

**Grain production and
assimilate utilization of wheat
in relation to cultivar characteristics,
climatic factors and nitrogen supply**

J.H.J. Spiertz



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Proefschrift

ter verkrijging van de graad van
doctor in de landbouwwetenschappen,
op gezag van de rector magnificus,
dr. H.C. van der Plas,
hoogleraar in de organische scheikunde,
in het openbaar te verdedigen
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Abstract

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The effects on grain production of cultivar characteristics, nitrogen supply and some climatic factors were studied in field trials and under controlled environmental conditions. A rise in temperature considerably increased the rate of grain growth but shortened its duration, whilst the positive effect of light intensity on the grain yield was greater at high temperatures.

Additional nitrogen raised post-floral photosynthesis. The nitrogen assimilation by the grains was increased by warmth, resulting in a higher nitrogen concentration of the grains and in earlier senescence of the leaves. Differences between a semi-dwarf cultivar and a standard were mainly expressed in the dry matter distribution before and after anthesis and so in a higher harvest-index.

Free descriptors: *Triticum aestivum* L., wheat, leaf area duration, crop photosynthesis, grain growth, water-soluble carbohydrates, nitrogen uptake, grain protein, grain yield, harvest-index, temperature, light intensity, semi-dwarf cultivar.

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Stellingen

1. Hoge temperaturen versnellen de groei van de tarwekorrel, maar bekorten de levensduur van de tarwehalm; het effect op de korrelopbrengst is afhankelijk van de hoeveelheid ingestraalde zonne-energie.

Dit proefschrift.

2. De groeisnelheid van de korrels in de eerste weken na de bloei wordt veelal niet beperkt door de beschikbaarheid van assimilaten, maar bepaald door de temperatuur.

Dit proefschrift.

3. Bij tarwe wordt de afrijping van de korrel hormonaal gestuurd, terwijl de afsterving van vegetatieve organen meestal een gevolg is van een negatieve eitwit- en/of koolhydratenbalans.

R.W. King, 1976. *Planta* (Berlin) 132: 43-51.

T.R. Sinclair & C.T. de Wit, 1975. *Science* 189: 565-567.

4. Bij de huidige tarwerassen is een hoog korrelaantal per m² (> 20 000) noodzakelijk om maximale korrelopbrengsten te verkrijgen, daar de toename van het individuele korrelgewicht genetisch begrensd is.

P.M. Bremner & H.W. Rawson, 1978. *Aust. J. Pl. Physiol.* 5: 61-72.

A. Darwinkel, 1978. *Neth. J. agric. Sci.* 26 (in press).

5. De conclusie dat door stikstofgebrek in tarweplanten de ademhalingsverliezen zowel relatief als absoluut toenemen, is strijdig met de huidige inzichten in de fysiologie van de assimilatenhuishouding van granen.

K. Orlovius & W. Höfner, 1976. *Z. Pflernähr. Bodenk.* 5: 631-640.

I. Pearman, Susan M. Thomas & Gillian N. Thorne, 1977. *Ann. Bot.* 41: 93-108.

F.W.T. Penning de Vries, 1974. *Neth. J. agric. Sci.* 22: 40-44.

6. Bij tarwe en gerst zijn de stikstofopname per halm en de harvest-index voor stikstof betere selectiecriteria voor eiwitopbrengst per ha dan het eiwitgehalte van de korrels.

7. Rassenmengsels bieden meer mogelijkheden tot het vergroten van de ziekeresistentie in een graangewas dan een 'multiline' (menggras).

8. Het eenzijdige teeltsysteem in de Veenkoloniën heeft een te grote ecologische instabiliteit om opbrengstdervingen door ziekten uitsluitend met een intensiever gebruik van gewasbeschermingsmiddelen te voorkomen.

9. In de nota Landelijke Gebieden wordt er ten onrechte aan voorbijgegaan dat een 'aangepaste' ontwikkeling van landbouwbedrijven een grotere bijdrage levert aan de instandhouding van karakteristieke cultuurlandschappen dan een conserverende natuurbescherming.

Nota Landelijke Gebieden, 1977. Ministerie van Volkshuisvesting en Ruimtelijke Ordening.

10. Bij het vergroten van de mobiliteit van onderzoekers wordt in de nota van de Raad van Advies voor het Wetenschapsbeleid te veel waarde gehecht aan verandering van werkring en in de praktijk te weinig gebruik gemaakt van 'mobiele' inter- en extra-institutionele onderzoekteams.

Nota: De mobiliteit van wetenschappelijke onderzoekers, september 1976. Advies van de Raad van Advies voor het Wetenschapsbeleid (RAWB) aan de Minister van Wetenschapsbeleid.

11. Het itereren van beleidsadviezen over een lange keten van adviserende organen ontkracht de inhoud van adviezen, schaadt de besluitvaardigheid en verhult de verantwoordelijkheid van bestuurderen.

12. Alternatieve levens- en maatschappijbeschouwingen zijn een onvoldoende basis voor het ontwikkelen van 'alternatieve' landbouwmethoden die werkelijk een alternatief bieden voor de 'gangbare' landbouw.

Proefschrift van J.H.J. Spiertz

Grain production and assimilate utilization of wheat in relation to cultivar characteristics, climatic factors and nitrogen supply.

Wageningen, 10 november 1978

Woord vooraf

Het onderzoek dat de basis vormde voor dit proefschrift, was onderdeel van een breder onderzoekprogramma op het gebied van produktiepatronen bij granen dat uitgevoerd werd bij de Vakgroep Landbouwplantenteelt en Graslandcultuur. Verscheidene medewerkers van deze vakgroep en studenten hebben direct of indirect in belangrijke mate aan mijn onderzoek bijgedragen. Voor de medewerking en belangstelling wil ik hen gaarne danken. Speciaal richt ik me tot Johan Ellen, met wie ik vanaf de start van het onderzoek heb samengewerkt; door jouw inzet en kundigheid heb je veel bijgedragen aan het onderzoek.

Prof. 't Hart en ir. Kupers, u ben ik zeer erkentelijk voor het vertrouwen en de ruimte die u mij geboden heeft bij het functioneren binnen en buiten de vakgroep. Het proefschrift is tot stand gekomen mede dank zij uw aanhoudende stimulans.

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Ir. Wansink, secretaris van de Nationale Raad voor Landbouwkundig Onderzoek, gaf mij de ruimte om in een periode van 'non-actief' bij de vakgroep toch actief betrokken te blijven bij de voortgang van het onderzoek. De tijdelijke personele ondersteuning door ir. Jan Vos heeft zelfs geleid tot een nieuw project waarin meer aandacht wordt gegeven aan de kwantitatieve betekenis van de ademhalingsprocessen voor de korrelgroei bij tarwe.

Dr. Gaastra, directeur CABO, gaf voorrang aan de afronding van het proefschrift in mijn nieuwe functie.

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Martha van Rinssum verrichtte op een zeer drukke post steeds voortreffelijk typewerk;

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De redacteuren van de Netherlands Journal of Agricultural Science, dr. van den Bergh en ir. Dirven, en de bureau-redacteur, de heer Van der Heij, maakten een tijdige plaatsing van de artikelen mogelijk. De heren Aalpol en Van den Heuvel van het Pudoc verzorgden de redactie van het proefschrift, terwijl mevrouw Brouns de correctie van de Engelse tekst van de 'omlijstende' hoofdstukken voor haar rekening nam.

Curriculum vitae

De auteur werd op 25 april 1941 geboren te Jabeek en behaalde in 1959 het diploma HBS-B aan het lyceum St.-Jan te Hoensbroek. Van 1959 tot 1967 studeerde hij aan de Landbouwhogeschool te Wageningen met als studierichting Akker- en Weidebouw; het doctoraal-examen omvatte de vakken: landbouwplantenteelt, algemene bodemkunde en bemestingsleer, bijzondere landhuishoudkunde en landbouwwerktuigkunde. In januari 1967 behaalde hij het ingenieursexamen met pedagogisch-didactische aantekening.

Tijdens zijn doctoraalstudie gaf hij les aan de Middelbare Landbouwschool te Cuyk. Van februari 1967 tot april 1978 was hij verbonden aan de Landbouwhogeschool. Zijn werkzaamheden bij de vakgroep Landbouwplantenteelt en Graslandcultuur betroffen enerzijds onderzoek en doctoraalonderwijs in de ecofysiologie van de zaadproductie bij grassen en granen, en anderzijds organisatorische functies voornamelijk in verband met de opeenvolgende herprogrammeringen, zoals secretaris van de richtingsonderwijscommissie (ROC) en studiecoördinator van de studierichting Landbouwplantenteelt.

Ook in het bredere kader van de Landbouwhogeschool werd een aantal organisatorische functies vervuld: onder meer lid Studieraad, lid Hogeschoolraad, voorzitter Cie Planning Postsecundair Onderwijs, voorzitter Cie Hoger Onderwijs in de Toekomst en voorzitter Cie Onderwijs en Wetenschappen. Vanwege laatstgenoemde functie werd deelgenomen aan het overleg in de Cie Algemene Vraagstukken Wetenschappelijk Onderzoek (CAVWO) van de Academische Raad.

Buiten de Landbouwhogeschool werd van 1975 tot en met 1977 medegewerkt aan de opbouw van een overlegstructuur voor het Plantaardig-Productie-Onderzoek in het kader van de Nationale Raad voor Landbouwkundig Onderzoek.

Sinds april 1978 is hij werkzaam bij het Centrum voor Agrobiologisch Onderzoek (CABO) te Wageningen.

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Relation between green area duration and grain yield in some varieties of spring wheat

J.H.J. Spiertz, B.A. ten Hag and L.J.P. Kupers, Netherlands Journal of Agricultural Science 19 (1971): 211-222

Effects of successive applications of maneb and benomyl on growth and yield of five wheat varieties of different heights

J.H.J. Spiertz, Netherlands Journal of Agricultural Science 21 (1973): 282-296

Grain growth and distribution of dry matter in the wheat plant as influenced by temperature, light energy and ear size

J.H.J. Spiertz, Netherlands Journal of Agricultural Science 22 (1974):207-220

The influence of temperature and light intensity on grain growth in relation to the carbohydrate and nitrogen economy of the wheat plant

J.H.J. Spiertz, Netherlands Journal of Agricultural Science 25 (1977):182-197

Effects of nitrogen on crop development and grain growth of winter wheat in relation to assimilation and utilization of assimilates and nutrients

J.H.J. Spiertz and J. Ellen, Netherlands Journal of Agricultural Science 26 (1978): 210-231

Cultivar and nitrogen effects on grain yield, crop photosynthesis and distribution of assimilates in winter wheat

J.H.J. Spiertz and H. van de Haar, Netherlands Journal of Agricultural Science 26 (1978): 233-249

1 Introduction

1.1 GENERAL

Wheat is among the most important crops for world food and feed supply (Table 1). Much wheat is grown under seasonal conditions comparable with those in which it evolved. In Mediterranean climates, vegetative development and ear initiation occur on cool, short winter days. Ear differentiation takes place under conditions of increasing daylength and temperature, while grain filling occurs under conditions of high solar radiation and warmth. In maritime climates at moderately high latitudes, as in Western Europe, ear differentiation takes place under long and still increasing daylengths, but often with relatively low temperatures and poor light conditions. During grain filling, mostly after midsummer, average day temperatures are moderate. However, due to annual and seasonal variations the temperature range is quite large. Under more continental climates, the winter wheat crop is exposed to extreme low temperatures during the winter period and to

Table 1. Acreage, yield and production of arable crops. Source: FAO-Yearbook, 1975.

