sterk afhankelijk van temperatuur, lichtintensiteit en vochtvoorziening. Deze factoren bepalen zowel de produktiesnelheid als de duur van de produktieve periode. Vooral de omstandigheden tijdens de bloei en de lichtintensiteit na de bloei zijn vaak beperkend voor (het instandhouden van) de produktiviteit. De weersomstandigheden in Nederland zijn in het algemeen gunstiger tijdens de tweede helft van de vegetatieve groei en de ontwikkeling van de bloeiwijzen dan tijdens de bevruchting, zetting en vulling van de korrels.

Algemeen patroon van groei, ontwikkeling en kwaliteit

De vorming en uitgroei van bovengrondse vegetatieve delen vinden plaats van opkomst (medio mei) tot enige weken na de vrouwelijke bloei. Deze periode gaat gepaard met de opbouw van stevigheidsweefsel dat in de loop van het groeiseizoen steeds slechter verteerbaar wordt. Als de vegetatieve delen uitgegroeid zijn, houdt de vorming van slecht verteerbaar structuurweefsel in deze delen op, maar de kwaliteit van de celwanden blijft langzaam achteruitgaan.

De groeipunten van hoofdas en zijassen worden eind mei of begin juni

generatief. De pluim en de kolf ontwikkelen zich vervolgens en bloeien eind juli of begin augustus. De daaropvolgende ontwikkeling van de kolf gaat gepaard met de vorming van structuurweefsel dat ook bij de oogst nog goed verteerbaar is. Deze celwandvorming houdt tijdens het begin van de korrelvulling op. Als de bevruchting en korrelzetting geslaagd zijn, worden de endospermcellen in de korrels gevuld met volledig verteerbaar zetmeel. De sucrose die nodig is voor de vorming van zetmeel, wordt deels tijdens de korrelvulling geproduceerd en is deels afkomstig uit de stengel, de kolfsteel, de kolfspil en de schutbladen. In deze organen worden onder gunstige omstandigheden aanzienlijke voorraden oplosbare assimilaten opgeslagen. Afhankelijk van de fotosynthesesnelheid tijdens de korrelvulling worden deze assimilaten geredistribueerd en aangewend voor de korrelgroei. Bij voldoende hoge produktie tijdens de korrelvulling neemt het gehalte aan structuurweefsel zo snel af dat daarmee de afname van verteerbaarheid van dit weefsel meer dan gecompenseerd kan worden. Het resultaat is dat de verteerbaarheid van de hele plant na de bloei iets toeneemt totdat de produktiesnelheid in oktober tengevolge van de lage lichtintensiteit of de veroudering van het blad zo laag is dat een geringe afname van de verteerbaarheid weer mogelijk is.

De perioden waarin slecht verteerbare celwanden, goed verteerbare celwanden of volledig verteerbare bestanddelen van de celinhoud gevormd worden, vallen dus voor een deel niet samen en zijn verschillend van duur. De hoeveelheid en kwaliteit van deze bestanddelen zijn dan ook deels afzonderlijk te beïnvloeden. De verteerbaarheid van een gewas is afhankelijk van de verteerbaarheid van de celwandbestanddelen en de verhouding tussen celwandopbrengst en droge-stofopbrengst. Uit de in dit proefschrift beschreven proeven komt naar voren dat de celwandverteerbaarheid van het hele gewas vooral afhankelijk is van het genotype en de fysiologische ouderdom van de plant en de temperatuur. De gemiddelde temperatuur tijdens het groeiseizoen vertoont te weinig variatie om jaarverschillen in celwandverteerbaarheid te veroorzaken. Binnen één hybride en bij normale zaai- en oogsttijdstippen is de verteerbaarheid dus afhankelijk van de gewichtsverhouding tussen structuurweefsel en celinhoud. Grofweg betekent dit dat de verteerbaarheid aangeeft hoe gunstig de produktieomstandigheden na de korrelzetting waren ten opzichte van die voor de korrelzetting.

De duur van deze beide perioden wordt bepaald door de ontwikkelingssnelheid van het gewas. Deze snelheid wordt op haar beurt weer beïnvloed door milieufactoren, maar ook door genotype. Omdat bepaalde ontwikkelingsstadia slechts enkele dagen duren of omdat sommige overgangen abrupt zijn, wordt de ontwikkeling

vaak beïnvloed door het weer van slechts enkele dagen.

Naast verteerbaarheid is het droge-stofgehalte een belangrijk kwaliteitskenmerk, omdat daardoor de processen in de silo en in de herkauwer beïnvloed worden. Het uiteindelijke droge-stofgehalte is veel afhankelijker van de ontwikkeling dan de uiteindelijke verteerbaarheid. Tot aan de korrelzetting neemt de hoeveelheid water in de bovengrondse delen toe, hoewel het vochtgehalte langzaam daalt. Daarna neemt de hoeveelheid droge stof nog steeds toe, maar het gewas verliest water, vooral als er forse kolven ontwikkeld zijn. De snelheid van vegetatieve en generatieve ontwikkeling, de omvang van stengel en kolf en de snelheid van korrelvulling, afrijping en afsterving bepalen het droge-stofgehalte bij de oogst. Het gehalte aan onoplosbare droge stof in de verse massa van de vegetatieve delen is waarschijnlijk belangrijker voor conserveringsverliezen dan het droge-stofgehalte van het hele gewas. Daarom speelt ook de mate van droge-stofredistributie een rol.