Crop		Acreage (x 1000 ha)	Yield (kg/ha)	Production (x 1000 ton)
Wheat	World	228169	1557	355172
	Europe	25864	3025	78245
Rice	World	140880	2441	343871
	Europe	380	4987	1893
Maize	World	114534	2816	322536
	Europe	12079	3842	46406
Barley	World	91504	1695	155083
	Europe	19038	3056	58187
Millet	World	71354	657	46871
	Europe	24	1340	32
Pulses	World	69560	661	45995
	Europe	4326	641	2774
Soybeans	World	46463	1971	68356
	Europe	323	1369	442
Sorghum	World	44599	1203	53632
	Europe	134	3563	477
Oats	World	31644	1549	49007
	Europe	6446	2617	16870
Potatoes	World	21783	13374	291321
	Europe	6400	18247	116784
Rye	World	15021	1601	24044
	Europe	5389	2406	12966
Sugar cane	World	12681	50268	637427
	Europe	5	64585	342
Cassava	World	11551	9108	105209
	Europe	-	-	-
Sugarbeet	World	8892	28097	249851
	Europe	3716	35301	131175

heat and drought during grain filling in midsummer. Thus the wheat plant has been adapted by selection to a wide range of climatic conditions, especially to variations in temperature and daylength.

As Evans & Wardlaw (1976) stated there have been fashions in the emphasis on which physiological process limits cereal yield and also on the stage of the crop life cycle regarded as most critical. Early studies by agronomists to gain insight into the factors and processes that determine grain yields were based on yield component analysis (Engledow & Wadham, 1923). Later growth analyses in terms of dry weight increase per unit leaf area became an important research tool. Growth analysis of cereals were initiated and promoted by Watson and co-workers at Rothamsted Experimental Station, England. They introduced the concept of leaf area index (LAI), which is defined as the ratio of foliage area to ground area. This is considered as an important growth parameter for determining yield in relation to environmental factors (Watson, 1952). The main results of this approach were summarized by Thorne (1965).

In subsequent years much more emphasis has been given to the final stage of the cereal life cycle; various research workers (Birecka & Dakic-Wlodkowska, 1964; Stoy, 1965; Thorne, 1966) have demonstrated that grain growth largely depends on post-floral assimilation. Then grain yield was assumed to be limited primarily by photosynthesis and the supply of assimilates. Thus, particular attention was given to crop photosynthesis throughout the grain-filling period as a major determinant of grain yield (Puckridge, 1971; Baldy, 1972; Lupton, 1969; Apel et al., 1973; Austin et al., 1977; de Vos, 1977). More recently, however, much evidence has been found to show that the capacity of the grain to store assimilates may limit yield just as much as the capacity of the crop to provide the grains with assimilates does (Bremner, 1972; Rawson et al., 1976; Fischer et al., 1977). Other crop physiologists have given more attention to processes such as assimilate transport (Jenner & Rathjen, 1975; Wardlaw, 1968) and hormonal regulation of grain growth (Radley, 1976; Goldbach & Michael, 1976; King, 1976).

An early, more comprehensive whole-plant physiological approach of grain production in wheat was chosen by Miller (1939) and by Stoy (1965). This whole-plant approach was also followed in my study of the effects of climatic factors and nitrogen supply on grain production in contrasting wheat cultivars.

1.2 PURPOSE OF STUDY

The sequence of experiments can be classified in three groups. The aim of the first group of experiments was to study:

- the relation between green area duration and grain yield, considering the various green organs of the wheat plant and differences between cultivars;
- the influence of a prolonged green area duration on grain growth and yield, by means of late nitrogen applications and disease-control with fungicides.

These experiments were carried out in the field.

After some preliminary shading experiments in the field a second group of experiments, carried out in a controlled environment, were directed to study the effects of light

intensity and temperature on rate and duration of grain growth and consequently on assimilation and utilization of carbohydrates and nitrogen compounds. A sink-source approach was included in the analysis of plant behaviour.

A third group of experiments was carried out in the field under the favourable soil conditions of the Flevopolder. The aim of these experiments was to analyse:

- the significance of annual variations in climatic factors for the pattern of grain production;
- the effect of various nitrogen treatments on crop development, grain growth and on production and utilization of assimilates and nutrients;
- the effect of cultivar differences on dry matter distribution (carbohydrate and nitrogen economy) in relation to the pattern of grain production and grain yield.

The field experiments were carried out at the experimental farms of the Agricultural University in the Flevopolder and in Wageningen. The experiments under controlled environmental conditions were done in the phytotron of the Department of Field Crops and Grassland Husbandry of the Agricultural University at Wageningen.

1.3 LITERATURE

The developments in the various fields of crop physiology concerning grain production of cereals are covered by the following reviews: Baldy (1972, 1973), Thorne (1974), Evans et al. (1975), Austin & Jones (1976), Evans & Wardlaw (1976) and Biscoe & Gallagher (1977).

Since there are extensive reviews on more general aspects, the following review just gives a background for the experimental work presented in Chapter 3. The most recent literature has been partly included in this chapter and partly in the General discussion (Chapter 4).

1.3.1 *Growth of vegetative organs*

The vegetative phase of the wheat plant extends from shoot emergence to ear initiation, but growth of some vegetative organs (e.g. roots, top leaves and stem) continues until anthesis and afterwards. In the early vegetative phase leaf and root growth predominate. Root growth may exceed shoot growth at low temperatures (Welbank, 1971), but as temperature rises the growth of shoots increases more than that of roots (Brouwer, 1966). Shoot growth thus appears to have a higher optimum temperature than root growth; this difference may result from increased competition for assimilates between root and shoot at higher temperatures (Friend, 1966). Low light intensities reduce root growth and tillering (Baldy, 1973). Similarly, limited nitrogen supply may reduce shoot growth, but increase root extension and the ratio root:shoot (Brouwer, 1966). Lower root numbers caused by nitrogen deficiency are compensated by greater lateral lengths in the seminal but not the nodal root systems (Tennant, 1976).

Usually growth of the root system continues until heading, after which root growth may cease and roots may even degenerate during the grain-filling period (Welbank, 1971). With an adequate water and nutrient supply, however, root growth and nutrient uptake

continue well into the grain-filling period (Campbell et al., 1977).

The rate of leaf formation as well as the size of the mature lamina depend on temperature, light intensity, daylength and nutritional status under which the plant is grown (Watson, 1971; Friend & Helson, 1976). Maximum leaf area per shoot is attained when the flag leaf has fully emerged (Watson et al., 1963; Puckridge, 1971). Leaf arrangement is an important aspect of canopy structure. Leaves formed prior to ear initiation originate close to the crown, but elongation of stem internodes separates the leaves in the vertical plane, leading to a more effective light distribution within the canopy.

Throughout the early life of the wheat plant, the leaf blades are the main photosynthetic organs and crop growth rate depends both on the rate of expansion of leaf area and the rate of photosynthesis per unit leaf area. The increase of the leaf area index (LAI) is closely paralleled by the increase in canopy photosynthesis (Puckridge, 1971). Towards the end of the life cycle, photosynthesis by the stems, leaf sheaths and ears tends to become increasingly important as the leaves senesce (Austin et al., 1976).

The stem grows concurrently with the leaves, roots and ear; rapid ear growth coincides with that of the top internodes (Wardlaw, 1974). Consequently, growth of the stem under limiting substrate conditions may compete with that of the ear (Rawson & Hofstra, 1969; Patrick, 1972).

1.3.2 Growth and development of the ear

The double-ridge stage is usually considered as a key stage in the development of the wheat plant, by marking the end of vegetative development and the beginning of ear development. Kirby (1974) suggested that ear development can be described quantitatively in terms of (a) the rate of spikelet initiation, (b) the duration of spikelet initiation and (c) the total number of primordia. Both leaf and spikelet initiation proceed at more or less constant rates, but spikelets initiate considerably faster than leaves. The rate of ear development is affected by light intensity, daylength and temperature (Friend et al., 1963; Puckridge, 1968; Rawson, 1970; Lucas, 1972). The number of fertile spikelets formed increases with higher light intensities (Friend, 1965); at high planting densities and in densely tillered stands, therefore, the number of fertile spikelets may be reduced by mutual shading. Nitrogen may affect spikelet number, but only when applied before the stage of ear initiation; late nitrogen dressings may increase the number of florets per spikelet (Langer & Liew, 1973). After the terminal spikelet has been formed, environmental conditions no longer influence spikelet number, but they may affect the number of florets differentiated within each spikelet (Kirby, 1974).

Differentiation of the spikelet primordia starts in the spikelets in the lower-mid part of the ear. A maximum of nine florets per spikelet may be formed, though some of the last-formed primordia do not produce fertile florets (Kirby, 1974). High temperatures at anthesis may cause sterility and it appears that pollen development is particularly sensitive to water stress and high temperatures (Fischer, 1973). Seed set is promoted by high light intensity during fertilization (Wardlaw, 1970) and is very susceptible to water stress (Asana & Saini, 1962). However, many other factors such as the position on the ear, may also affect the number of grains set (Rawson & Evans, 1970; Bremner, 1972).

After cell wall formation, the endosperm increases rapidly in cell number and size (Wardlaw, 1970). Sofield et al. (1977) found a rapid increase in the amount of water in the grains during the period of active cell division and expansion of the endosperm, after which there was little net change in the amount of water until completion of dry weight accumulation. Starch storage begins one to two weeks after anthesis, depending on temperature. In the grain-filling period, in which most of the dry matter of the grain is accumulated, grain volume continues to increase but at a reduced rate. From the beginning of starch synthesis onwards there is a period of almost linear increase in dry weight, followed by an asymptotic increase to final grain weight. In this last phase, the amount of water of the grains decreases and grain growth stops at about 40% water in the grain (Jennings & Morton, 1963; Sofield et al., 1977). We do not know yet whether the decrease in grain water content at maturity causes or is a consequence of the cessation of grain growth. Radley (1976) suggested that the initiation of water loss from the grain at maturation might result from an increase in the permeability of the pericarp. However, Sofield et al. (1977) concluded that grain growth was terminated by blockage of the transport system by lipids. Other authors suggested that the accumulation of abscisic acid in the grain affects its maturation (Goldbach & Michael, 1976; King, 1976; Radley, 1976).

Temperature has a pronounced effect on the rate and duration of grain-filling (Campbell & Read, 1968). In the experiments of Asana & Williams (1965) the main effect was due to day temperature, but Peters et al. (1971) found that a rise in night temperature shortened the period of grain filling drastically. Phytotron experiments have shown, however, that it is daily temperature that has a predominant effect on duration of grain filling (Sofield et al., 1974; Spiertz, 1974; Warrington et al., 1977).

Grains in different positions within an ear grow at different rates and have different mature grain weights. Grains in second florets begin later but may grow faster and attain a larger weight than those in basal florets (Rawson & Evans, 1970; Bremner, 1972); grain weight decreases from the second floret to the apical floret. Grains in the upper spikelets grow more slowly than those in the central spikelets; when the supply of assimilate from the leaves is reduced by defoliation or shading, grain growth is most severely reduced in the upper spikelets (Bremner, 1972).

Final grain size depends to some extent on the number of grains per ear. Bingham (1967) found that the weight of grains in specific position increases as grain number per ear decreases. This observation suggests that grain growth may have been limited also by the supply of assimilates. However, grain yield per ear fell considerably as the grain number was reduced, indicating a restricted compensation capacity of the remaining grains.

1.3.3 *Source - sink relations and the distribution of assimilates in the wheat plant*

The terms 'source' and 'sink' are often used rather loosely and with various meanings. Warren Wilson (1972) suggested that sources and sinks should be defined in terms of losses and gains of a particular substance in a particular plant part. Other authors prefer a definition in metabolic terms, such as:

- sources produce assimilates by assimilation of carbon and nitrogen compounds or by mobilization of stored materials, while

- sinks utilize assimilates in growth of structural and storage material and in respiration. Thus the regions of production and consumption of assimilates in the plant are referred to as 'source' and 'sink', respectively (Wareing & Patrick, 1975).

Usually in cereals the grains are considered as sink and the photosynthetic active parts of the plant as source. This concept is an oversimplification because there are alternative sinks in the wheat plant (stem, roots, tillers). However their priority and capacity for utilization of assimilates is lower than for the ear. Rawson et al. (1976) found that the response of leaf photosynthesis to the level of assimilate requirement by the ear was influenced by the treatment of the vegetative tillers. Thus, the net photosynthesis rate of the flag leaf was decreased by a reduction in grain number or increased by inhibition of photosynthesis in the ear, only when the vegetative tillers were kept defoliated; when these tillers were allowed to grow normally, there was no influence of ear treatment on leaf photosynthesis. This observation might explain the contrast between the findings of King et al. (1967) and others, who observed a strong dependence of the rate of photosynthesis in the flag leaf of wheat on the level of requirement for assimilate by the developing grains, and the studies by Apel et al. (1973) and Austin & Edrich (1975) in which photosynthesis was independent of the level of assimilate requirement.

A close correlation between final grain yield and various parameters of leaf area after anthesis (Welbank et al., 1966; Simpson, 1968), together with the fact that most of the dry matter in cereal grains is photosynthesized after anthesis (Thorne, 1965) have frequently led to the conclusion that grain yield is limited by the supply of photosynthate during grain filling. This conclusion may not be made if initial ear size or potential grain size is correlated with leaf area at anthesis and with leaf longevity. Treatments involving partial defoliation (Boonstra, 1929) or partial grain removal and inhibition of grain set (Bingham, 1967) usually lead to disproportionately small effects on final yield owing to photosynthetic or yield component compensation, respectively.

Reviewing the literature, Gifford (1974) concluded that source and sink limitations usually co-exist and are only partial limitations. However, Stoy (1977) emphasized that the photosynthetic performance of the sources as well as subsequent partitioning of the assimilates obviously are controlled mainly by the metabolic activity of the sinks. Stoy's conclusion might refer especially to the first weeks of grain growth when a pool of readily mobilisable reserves, mainly in the stem, may compensate for short-term deficiencies in photosynthetic capacity. During the second half of the grain-filling period, the interaction between environment and genotype might determine the rates of leaf senescence and grain maturation and so the relative limitation by source or sink capacity. Constraints on water and nutrient supply affect photosynthetic capacity of the leaves more than the storage capacity of the grains, which is reflected by a fast depletion and relocation of carbohydrate reserves from the stem (Asana & Saini, 1962; Gallagher et al., 1976), and of nitrogen compounds, mainly from the leaves (Campbell & Read, 1968).

The distribution of dry matter between the various parts of the wheat plant has been considered to be constant within a specific development phase (van der Sande Bakhuyzen, 1937). The initial interdependence between roots and leaves is disturbed from ear initiation

onwards. Successively stem, ear and developing grains become major sinks for carbohydrates and nitrogen compounds. Recently Sinclair & de Wit (1975) made a comparative analysis of photosynthate and nitrogen requirements in the production of grains by various crops. They concluded that the requirement for nitrogen by the grain, especially with high protein grains, was so great that mostly nitrogen must be translocated from the vegetative plant tissue to the kernels to sustain grain growth. A rapid loss of nitrogen from the vegetative organs of the plant could cause a decline in physiological activity and thereby limit the length of the grain-filling period. Periodic analysis of the changes in nitrogen content of the various parts of the wheat culm showed a loss of nitrogen from the leaves and stem concomitant with an increase in grain nitrogen (van der Sande Bakhuyzen, 1937; Williams, 1955).

The increase in the amount of grain nitrogen, however, frequently exceeds the loss by the leaves and stem during grain development. The balance of grain nitrogen must therefore come from nitrogen reserves in the roots or from current root uptake. Depletion of the leaf nitrogen pools leads to a progressive leaf senescence from the base to the top of the wheat culm. Thus a balanced nitrogen economy of the wheat culm is a prerequisite for the photosynthetic active functioning of the leaves during the grain-filling period.

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2 Experimental studies

SUMMARIES OF THE ARTICLES

Relation between green area duration and grain yield in some varieties of spring wheat
J.H.J. Spiertz, B.A. ten Hag and L.J.P. Kupers, *Netherlands Journal of Agricultural Science* 19(1971): 211-222.

In two experiments with spring wheat the relation was studied between green area duration (D) and grain yield during the period after heading. For this, the green areas of leaf, internode and ear were determined as accurately as possible in samples.

The relation between grain yield and green area duration of the separate green organs and of combinations of these was quantified by regression and correlation calculations. These calculations have shown that of the separate parts of the culm the D values of flag leaf and peduncle were closely correlated with the grain yield.

By using the combined D value of flag leaf and peduncle as a yield determining factor, 81 and 61% of the variance in the grain yield could be statistically predicted in 1967 and 1968, respectively. By including all the separate D values in a multiple correlation calculation the coefficients of determination of the variance in the grain yield could be increased to 83% in 1967 and to 74% in 1968. In 1968, next to the D values of flag leaf and peduncle, the D value of the ear was closely correlated to the grain yield.

The photosynthetic efficiency of the green area was compared by the grain-leaf ratio.

Effects of successive applications of maneb and benomyl on growth and yield of five wheat varieties of different heights

J.H.J. Spiertz, *Netherlands Journal of Agricultural Science* 21(1973): 282-298.

The effect of some fungicide treatments on the production pattern of five wheat varieties with different culm lengths was investigated in a field experiment. The fungicide treatments consisted of: a sequence of 2 pre-floral sprayings with 2 kg maneb per ha and 2 post-floral sprayings with 1 kg benlate per ha. The varieties were Juliana (117 cm culm length), Manella (82 cm), Lely (80 cm), Mex.-cross (69 cm) and Gaines (79 cm). There was hardly any mildew in the crop but *Septoria tritici* and *Septoria nodorum* were very much in evidence in all the varieties. Of the group of ripening diseases, black moulds and *Fusarium* were found to a lesser degree.

The combined application of maneb and benomyl greatly delayed the spread of *Septoria* in the crop, as a result of which the flag leaf in particular remained green for a longer period and the grain filling period was lengthened. The growth rate of the grains during

the phase from the milk-ripe stage to the dough-ripe stage was raised from $204 \text{ kg ha}^{-1} \text{ day}^{-1}$ to $230 \text{ kg ha}^{-1} \text{ day}^{-1}$. The effect of the application was greater in the varieties most susceptible to *Septoria* (Lely and Gaines) than in the other varieties. The increases in grain yield of the varieties Juliana, Manella, Lely, Mex.-cross and Gaines were 14%, 23%, 32%, 16% and 42%, respectively. By statistical analysis 85% of the variance in the grain yield within the varieties could be attributed to the green area of the flag leaf. Thus, the main effect of *Septoria* seems to be a reduction of the photosynthetic area, causing a decreased supply of assimilates to reach the grain, and in this way lowering the 1000-grain weight.

The degree of disease infection was not significantly correlated with culm length or the amount of leaf area, so the tolerance and resistance characteristics of the varieties were not immediately due to differences in crop structure. Specific variety differences were still present, even after reduction of the disease infection with the fungicides.

Grain growth and distribution of dry matter in the wheat plant as influenced by temperature, light energy and ear size

J.H.J. Spiertz, *Netherlands Journal of Agricultural Science* 22(1974): 207-220.

An experiment was carried out under controlled growing conditions to study the plant response during the post-floral stage to temperature, light intensity and ear size. Within the range of 15 to 25 °C a raise in temperature increased the growth rate of the grains but the duration of the post-floral development of the plant was very much shortened. The final result was that higher temperatures caused lower grain yields. An increase of light intensity from 92 to 147 $\text{cal cm}^{-2} \text{ day}^{-1}$ has shown a more positive effect on grain weight than an increase from 147 to 175 $\text{cal cm}^{-2} \text{ day}^{-1}$. The artificial reduction of ear size by removing spikelets from the ear increased the thousand-grain weight but not enough to compensate for the reduction in number of kernels per ear.

The effects of the main factors - temperature, light intensity and ear size - and of the combined treatments on the supply and storage of carbohydrate are discussed within the framework of a sink-source model.

The influence of temperature and light intensity on grain growth in relation to the carbohydrate and nitrogen economy of the wheat plant

J.H.J. Spiertz, *Netherlands Journal of Agricultural Science* 25(1977): 182-197.

The response of grain growth to temperature and light intensity was studied under controlled conditions within the ranges from 10 to 25 °C and from 64 to 188 W m^{-2} , respectively. Warmth hastened the senescence of the wheat plant and enhanced the initial growth rate of the grains. Additional light promoted the rate of grain growth more at high than at low temperatures; under the latter conditions there was a considerable accumulation of carbohydrates in the stem (up to 40%) from anthesis onwards. The rate of grain growth ranged from 0.70 to 1.64 $\text{mg day}^{-1} \text{ kernel}^{-1}$. The duration of grain growth was prolonged by decreasing the temperature from 25 to 10 °C; the increase in growth duration from about 30 to 80 days corresponded with a relatively stable temperature sum. Temperature and light

also affected the redistribution of assimilates and the chemical composition of the grain. The rate of protein synthesis was promoted more by warmth than the rate of starch synthesis. This resulted in an increased nitrogen content of the grain. The final content of total non-structural carbohydrates (starch and sugars) was slightly decreased by warmth. Additional light raised the carbohydrate content of all parts of the plant and so decreased the nitrogen content of these parts. However, light intensity had less effect on nitrogen distribution and yield than temperature had.

Effects of nitrogen on crop development and grain growth of winter wheat in relation to assimilation and utilization of assimilates and nutrients

J.H.J. Spiertz and J. Ellen, *Netherlands Journal of Agricultural Science* 26(1978): 210-231.

Grain growth and yield components of winter wheat (cv Lely) were studied in a field experiment in 1976 with four regimes of nitrogen dressing (50, 100, 100 + 50 and 100 + 100 kg N ha⁻¹). Growing conditions were characterized by a high level of solar radiation, warmth, ample nutrient supply and no damage by diseases.

Nitrogen raised grain number per m² from 16,700 to 20,600 and grain yield from 640 to 821 g dry weight m⁻². Grain growth duration was short, due to warmth, but the rate of grain filling was very high: from 24.0 to 29.2 g m⁻² day⁻¹ during the effective grain filling period. A high grain yield was associated with a high nitrogen percentage of the grains, which resulted in a grain protein yield ranging from 63.8 to 107.1 g m⁻² with an increased nitrogen dressing from 50 to 200 kg ha⁻¹.

The carbohydrate demand of the grains was provided by current photosynthesis and re-location of stem reserves. The latter was reflected in a decline of the stem weight after the mid-kernel filling stage. Nitrogen and phosphorus demand of the grains were supplied by withdrawal from the vegetative organs (leaves, stem, chaff) and to a large extent by post-floral uptake and assimilation.

Under the prevailing growing conditions the grains turned out to be very strong sinks for carbohydrate, nitrogen and phosphorus as shown by the harvest-indices. Additional nitrogen dressings increased the harvest-indices of dry matter, nitrogen and phosphorus from 0.40 to 0.48, from 0.75 to 0.81 and from 0.91 to 0.93, respectively.

It was suggested that a more restricted vegetative crop development at high nitrogen levels and a longer duration of root activity, photosynthesis and grain growth after anthesis would considerably favour grain yield.

Cultivar and nitrogen effects on grain yield, crop photosynthesis and distribution of assimilates in winter wheat

J.H.J. Spiertz and H. van de Haar, *Netherlands Journal of Agricultural Science* 26(1978): 233-249.

A comparison between the crop performance of a semi-dwarf (Maris Hobbit) and a standard height cultivar (Lely) at various levels of nitrogen supply was made. Grain yields of Hobbit were considerable higher, due to a higher number of grains and a heavier

grain weight. Owing to the higher grain yield and a lower stem weight the harvest-index of Hobbit was higher compared to Lely: 0.47 and 0.40, respectively. The content of water-soluble carbohydrates in the stems of both cultivars appeared to be very high until 3 weeks after anthesis, despite the occurrence of low light intensities. It was suggested that due to the weather of 1977 low temperatures restricted early grain growth and respiration more than photosynthesis was affected by light intensity. Lely used more assimilates for structural stem material than Maris Hobbit did.

Quantity and time of nitrogen application affected grain number strongly, but grain weight to a less extent. So within each cultivar grain number per m² was the main determinant of grain yield. Late nitrogen dressings promoted photosynthetic production, grain weight and protein content of the grains. The low protein percentages of the grains were attributed to the low temperatures during the grain filling period. The distribution of nitrogen within the wheat plant was only slightly influenced by nitrogen dressings and cultivar differences.