Het hierboven beschreven algemene beeld van produktie en kwaliteit is gebaseerd op de resultaten van veld- en fytotronproeven, waarin de effecten van niveau van en veranderingen in temperatuur, lichtintensiteit en daglengte op de ontwikkeling, droge-stofproduktie, droge-stofverdeling, de verteerbaarheid en het droge-stofgehalte werden onderzocht. Tevens werd in enkele proeven het ras of de teelttechniek gevarieerd. Deze proeven leverden inzicht in het algemene patroon van produktie en kwaliteit en in de factoren die daarop van invloed zijn. Er werd ook informatie verkregen over specifieke ecofysiologische reacties van een maïsgewas op tijdelijke veranderingen in klimaatsfactoren.

Effecten van klimaatsfactoren

Hogere temperaturen dan normaal tijdens de periode voor de pluimaanleg verhogen de opbrengst van snijmais in Nederland sterk, omdat zij de groei van de zaailing versnellen en de produktiviteit later in het groeiseizoen bevorderen. Hogere temperaturen kort voor de pluimaanleg leiden tot meer bladeren. Een groter aantal bladeren kan opbrengstverhogend werken, maar heeft een negatieve invloed op verteerbaarheid en droge-stofgehalte. Nadat de pluim en de kolven geïnitieerd zijn, leidt een verhoging van de temperatuur tot een verhoging van de produktiesnelheid en een versnelling van de ontwikkeling. Omdat de temperatuurcoëfficiënt van de fotosynthesesnelheid veel lager is dan van de ontwikkelingssnelheid is het uiteindelijke effect op de opbrengst negatief, tenzij het groeiseizoen aan het einde duidelijk begrensd wordt, bijvoorbeeld door nachtvorst of lage lichtintensiteit. Permanent hogere temperaturen leiden ook tot een lagere verteerbaarheid van de celwanden van-

wege een hoger ligninegehalte en een veranderde fysisch-chemische structuur. Dit effect van temperatuur op de celwandverteerbaarheid is veel minder uitgesproken wanneer er slechts sprake is van een tijdelijke verhoging van de temperatuur. Hoge temperaturen na pluimaanleg kunnen in verschillende gewasstadia ook negatief werken op de ontwikkeling van de kolf.

Korte perioden met weinig licht vroeg in het groeiseizoen reduceren sterk de afmetingen van de stengel zonder dat ze de uiteindelijke opbrengst en kwaliteit verlagen. Weinig licht tijdens cruciale momenten in de generatieve ontwikkeling heeft wel verregaande consequenties voor zowel opbrengst als verteerbaarheid en droge-stofgehalte. Tijdens de korrelvulling kan maïs ook nog zeer heftig reageren op verminderde instraling. Uit sommige proeven bleek echter dat na verloop van tijd een opvallende aanpassing of zelfs herstel mogelijk is. Lage lichtniveaus aan het eind van de veldperiode kunnen de gevoeligheid voor *Fusarium* sterk vergroten.

Langere perioden met een lage lichtintensiteit geven grote opbrengstdepressies. Mits niet te vroeg in het groeiseizoen begonnen, verlagen dergelijke condities de verteerbaarheid en vertragen het waterverlies van het gewas.

Met behulp van daglengteveranderingen in het voorjaar bleek het mogelijk de vegetatieve en generatieve ontwikkeling van de hoofdas en van de (kolfdragende) zijassen meer of minder synchroon te laten verlopen. Tegelijkertijd wordt dan ook de omvang van de vegetatieve en reproductieve organen beïnvloed. Onderzoek naar de consequenties van dergelijke effecten kan behulpzaam zijn bij het verbeteren van de ideotypebeschrijving van snijmaïs.

Het ideale weer voor de snijmaïsteelt in Nederland

Het Nederlandse klimaat is geschikt voor de produktie van snijmaïs met een hoge voederwaarde. De produktiviteit wordt echter ernstig belemmerd door de lage bodem- en luchttemperaturen in het voorjaar en de lage luchttemperatuur in het najaar. In september en oktober is de lichtintensiteit echter sterker beperkend dan de temperatuur. Omdat de eerste schadelijke nachtvorsten gewoonlijk pas laat in het najaar optreden, is het groeiseizoen in de gematigde gebieden lang; daardoor zijn hoge droge-stofopbrengsten toch mogelijk. Het ideale weertype voor maïs in Nederland wordt gekenmerkt door voldoende (maar niet te veel) en regelmatig verdeelde neerslag, hoge temperaturen vanaf inzaai tot vlak voor de pluimaanleg en tijdens de korrelvulling, en veel straling, vooral vanaf de pluimaanleg tot aan de oogst.

Het lijkt mogelijk op grond van het geteelde ras, gewaskenmerken en het weer de verteerbaarheid van snijmaïs met een redelijke betrouwbaarheid te

voorspellen.

Ideotype van snijmaïs voor Noordwest-Europa

Het ideotype van maïs voor de snijmaïsteelt in Noordwest-Europa bezit de volgende eigenschappen:

- goede koudetolerantie en "early vigour", alsmede een goede tolerantie voor hoge standdichtheden
- snelle bladafsplitsing, lang groenblijvend bladapparaat en de hoogst mogelijke fotosynthesesnelheid
- vroege bloei, een kleine pluim en een grote kolf met een lage korrelvullingssnelheid
- een korte, dikke stengel met veel en stevig merg
- geringe vatbaarheid voor ziekten en plagen
- een hoge verteringssnelheid en verteerbaarheid van de celwanden
- een beperkte vorming van steunwortels.