Nitrogen harvest-index ranged from 0.74 to 0.79. Grain nitrogen was derived from the vegetative organs (63-94%) and from uptake after anthesis (6-37%). The importance of carbohydrate and nitrogen economy for grain yield are discussed.

3 General discussion

3.1 SIZE AND ACTIVITY OF THE GREEN ORGANS IN RELATION TO GRAIN PRODUCTION

Following the work of Watson et al. (1963), Thorne et al. (1969) and Welbank et al. (1966), we studied the relation between green area duration and grain yield in spring wheat, as affected by sowing date and genotypic differences. The relation between grain yield and green area duration of the various green organs were quantified by regression and correlation calculations (Spiertz et al., 1971). The results showed that green area duration, calculated for the period from heading to ripening, was more closely correlated to grain yield than the green area duration from flowering to ripening. It was suggested that photosynthesis during the pre-anthesis period would affect final grain yield by influencing the number of grains set and the amount of reserves temporarily stored in the stem.

Since the green areas of the various parts of the culm were closely inter-related, it was not possible to calculate the exact contribution of each organ to grain growth. Judging from the degree of correlation between green area duration and grain yield, we considered the following organs to be important in grain filling: especially peduncle and flag leaf, followed by the ear, last leaf and last internode but one. The coefficient of determination of the variance in grain yield (R^2) amounted to 0.83 and 0.74 in two successive years. By late sowing vegetative growth was reduced more than ear formation, so that the number of grains per unit green area was higher. Consequently the grain-leaf-ratio was higher. However, in spite of a higher photosynthetic efficiency the late-sown crops yielded less, because of a considerably lower green area duration.

Similarly good correlations between grain yield and green area duration were reported by Fischer & Kohn (1966), Simpson (1968) and Hsu & Walton (1971). In later experiments the correlation of grain yield with green area duration was not as good. Especially under growing conditions favourable for leaf growth - viz. high rates of nitrogen supply - apparently grain yield was limited by factors other than the amount of green area. Thorne & Blacklock (1971) suggested that grain yield ceased to be well correlated with green area duration after anthesis when grain yields exceeded about 500 g.m^{-2} and leaf area index (two-sided) at anthesis was higher than about seven. However, such criteria depend on growing conditions (light intensity), cultivar differences, occurrence of diseases, etc.

Generally the correlation of grain yield with green area duration is high, when variation in grain yield is mainly caused by the weight of the individual grain and not by grain number. This phenomenon was shown by an experiment with five cultivars of winter wheat (Spiertz, 1973). Correlations between grain yield and leaf area were positive within the cultivars and negative between them. The correlation was negative because a low grain yield in the cultivar Juliana was associated with a high leaf area duration after anthesis.

The reverse occurred with the cultivar Gaines. The variance in grain yield within the cultivars could be attributed for 85% to the variance in green area of the flag leaf at the end of the kernel-filling period. This percentage increased when various degrees of leaf infection were produced in a cultivar susceptible to *Septoria* sp. by a different frequency of fungicide application. The very susceptible cultivar Lely showed a correlation of 0.99 between grain yield and percentage green area of the flag leaf on 20 July, whilst the more resistant cultivar had a correlation coefficient of 0.33. The main effect of diseases like *Septoria* seems to be a reduction of the photosynthetic area, causing a decreased supply of assimilates to the grain and as a consequence a lower grain weight.

More recently Ledent (1977a) studied the relation between grain yield and a number of plant characters in wheat canopies in the field and in controlled environments. Simple correlations, stepwise regression analysis and factor analysis indicated that the plant characters most closely related to grain yield were grain number, stem dry weight and weight of sheaths of flag leaf and second leaf. Areas of leaves and internodes were less strongly related to grain yield in the cultivars studied. McNeal & Berg (1977) found with near-isogenic populations that flag leaf area, by itself, was not a good index for plant performance. Differences in other characters (heading and plant height), however, might have been more important in these near-isogenic populations.

Removal of parts of leaf laminae or cutting vascular bundles in the upper leaves or sheaths of wheat culms had little effect on mean weight per kernel. Removal of entire laminae, complete leaf removal, and cutting vascular bundles at the base of the ear significantly decreased mean kernel weight (Ledent, 1977b). In most cases, the decreases varied by 10 to 20%. These findings confirm the results of Walpole & Morgan (1974); they could not detect any significant effect on grain weight in the 14 days after defoliation. Later the more severe defoliations reduced grain weight, and reductions in final grain yield ranged from 16.6 to 45.5%. Generally, effects of a reduction in photosynthetic capacity on grain yield will depend on the extent to which the 'source' limits grain growth.

Canopy photosynthesis appears to increase asymptotically with increase in LAI, reaching a maximum level at LAI values above 4 (Evans et al., 1975). The relation between net photosynthesis and LAI was unaffected by either cultivar or by sowing density (Puckridge & Ratkowsky, 1971). In our experiments (Spiertz & van de Haar, 1978) additional nitrogen applied at the boot stage promoted net photosynthesis more than it promoted LAI, especially in the later stages of grain growth. This finding shows the importance of maintaining the photosynthetic activity of the green organs during ageing rather than increasing the area of the green organs as such. Toward the end of grain filling, stem and ear photosynthesis can become the major source of current photosynthesis, but even in the earlier stages of grain growth, stem photosynthesis can be a substantial component (Evans & Rawson, 1970). This contribution from the stem might explain the high dry matter yields found under growing conditions which did not favour leaf growth (Spiertz & Ellen, 1978), but promoted the formation of a high number of culms.

Grain growth can be also considerably affected by the carbon dioxide concentration (Gifford, 1977). CO₂-enrichment (0.20 ml.l⁻¹) gave a 32% larger total crop weight at

maturity and a 43% increase in grain yield, whilst a reduction ($\sim 0.15 \text{ ml.l}^{-1}$) gave a 43% reduction in total crop weight and 44% reduction in grain yield. Most of the grain yield response was brought about by an increased fertility of the side-tillers; obviously incident radiation was not limiting. Osman (1971) showed that net photosynthesis was more closely related to light interception and crop growth rate than to leaf area index. Photosynthesis-light curves turned out to be different for the various leaf layers. Lower, and thus shaded, leaves had a lower level of maximum photosynthesis than top leaves, due to a higher mesophyll and carboxylation resistance.

Hence the characters of the vegetative organs are only partly correlated with grain yield. The degree of correlation depends on growing conditions and on the demand for assimilates by the grains.

3.2 RESPONSE OF GRAIN NUMBER AND GRAIN GROWTH TO CLIMATIC FACTORS AND NITROGEN SUPPLY

Grain yield is a function of the number of grains per unit ground area and the mean weight per grain at harvest. The *number of grains* per unit ground area is composed of grain number per ear and number of ears per unit ground area. Biscoe & Gallagher (1977) concluded that the weather influences the physiological and developmental processes which determine the number of grains more than the processes determining their size. This conclusion is confirmed by comparing the variance in grain yield and grain number between years in our field experiments (Fig. 1). The relationship between grain yield (Y) and grain number (N) for the cultivar Lely under disease-free conditions in the growing seasons from 1972-1977 could be expressed by the following formula:

$$Y = 52.8 + 0.0357 N \quad (R = 0.85)$$

The main environmental factors in these experiments were weather and nitrogen supply. If other factors like disease, drought and nitrogen stress interfere during the post-floral period, then the rate and duration of grain growth would be far more important (Spiertz, 1973).

Apparently, poor light conditions during the pre-floral period can severely reduce yields in wheat (Willey & Holliday, 1971; Fischer, 1975). Evans (1978) found that ear number (ranging from 402 to 1070 per m^2) was closely related to irradiance during the early reproductive stage (from 35 to 15 days before anthesis). Grain number per ear was influenced mostly by irradiance during the late reproductive stage (from 15 days before to 5 days after anthesis). However, Fischer et al. (1977) concluded that grain yield in normal crops was limited by both sink and post-anthesis source. They established a wide range in grain numbers (4000 to 34000 per m^2) by thinning, shading, application of carbon dioxide and crowding. Grain yield increased, reaching a maximum at a grain number well above those of crops grown with optimal agronomic management but without manipulation. Kernel weight fell linearly with increase in grain number over the whole range of grain numbers studied, but the rate of fall varied with the season. In our experiments additional nitrogen applied at the boot stage increased mostly the number of grains as well as grain weight (Ellen & Spiertz, 1975; Spiertz & Ellen, 1978). Thus there are management treatments which break

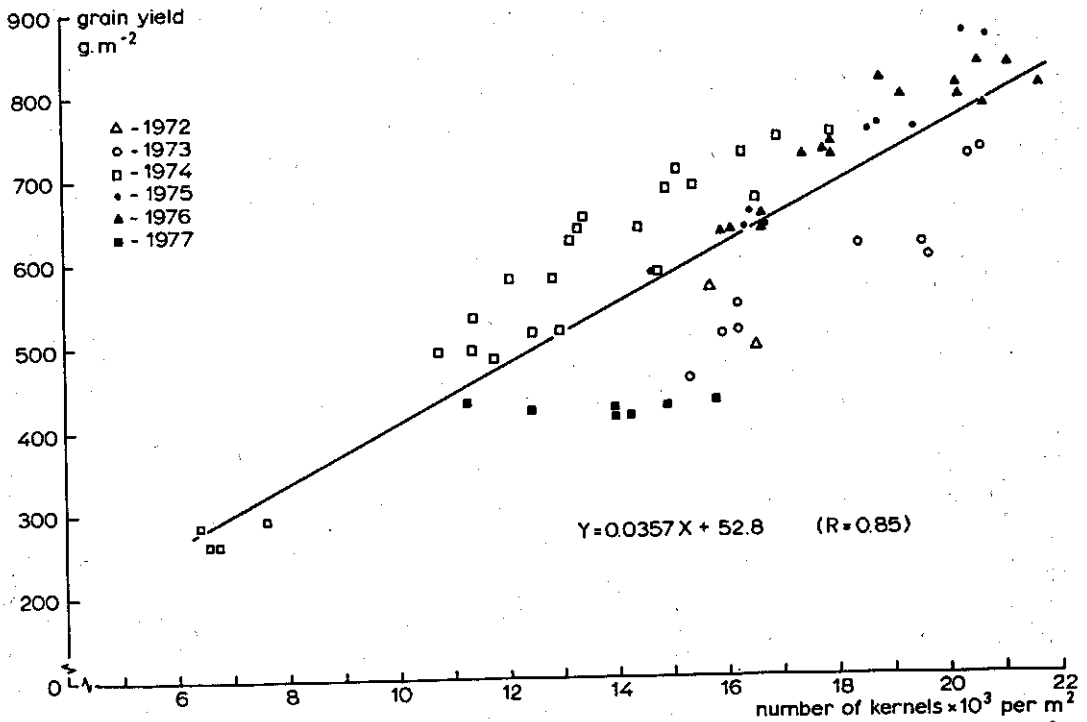


Fig. 1. Simple linear regression of grain dry matter yield (g.m^{-2}) on grain number per m^2 for six successive years with the cultivar Lely.

the compensation mechanism. The same phenomenon was seen in the experiment to study difference between cultivars (Spiertz & van de Haar, 1978). Darwinkel (1978) varied plant density from 5 to 800 plants per m^2 and found also a linear relation between grain yield and grain number up to about 18000 grains per m^2 . Above this level an increase in grain number was completely compensated by a decrease in kernel weight. The extent to which the grains are filled depends on the location within the ear and on the supply of assimilates. Bremner & Rawson (1978) suggested that the different potentials for growth of grains within a spikelet have a minor influence on mature grain weight, but that the relative ease with which assimilate reaches the grain has a major influence. The latter depended largely on the distance of the grains from the spike rachis.

The effects of environmental factors on the rate and duration of grain growth were studied in growth chambers within the ranges from 10 to 25 °C and from 64 to 188 W.m^{-2} . A rise in temperature increased the growth rate of the grains considerably, but the duration of the post-floral period was very much shortened (Spiertz, 1974, 1977). Duration of grain growth was reduced from 80 to 30 days by a rise in temperature from 10 to 25 °C. Similar temperature effects were found in phytotron experiments with other cultivars of spring wheat (Sofield et al., 1974, 1977a; Ford & Thorne, 1975; Warrington et al., 1977; Chowdhury & Wardlaw, 1978). Thus response in grain growth of the wheat plant to temperature seems to be very predictable.

Growth rate of the grains was closely associated with mean daily temperatures after anthesis, as long as assimilate supply to the grains corresponded to the demand (Spiertz, 1977). Demands of the grains for assimilates increased with a rise in temperature. Therefore the effect of light intensity on rate of grain growth was greater at higher temperatures. In the phytotron experiments, the highest level of photosynthetic radiation (16 hours:188 W.m⁻²) turned out to be insufficient for an adequate supply of photosynthate at high temperatures. This shortage of assimilates was also reflected in a fast depletion of stem reserves. So final grain yield depends on the balance between supply of assimilates and storage capacity of the ear.

The question remains to what extent temperature affects rate and duration of grain growth in the field crop. Under growing conditions in the Netherlands great differences are observed in temperature and light intensity from year to year (Fig. 2). In winter wheat experiments with the cultivar Lely, the rates of grain growth between years from 1972-1977 were compared. Per year plots with an optimum nitrogen dressing were selected; other growing factors were rather favourable in these field experiments in the Flevopolder. The rate of grain growth (dry matter) per unit ground area ranged between years from about 200 up to 350 kg.ha⁻¹.d⁻¹ (Fig. 3). After correction for differences in solar radiation between years, by expressing the rate of grain growth per unit of light intensity ($\mu\text{g.J}^{-1}$), also under these field conditions temperature was positively related to grain growth during the so-called linear phase of grain filling (Fig. 4A). The duration of grain growth turned out to be inversely related to temperature (Fig. 4B). These responses of field crops to

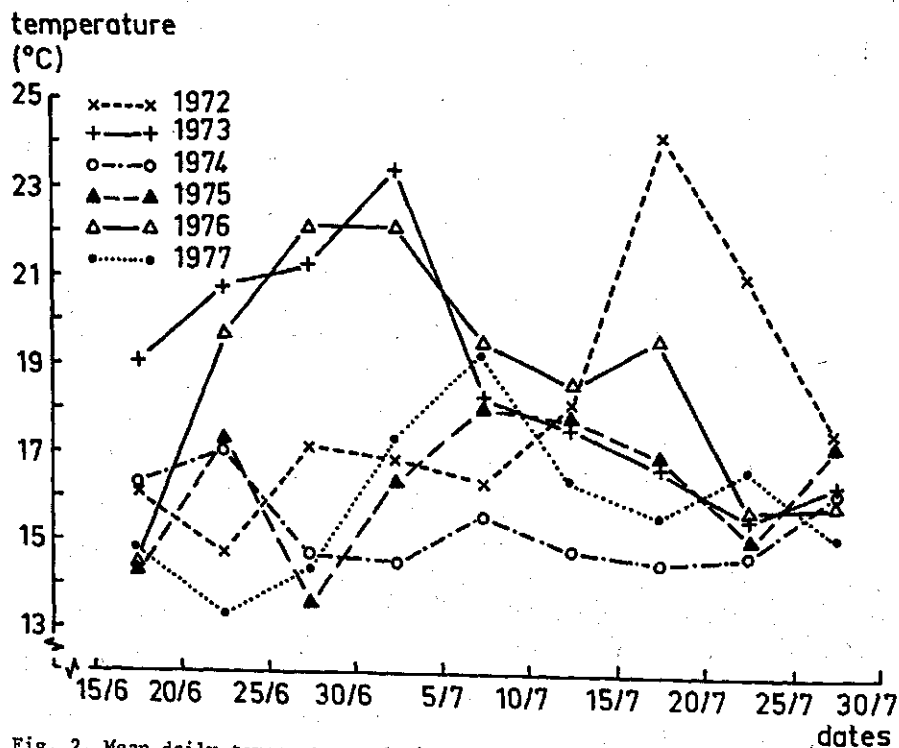


Fig. 2. Mean daily temperatures during the kernel-filling period in six successive years.

temperature agree very well with those found by Marcellos & Single (1972), Meredith & Jenkins (1976) and Pinthus & Sar-Shalom (1978). Under bright conditions assimilate supply is favoured more than the demands of the growing grains. Therefore individual grain weights in field crops are not affected by temperature as much as those in the phytotron experiments.

Evans (1978) found that grain yield of wheat grown in a constant daylength and temperature regime was more limited by irradiance between ear initiation and anthesis, when storage capacity is determined, than by irradiance during grain growth. Sofield et al. (1977a) found that with cultivars in which grain number was less affected by light intensity, growth rate per grain was highly responsive to irradiance, especially in the more distal florets. They concluded that growth rate per grain depended mainly on floret position within the ear, on differences in grain size between cultivars and on temperature. A higher rate of grain growth in cultivars with larger grains at maturity was also found in our field experiment with the cultivars Lely and Maris Hobbit (Spiertz & van de Haar, 1978).

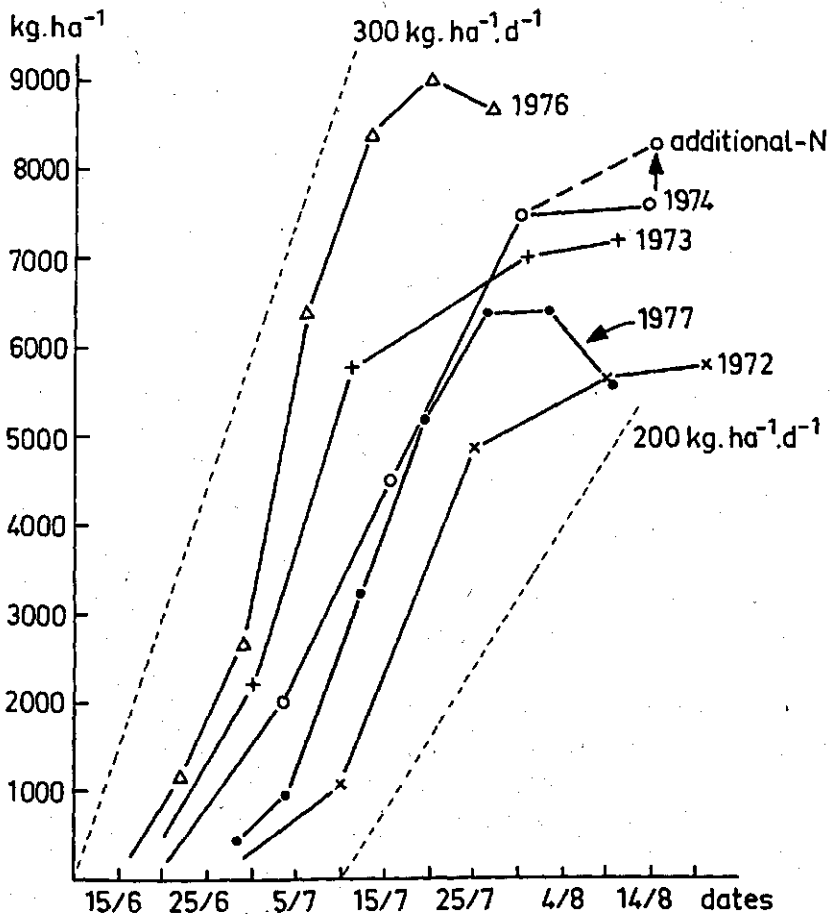


Fig. 3. Patterns and rates of grain growth for different climatic conditions in successive years with the cultivar Lely at optimal nitrogen dressings.

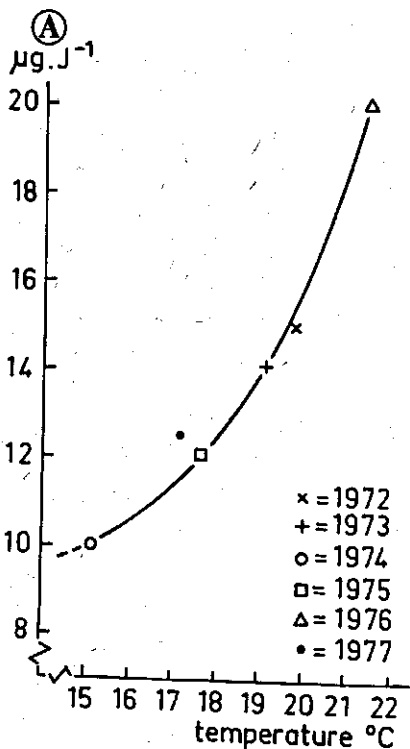


Fig. 4A. Relationship between the growth rate per unit light energy ($\mu\text{g} \cdot \text{J}^{-1}$) and the mean daily temperature ($^{\circ}\text{C}$) during the linear phase of grain filling.

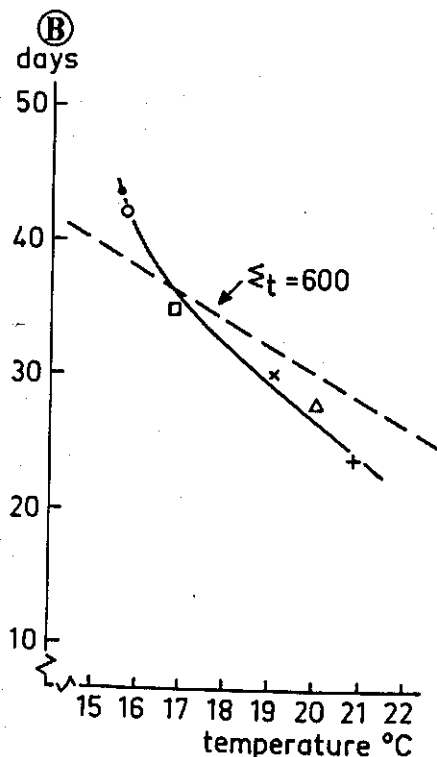


Fig. 4B. Relationship between the duration (days) from anthesis to ripeness and the mean daily temperature ($^{\circ}\text{C}$) during this period. $\Sigma t = 600$ sum of mean daily temperatures ($^{\circ}\text{C} \cdot \text{d}$).

Duration of grain growth is related to senescence of vegetative organs as well as to maturation of the grains. The earlier senescence of the green organs of the wheat plant at high temperatures can be retarded by late nitrogen dressings. In a field experiment (Spiertz & van de Haar, 1978) crop photosynthesis after mid-kernel filling declined much more slowly with an additional nitrogen dressing at the boot stage. Prolonged photosynthetic production can favour grain growth considerably (Ellen & Spiertz, 1975). The supply of assimilates is generally limiting at the end of the kernel filling if grain number is adequate ($> 20\ 000$ per m^2). The effect of late nitrogen dressings on the functioning of the leaves indicates that a fast senescence can also be caused by a negative balance between the nitrogen uptake of the plant and the requirements of the grains. One might conclude that at high temperatures the rapid senescence of green tissue causes a shortage of carbohydrates, which can reduce the growth rate and even stop grain growth towards the end of the kernel-filling period. At lower temperatures under optimal water and nutrient supply maturation of the ear often preceded the senescence of green organs and other vegetative tissue (Spiertz, 1977; Sofield et al., 1977a).

From studies by Jenner & Rathjen (1975, 1977), it was concluded that the developmental pattern of grain growth is determined internally by metabolic processes rather than

externally by the supply of sucrose and amino acids from the rest of the plant. They found from ^{14}C -studies that the rate of starch production in the cultured endosperm rose to a maximum at about the mid-point of grain development and then fell progressively to near zero. Other research workers studied the relationship between grain water content and the cessation of grain growth (Geslin & Jonard, 1948; Andersen et al., 1978).

It was shown that this relationship was affected by the abscisic acid (ABA) concentration in the wheat grains. Radley (1976) and King (1976) found that the water loss of the grains is preceded by an increase in the ABA-concentration. Application of ABA to the ear had no effect on the rate of grain growth but resulted in an earlier cessation of grain growth and hastened the drying of the grain. Goldbach (1975) found that temperatures of 26°C compared with 18°C accelerated the increase in ABA-concentration up to the start of ripening. Late application of nitrogen decreased ABA-concentration. However, it is important to know whether the fall in the amount of water in the grain and rise of the ABA-concentration at maturity caused or was a consequence of the cessation of grain growth.

Sofield et al. (1977b) found no evidence of an increased rate of water loss by the grain at the stage of maximum grain dry weight. They suggested that the rapid fall in water content at the cessation of grain growth was due to a blockage of the chalaxal zone of entry into the grain by deposition of lipids. This suggestion agrees with the finding of Jennings & Morton (1963) that lipid content increased as wheat grains reached maturity.

Although the controlling factors of the cessation of grain growth are not completely understood, the strong dependence of the duration of grain growth on temperature often limits grain yield. It may be worthwhile to look for genetic variability in this character.

3.3 ASSIMILATION AND UTILIZATION OF CARBOHYDRATES AND NITROGEN COMPOUNDS

The two main organic storage products in the wheat plant are carbohydrates and nitrogen compounds. Both have a dynamic pattern of assimilation, distribution, relocation and storage. The mass fractions of water-soluble carbohydrates (w.s.c.), starch and nitrogen were determined in the various parts of the wheat culm of plants grown either in the phytotron or in the field. Although carbohydrate and nitrogen metabolism are partly interrelated, they will be discussed sequentially.

Accumulation of *carbohydrates* in the vegetative organs of the wheat plant is governed by the balance between photosynthetic production and the utilization of assimilates for growth and respiration. When there is a surplus of carbohydrates, these are mainly stored in the stem (Spiertz, 1974). Low temperatures and high light intensities increased the carbohydrate content of all parts of the plant. Under these artificial climatic conditions the mass fraction w.s.c. in the stem was raised to a level higher than 0.4 (40%) until 4 weeks after anthesis (Spiertz, 1977). The w.s.c.-mass fraction of leaves and roots showed an increase as rate of grain growth declined. With high temperatures w.s.c.-mass fractions decreased shortly after anthesis.

Also under field conditions high w.s.c.-contents were found in the stem up to a fortnight after anthesis under the bright conditions of 1976 as well as with the cool overcast weather of 1977 (Spiertz & Ellen, 1978; Spiertz & van de Haar, 1978). These results indicate that temperature governs indirectly, by the rate of initial grain growth, also the

utilization of the stem reserves. In 1976, a high level of radiation increased w.s.c.-content of the stem before anthesis, but decreased it after anthesis mainly because of rapid grain growth due to the high temperature. In 1977, low temperatures after anthesis retarded grain growth and obviously kept respiration at a lower level, so that the mass fraction of w.s.c. in the stem remained relatively high. Gifford (1977) concluded that the wheat crop adjusts yield components and possibly duration of grain filling to give near constancy of kernel weight in different photosynthetic environments. The adaptation mechanisms for regulating grain set and grain growth are still incompletely understood.

For many years there has been controversy about to what extent the carbohydrate produced by photosynthesis before anthesis contributes to the grain yield of cereals. Evans & Wardlaw (1976) concluded that reserves do contribute to grain yield to an extent that depends on the type of cereal and the environmental conditions. Reserves of assimilate present at flowering and available for later translocation to the grains could buffer grain growth against environmental stresses during grain filling. Estimates of the contribution of stem reserves to grain yield are derived from changes in stem weight after anthesis (Gallagher et al., 1976) or from ^{14}C studies in whole wheat plants (Austin et al., 1977) and in labelling only specific organs (Pearman et al., 1978). The pre-anthesis assimilate contribution was estimated to be no more than 20% (Stoy, 1963; Thorne, 1966; Birecka & Dakic-Wlodkowska, 1966). Later experiments gave estimates ranging from 27% (Rawson & Evans, 1971) to 57% (Gallagher et al., 1976) of the grain dry matter yield in wheat. The latter percentage was criticized by Bidinger et al. (1977). These authors carried out field experiments with in situ labelling of the whole crop canopy with $^{14}\text{CO}_2$ at frequent intervals before and after anthesis. They found a 12% (irrigated crops) and 22% (droughted crops) contribution by pre-anthesis assimilates, mainly from stem reserves, to the grain dry matter yield. Based on changes in dry weight of the stem after anthesis and corrections for losses due to respiration and translocation to the roots, we found that the dry matter contribution of stem reserves ranged from 760 to 1360 $\text{kg}\cdot\text{ha}^{-1}$, which corresponded to 9.0 and 21.3% of the final grain dry matter yield with nitrogen dressings of 200 and 50 $\text{kg}\cdot\text{ha}^{-1}$, respectively (Spiertz & Ellen, 1978). The largest part of stem weight losses was due to a sharp decline of the amount of water-soluble carbohydrates. The remaining proportion of dry weight losses may be caused by relocation of various other compounds (amino acids, organic acids, nutrients) and to a small extent by lignification processes.

Austin et al. (1977) found that photosynthesis during the 18 days following anthesis contributed on average 48% of the final grain dry weight. Of this quantity, about half was translocated to the grains within 10 days of initial assimilation. The remainder appeared to be stored temporarily in the stems and leaves and was translocated to the grains from 4 weeks after anthesis onwards. These authors also found that relocation of dry matter from the vegetative organs to the grains was greatest in genotypes which lost most dry weight of stems and leaves. The phenomenon of a surplus of assimilates during the first weeks after anthesis was also observed in our experiments (Spiertz & van de Haar, 1978). Differences between a semi-dwarf and a standard cultivar were, however, more pronounced in stem and ear weight at anthesis than in dry weight loss of the stem during grain filling. This finding is confirmed by ^{14}C -studies of Makunga et al. (1978); they suggest

that the lower stem weight of semi-dwarf cultivars is a more important cause of differences in harvest index than the greater movement of post-anthesis photosynthate to the grain. Cultivars with more grains per ear had larger ear weights at anthesis and incorporated more ^{14}C into the ear before anthesis during floret differentiation. Ruckenbauer (1975) found that more ^{14}C reached the ear of Maris Hobbit than that of Maris Huntsman, but Hobbit had also more grains per ear.

Considering the function of leaves in assimilate distribution and utilization of the plant, *nitrogen compounds* play a complex role. Referring to the model proposed by Thornley (1977) nitrogen compounds can be divided into three categories: (1) storage material (2) biologically active material, (3) inert material. Nitrogen compounds accumulated and stored in the green organs of the wheat plant, especially the leaves (blade and sheath) are usually the main nitrogen source for the growing grains (Nair et al., 1978). At the same time some nitrogen compounds are biologically active and determine the activity and duration of physiological processes, viz. photosynthesis and nitrate assimilation.

In our experiments in the phytotron as well as in field experiments we found that high temperatures raised the rate of nitrogen uptake by the grains more than the carbohydrate accumulation (Spiertz, 1977; Spiertz & Ellen, 1978). So warmth during the grain-filling period promoted the nitrogen mass fraction of the grain. Already in 1914 Le Clerc & Yoder demonstrated with their curious tri-local soil-exchange experiment that climate has a much greater influence on the protein content of wheat grain than soil fertility.

Under controlled environmental conditions Campbell & Read (1968) found that increasing either day temperature (from 21 to 27 °C) or night temperature (from 13 to 21 °C) raised the protein content of the grain. There were only small interactions with light intensity and soil moisture stress. It was stated that reduced light intensity lowers the grain nitrogen content to about the same extent as grain weight, with the result that the mass fraction of nitrogen is little affected (Bremner, 1972). However, in our phytotron experiment (Spiertz, 1977) and in the experiments of Kolderup (1975) and Sofield et al. (1977b) there was also a clear inverse relation between light intensity and the mass fraction of nitrogen in the grain. Striking was the weak response of nitrogen yield and distribution of nitrogen to environmental conditions. Obviously, nitrogen economy is more under genetic control than carbohydrate economy; the latter seems to reflect the photosynthetic conditions.

In the phytotron experiment with regular nitrogen supply to the plants, about 65% of the grain nitrogen was derived from the vegetative aerial parts, whilst 35% was uptake from the roots or the soil after anthesis. These proportions correspond with data of Deherain & Dupont (1902). In our field experiments with late N applications, we found about 50% ($100 \text{ kg} \cdot \text{ha}^{-1}$) of the nitrogen uptake after anthesis in the less leafy crop of 1976 (Spiertz & Ellen, 1978) and about 20% ($25 \text{ kg} \cdot \text{ha}^{-1}$) in the crops with an early vigorous development in 1977. Austin et al. (1977) and Pearman et al. (1977) reported for British growing conditions that post-anthesis nitrogen uptake accounted for only 17% and 15 to 28%, respectively. The post-anthesis nitrogen uptake is strongly affected by root activity, moisture level and nitrogen supply, as shown by extensive studies of Campbell et al. (1977a, b) and Campbell & Paul (1978).

A late nitrogen dressing at the boot stage to a crop with an intermediate plant density turned out to favour grain number as well as supply of assimilates to the grains (Spiertz & Ellen, 1978; Spiertz & van de Haar, 1978). The latter was due to a retarded depletion of the nitrogen content in the green organs of the wheat plant and a prolonged photosynthetic capacity. Supply with nitrogen compounds was more favoured than carbohydrate supply to the grains. Therefore nitrogen harvest index (percentage grain nitrogen) was raised from 0.75 to 0.81 and from 0.74 to 0.79 in the years 1976 and 1977, respectively. This efficiency of nitrogen distribution was also found by Dalling et al. (1976), whilst Austin et al. (1977) reported a nitrogen harvest index of 0.68 as an average value for various genotypes. Canvin (1976) stated that nitrogen harvest index is not a constant feature of a cultivar and that there is as much variation within a cultivar as there is between cultivars.

3.4 AGRONOMIC POSSIBILITIES AND LIMITATIONS FOR INCREASING GRAIN YIELD

Discussions of whether assimilate supply (= source) or storage capacity (= sink) limits yield refer mostly to the grain-filling stage, since most grain growth is supported by concurrent photosynthesis rather than by stored reserves of carbohydrate (see Section 3.3). However, the sink or storage capacity for assimilates at the grain filling stage is to a large degree determined by the extent of photosynthesis, nitrogen assimilation and dry matter distribution before anthesis, especially from ear initiation onwards (see Section 3.2). Thus, whether source or sink limits grain development depends on the balance between growth and development of the crop during the various stages of the life cycle. Productive cultivars are adapted to the growing conditions in such a way that their production pattern has a large potential for maximizing the utilization of irradiance and the storage of photosynthates in the grain.

The comparison of grain numbers and grain yields of the cultivar Lely (Fig. 1) in various seasons showed that, under growing conditions in the Netherlands with disease-free crops, grain number per unit ground area is mostly limiting. This relationship suggests that for achieving top yields a grain number per m^2 of about 20 000 is required. Darwinkel (1978) found a minimum value of 18 000 grains per m^2 , but this figure was established under the poor light conditions of 1977. Under high irradiation in controlled environments with micro-crops Evans (1978) found a linear relationship between grain number and grain yield up to 28 600 grains per m^2 .

Grain number per ear (and per unit ground area) depends greatly on the availability of assimilates, but also on the distribution within the shoot. It was shown (see Section 3.3) that there exist genotypic differences in sink-strength of the developing ear, which are reflected in a higher ear weight and a lower stem weight at anthesis. This trend has been present already for many years in Dutch cultivars, as illustrated by the dry matter distribution in the cultivars Juliana and Lely (Kramer, 1978). Our own results and the results of current research in England indicate that further progress with semi or triple dwarf types is possible.

Another approach to increase the number of grains per ear was outlined by Donald (1968) in his concept of a wheat ideotype: single culm, strong stem, dwarf stature and large spike. The first unicum type of wheat was crossed in Israel. Atsmon & Jacobs (1977) reported an average grain number per ear of 106 within a range from 80 to 180. These huge numbers of grains were due to a higher number of grains per spikelet and more spikelets per ear. The high grain number per ear was associated with an average grain dry matter weight of 62.5 mg per kernel and a grain dry matter yield per plant of 4.4 g. However, vegetative parts were robust and vigorous, including broad, thick, dark green leaves and thick, stiff straw. The larger and proliferous ear had a considerably higher chaff weight. This unicum fulfils only part of Donald's concept of the ideotype, because it is not a weak competitor and ultimately sensitive to mutual light competition. Agronomically it is questionable whether a low plant density with large ears is more favourable than a dense crop with smaller ears if grain number per unit ground area is equal. Further the lack of tillering capacity may be a disadvantage of winter wheat under poor or variable establishment conditions.

Assuming that grain number per unit ground area can be increased, then the increased demand for assimilates must be considered. High temperatures enhance the conversion of precursors (sucrose and amino acids) into storage products (starch and protein) in the grain, but also the rate of respiration (Spiertz, 1977; Apel & Tschäpe, 1973). Under these growing conditions the utilization of assimilates can be greater than current photosynthesis and nitrogen assimilation (Spiertz & Ellen, 1978). The demands for carbohydrates are buffered by the stem reserves, but high requirements for nitrogen would accelerate senescence and shorten the grain-filling period (Fig. 5).

As photosynthesis depends on solar radiation and ambient CO_2 -concentration, there is no evidence for a considerable increase of net crop photosynthesis. Sibma (1977) inferred from a comparison between potential gross production and crop growth rate derived from light interception that photosynthetic production of wheat can be increased by prolonging the growth period. If water is available additional nitrogen dressings at the boot stage and adequate disease control favour net photosynthesis at the end of the growing period (Spiertz, 1973; Ellen & Spiertz, 1975; Spiertz & van de Haar, 1978). However, it has already been observed that in the field the ears sometimes mature before the vegetative organs senesce.

High grain yield, associated if possible with a high content of grain protein, requires either large nitrogen reserves in the vegetative organs or a continued uptake of nitrogen after anthesis. Assuming as a goal 10 tons of grain dry matter per ha with a nitrogen mass fraction of 0.025 (2.5%), then a nitrogen supply of $250 \text{ kg} \cdot \text{ha}^{-1}$ is required. Normally in a good winter wheat crop, nitrogen yield at anthesis amounts to about $150 \text{ kg} \cdot \text{ha}^{-1}$ of which about $100 \text{ kg} \cdot \text{ha}^{-1}$ is available for relocation to the grains (Cofc, 1960; Spiertz & Ellen, 1978). So a large quantity of nitrogen must be absorbed and assimilated after anthesis; this absorption also needs a prolonged activity of the roots.

Up to now mostly potential grain yields of wheat have been calculated from the photosynthetic potentials (de Wit, 1965; Evans, 1970). The consequences of these potential yields for the nitrogen economy of the wheat plant are mostly overlooked. The majority of the studies on nitrogen in the wheat plant concern the nitrogen content of the grain and

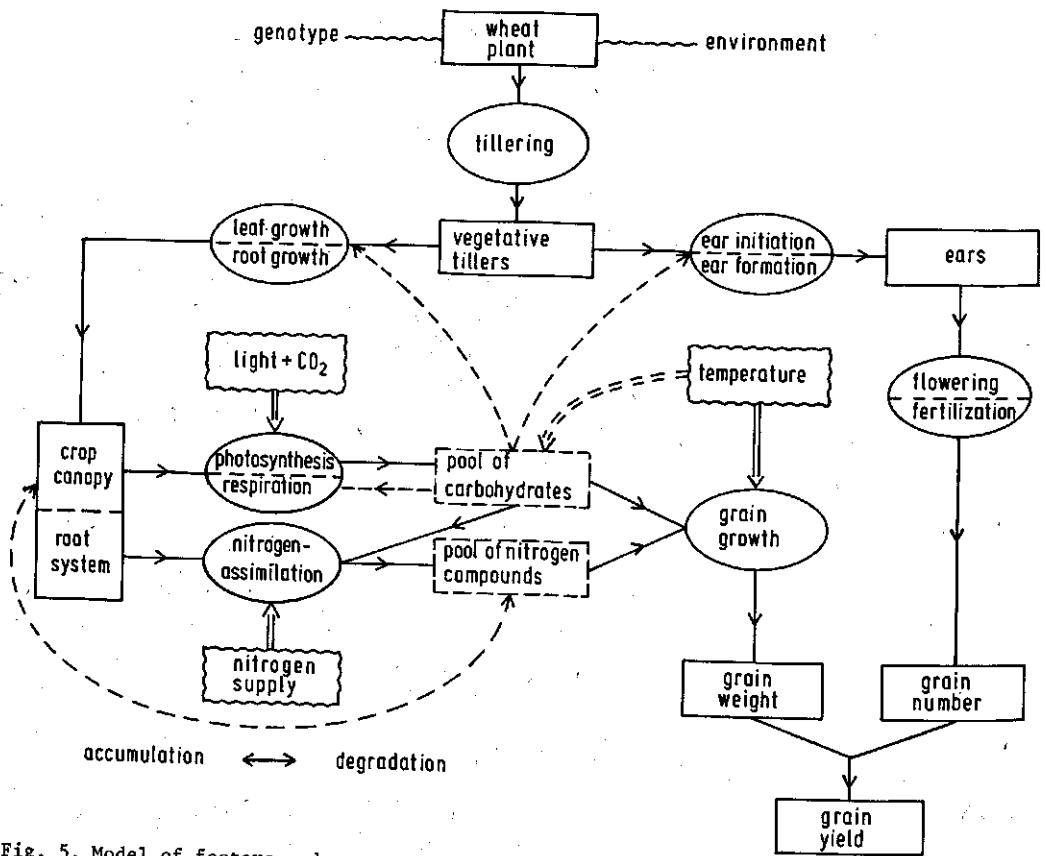


Fig. 5. Model of factors and processes related to grain growth of wheat. \square , crop components; \circ , processes; --- , environmental factors; --- , dependence on; \Rightarrow , direct effect; \dashrightarrow , indirect relation; \rightarrow , direct relation; \dashrightarrow , indirect relation.

not the nitrogen economy of the whole plant. Further research on achieving higher grain yields has to consider not only photosynthetic production but also nitrogen economy and root activity.

The gap between actual and potential grain yield has been narrowed in the past by providing better growing conditions through improved cultivation methods, such as fertilizer application, weed control, soil tillage, irrigation, etc. In the last decade the application of fungicides, when genetic disease-resistance failed, contributed to still higher and more stable grain yields. Further progress has to be made by preventing damages through pathogens of the roots.

Improvement of growing conditions and of genotypes will lead to higher and more stable grain yields of wheat and as a result to a better use of solar energy and of the available land acreage.

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Summary

The main purpose of growing a wheat crop has always been to produce grain. Final grain yield is a function of number of ears per m^2 , number of grains per ear and mean individual grain weight.

Since research workers found that grain growth is based largely on post-floral assimilation, much emphasis has been given to the significance of the size and the longevity of the photosynthetic active organs for the grain yield. Following the concepts about leaf area index (LAI) and leaf area duration (LAD) of Watson and co-workers, we studied the relation between grain yield and green area duration of the various green organs under growing conditions in the Netherlands. By multiple regression analysis, up to 83% (R^2) of the variance in grain yield could be attributed to the variance in green area duration of flag leaf, peduncle (incl. leaf sheath), ear, penultimate leaf and last internode. From these calculations it could be derived that the area durations of flag leaf and peduncle were most strongly associated with grain yield. However, within a wheat plant there is a high degree of co-variation between the green area durations of individual organs, so that it was not possible to estimate the exact contribution of these organs to grain growth. Even with a high correlation between green area duration and grain yield, it is not possible to determine whether grain growth is directly affected by environmental conditions or indirectly through the supply of assimilates by the vegetative (green) parts of the plant.

Therefore the effects of light intensity and temperature on the duration and rate of grain growth and on the assimilation and utilization of photosynthates were studied in phytotron experiments. High temperatures considerably increased the rate of grain growth, but likewise shortened the duration of grain growth. Thus the daily requirements of the grains for assimilates increased with a rise in temperature. As grain growth is sustained largely by current photosynthesis, light intensity affected grain yield more at high than at low temperatures. The restricted grain growth at low temperatures led to a surplus of assimilates, which accumulated in the vegetative organs; especially carbohydrates were stored temporarily in the stem.

A high temperature during grain filling promoted the accumulation of nitrogen in the grains relatively more than it promoted the storage of starch. Light intensity had only a minor effect on nitrogen accumulation and protein synthesis in the grain. The change in nitrogen content of the grains was caused by the effect of light intensity on carbohydrate supply.

Although warmth raised the rate of nitrogen uptake by the grain considerably, the nitrogen yield of the grains was hardly affected. This result indicates that without post-floral nitrogen uptake, the duration of the grain-filling period is determined by the amount of nitrogen reserves in the wheat culm at anthesis and by the rate of nitrogen

relocation from the vegetative organs to the grains.

The responses of spring wheat to temperature and light intensity in the phytotron were compared with the behaviour of winter wheat in field experiments during five growing seasons, which covered a large range of climatic conditions during the grain-filling period. It was found that also under field conditions temperature was the main determinant of the rate of grain growth and its duration. However, temperature effects on grain yield under field conditions were masked, due to co-variation between light intensity and temperature. From the pattern of carbohydrate accumulation in the stem and assimilate utilization by the grains, it was concluded that grain growth during the first three weeks of the grain-filling period was more governed by temperature than by the availability of assimilates. During the latter part of this period additional assimilates, made available by a prolonged photosynthetic activity, favoured grain growth.

I suggested that under the growing conditions for winter wheat in the Netherlands the storage capacity of the grains is limiting during the first weeks after anthesis (sink-limitation), whilst later on the supply of assimilates to the grains might be limiting (source-limitation), due to constraints of water, nitrogen and diseases. By late nitrogen applications and disease control with fungicides, the longevity of the photosynthetic active organs could be prolonged and grain yield enhanced. A late nitrogen application, however, increased the number of grains per ear.

Crop performance under various environmental conditions depends on differences between cultivars. The relative importance of various traits of a semi-dwarf and a standard wheat cultivar were assessed. The higher harvest-index of the semi-dwarf cultivar was brought about partly by a favoured ear growth during the prefloral period and partly by a faster grain growth during the first half of the grain-filling period. The semi-dwarf cultivar had a reduced stem weight; leaf and chaff weight were affected positively, but only to a small extent. There were only small differences in nitrogen yield and distribution between the cultivars. However, nitrogen content of the grains differed strongly due to differences in starch accumulation. The nitrogen content of the grains varied also strongly within a cultivar: a warm growing season increased the protein mass fraction (up to 0.14), whilst a cool growing season resulted in a low protein mass fraction (about 0.08). The nitrogen harvest-index did not vary widely between seasons and cultivars, when split nitrogen dressings were applied. This index ranged from 0.74 to 0.81.

A much greater variation occurred between seasons in the amount of nitrogen uptake after anthesis; this amount ranged on average between 20 and 50% of the final grain-nitrogen yield. Especially when vegetative growth was restricted, post-floral nitrogen uptake was needed to fulfill the requirements of the grains at a high yield level. A late uptake of nitrogen in the aerial parts of the wheat culm indicates nitrogen reserves in the root system or a prolonged activity of the root system.

The agronomic possibilities and limitations for increasing grain yield are discussed. Further progress in increasing grain yield has to be made in such a way that the wheat crop is adapted as much as possible to the environmental conditions. It is hypothesized

that further increase in grain yield might be expected from a higher grain number per unit ground area, from a longer root activity after anthesis and from a prolonged capability of the grains to accumulate assimilates and convert these into storage products.

Samenvatting

Korrelproductie en assimilatenhuishouding bij tarwe in relatie tot raseigenschappen, weersfactoren en stikstofvoorziening

Het hoofddoel bij de teelt van tarwe is steeds de produktie van korrels geweest. De korrelopbrengst is een functie van het aantal aren per m^2 , het aantal korrels per aar en het gemiddelde gewicht per korrel. Sinds door onderzoekers werd vastgesteld dat de korrelgroei grotendeels afhankelijk is van de postflorale fotosynthese, is er veel aandacht gegeven aan de betekenis van de grootte en de levensduur van de fotosynthetisch actieve organen voor de korrelopbrengst.

In aansluiting op de opvattingen van Watson en medewerkers over de bebladerings-index (leaf area index, LAI) en de bebladeringsduur (leaf area duration, LAD) werd de samenhang tussen de korrelopbrengst en het in de tijd geïntegreerde groene oppervlak van de afzonderlijke organen bestudeerd onder Nederlandse groei-omstandigheden. Door middel van meervoudige regressie-analyse kon tot 83% (R^2) van de variatie in korrelopbrengst toegerekend worden aan de variaties in de geïntegreerde groene oppervlakken van het vlagblad, de aarsteel, het voorlaatste blad en internodium. Uit deze analyse kon worden afgeleid dat het vlagblad en de aarsteel het sterkst gerelateerd waren aan de korrelopbrengst. Vanwege de hoge mate van co-variantie tussen groene oppervlakken van de individuele organen was het niet mogelijk de exacte bijdrage van de afzonderlijke organen te berekenen. Zelfs een hoge correlatie tussen groen oppervlak en korrelopbrengst geeft geen antwoord op de vraag of de groei van de korrels direct wordt beïnvloed door uitwendige omstandigheden dan wel indirect door de toevoer van de assimilaten uit de groene organen.

Hiertoe werden de invloeden van licht en temperatuur op de duur en snelheid van korrelgroei en op de stofwisselingsprocessen in de tarweplant bestudeerd door middel van fytotronproeven. Het bleek dat hoge temperaturen de groeisnelheid van de korrels sterk verhoogden, maar tevens de groeiduur bekortten. Daardoor werd de dagelijkse behoefte van de korrels aan assimilaten vergroot met het stijgen van de temperatuur. Omdat in de assimilatenbehoefte van de korrels grotendeels wordt voorzien door de fotosynthese tijdens de korrelvulling, is de hoeveelheid licht belangrijker voor de korrelopbrengst bij hoge dan bij lage temperaturen. De trage korrelgroei bij lage temperaturen veroorzaakte zelfs een overschot aan assimilaten, die opgeslagen werden in de vegetatieve organen; met name vond er opslag van water-oplosbare-koolhydraten in de stengel plaats.

Hoge temperaturen gedurende de korrelvulling bevorderden de opslag van stikstof in de korrels meer dan de toename van zetmeel. De lichtintensiteit had slechts een gering effect op de stikstofopname en eiwitsynthese in de korrel, maar beïnvloedde desondanks het eiwitgehalte van de korrel door een verandering van de koolhydratentoevoer naar de korrel. Ofschoon hoge temperaturen de stikstofopname in de korrel aanzienlijk versnelden, werd de totale hoeveelheid stikstof in de korrels nauwelijks beïnvloed. Dit duidt erop dat bij afwezigheid van stikstofopname door de tarweplant na de bloei de duur van de korrelvulling mede wordt bepaald door de stikstofvoorraad in de halm bij de bloei en door

de snelheid van herverdeling van stikstof vanuit de vegetatieve organen naar de korrel.

De reacties van (zomer-)tarwe op variaties in temperatuur en lichtintensiteit in het fytotron werden vergeleken met het gedrag van (winter-)tarwe onder veldomstandigheden gedurende zes jaren; deze jaren vertegenwoordigden een brede variatie in weersfactoren gedurende de korrelvulling. Er werd vastgesteld dat ook onder veldomstandigheden de temperatuur van bepalende invloed is op de snelheid en duur van de korrelvulling. De invloed van de temperatuur op de korrelopbrengst wordt echter gemaskeerd door de co-variantie tussen temperatuur en lichtintensiteit in het veld.

Uit het verloop van de koolhydratenaccumulatie in de stengel en de benutting van assimilaten door de korrel werd afgeleid dat de korrelgroei gedurende de eerste drie weken na de bloei meer gereguleerd wordt door de temperatuur dan door de beschikbaarheid van assimilaten. Gedurende de tweede helft van de korrelvullingsperiode reageerden de korrels positief in groeisnelheid op de extra assimilaten die beschikbaar komen bij een verlenging van de fotosynthese-activiteit. Dit wijst op een sub-optimale toevoer van assimilaten in deze fase. Er werd geconcludeerd dat onder Nederlandse groei-omstandigheden bij winter-tarwe de opslagcapaciteit van de korrels beperkend is gedurende de eerste weken na de bloei ('sink'-beperking), terwijl nadien de toevoer van assimilaten naar de korrel beperkend is ('source'-beperking). Tekorten aan water, stikstof etc. of het optreden van ziekten spelen hierbij een rol. Door late stikstofgiften en bestrijding van ziekten met fungiciden kon de levensduur van de fotosynthetisch actieve organen verlengd worden en daarmee de korrelopbrengst verhoogd. Een late, gedeelde stikstofgift vergrootte echter ook het aantal korrels per aar.

De produktiviteit van een gewas onder variërende uitwendige omstandigheden hangt sterk af van de raseigenschappen. De relatieve betekenis van enkele verschillende raseigenschappen werden vastgesteld door een vergelijking van een half-dwerg (semi-dwarf) en een standaardras. Het bleek dat de hogere harvest-index (aandeel van de korrel in de bovengrondse massa) van de half-dwerg ten dele werd veroorzaakt door een gunstigere aarvorming vóór de bloei en ten dele door een hogere groeisnelheid van de korrels gedurende de eerste weken na de bloei. De half-dwerg had een duidelijk lager stengelgewicht; daarentegen waren blad- en kafgewicht iets hoger dan bij het standaardras.

Tussen de rassen waren er slechts kleine verschillen in stikstofopbrengst en -verdeling, maar grote verschillen in de eiwitgehalten van de korrels. Het eiwitgehalte van de korrels bleek per ras sterk te reageren op weersinvloeden; een warm groeiseizoen verhoogde het eiwitgehalte sterk, terwijl in een koel seizoen dit gehalte laag bleef. De harvest-index voor stikstof varieerde nauwelijks tussen de seizoenen en tussen de rassen bij hoge, gedeelde stikstofgiften (van 0,74 tot 0,81). Tussen de groeiseizoenen bleek een grote variatie te bestaan ten aanzien van de hoeveelheid opgenomen stikstof na de bloei; deze hoeveelheid varieerde van 20 tot 50% van de stikstofopbrengst in de korrel. In het bijzonder als de groei van de vegetatieve organen beperkt werd, was postflorale stikstofopname nodig om bij een hoog opbrengstniveau aan de behoefte van de korrels te voldoen. Een dergelijke late opname van stikstof wijst op het vrijkomen van stikstofreserves uit het wortelsysteem en/of op een langere activiteit van het wortelstelsel.

De landbouwkundige mogelijkheden en beperkingen voor een verdere verhoging van de korrelobbrengst zijn besproken. Er wordt geconcludeerd, dat een verdere verbetering van de korrelobbrengst op een evenwichtige wijze moet worden nagestreefd, opdat de gewassen aangepast blijven aan de beperkingen van hun groeiomgeving. Tevens wordt opgemerkt dat een verdere toename van de korrelobbrengst kan worden verwacht van een groter aantal korrels per eenheid van grondoppervlak, van een langere activiteit van het wortelstelsel na de bloei en van een verlengde duur van opname en omzetting van assimilaten door de korrel.

Relation between green area duration and grain yield in some varieties of spring wheat

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Summary

In two experiments with spring wheat the relation was studied between green area duration (D) and grain yield during the period after heading. For this, the green areas of leaf, internode and ear were determined as accurately as possible in samples.

The relation between grain yield and green area duration of the separate green organs and of combinations of these was quantified by regression and correlation calculations. These calculations have shown that of the separate parts of the culm the D values of flag leaf and peduncle were closely correlated with the grain yield.

By using the combined D value of flag leaf and peduncle as a yield determining factor, 81 and 61 % of the variance in the grain yield could be statistically predicted in 1967 and 1968, respectively. By including all the separate D values in a multiple correlation calculation the coefficients of determination of the variance in the grain yield could be increased to 83 % in 1967 and to 74 % in 1968. In 1968, next to the D values of flag leaf and peduncle, the D value of the ear was closely correlated to the grain yield.

The photosynthetic efficiency of the green areas was compared by the grain-leaf ratio.

Introduction

The contribution of the various green organs in the wheat plant in ear filling for many years has been a subject of study for several workers. In these studies different methods were applied, among others, shading or clipping some parts of the culm (Boonstra, 1929; Asana and Mani, 1955; Birecka, 1968; Puckridge, 1968) and measuring the rate of photosynthesis and distribution of the assimilates with $^{14}\text{CO}_2$ (Birecka et al., 1963; Stoy, 1963; Carr and Wardlaw, 1965; Lupton, 1968; Rawson and Hofstra, 1969). These studies, especially the more recent ones, show that the carbohydrates in the grain are mainly provided by the flag leaf and the peduncle (including leaf sheath) and to a less extent by the ear, and the last leaf and internode, but one. The data on the size of the contribution by each of these organs in ear filling vary widely which may be partly due to differences in experimental conditions or techniques.

In various experiments it was found that the carbohydrates for ear filling are mainly formed during the period from heading onwards (Archbold, 1942; Thorne, 1965) and

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that from the carbohydrates formed before flowering 5 to 10 % are available to the grain by re-distribution (Stoy, 1965; Wardlaw and Porter, 1967; Lupton, 1968). Therefore, the greater part of the assimilates available for ear filling is dependent on the size and the duration of the green organs in the period after flowering.

Many of these experiments were done with single plants in pots or in the field, in which the growing conditions, dependent on the treatments always deviate to a more or less extent from crop conditions. In field experiments with 'undisturbed' crops the differences in grain yield between old and new varieties have been related by Watson et al. (1963) with the size and duration of the green parts of the culm. An usual measure of the latter is the green area duration (D), the green area per unit area of land integrated over the period of grain growth. The photosynthetic efficiency of the green organs for grain filling was estimated by deviding the grain yield by the green area duration, called the grain leaf ratio (G).

Welbank et al. (1966) found by calculating G values, first, a good correlation between the grain yield and the green area duration, and secondly, that the standard deviation of G was smaller if the green area duration only included the green area of the flag leaf and the peduncle (D_{Flax}) during the period after flowering.

With reference to this work from Great Britain, two experiments were conducted with spring wheat to study which D value was closed correlated to the grain yield, and in particular during which period D had to be calculated and which parts of the culm the D value would be composed of. By means of correlation and regression calculations the relationships between the D values of the important green parts and the grain yields have been analysed. Should the parameter, green area duration, show a close correlation with the differences in grain yield, this might lead the breeder to make more purposeful use of genetic differences in the concerning morphological characteristics in the wheat plant and it might give the cereal grower a better idea of the effect of certain cultivation measures, as e.g. a late nitrogen application, on the production pattern of the crop.

Material and methods

The field experiments were conducted in 1967 and 1968 with spring wheat on a fine-textured (about 35 % clay) soil on subrecent Rhine sediments. To vary the crop structure the following treatments were applied:

1967:

- 2 varieties: 'Opal' and 'Orca'
- 3 sowing dates: 17 March, 12 April and 5 May
- 3 seed rates: 160 kg, 180 kg and 200 kg per ha

Nitrogen fertilizing was the same for all the treatments, viz 30 kg N/ha at sowing, 20 kg N/ha in the F_0 stage and 20 kg N/ha in the $F_{10.1}$ stage (according to the Feekes scale);

1968:

- 3 varieties: 'Opal', 'Gaby' and 'Orca'
- 2 sowing dates: 4 March and 16 April
- 2 CCC levels: without CCC and 2 l CCC per ha, applied in the F_0 stage
- 2 N levels: 75 kg N/ha and 75 kg + 25 kg N/ha at the beginning of flowering.

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The former experiment had a split plot design and the second a block design; both experiments were set out in four replicates. The total number of plots in 1967 and 1968 was 72 and 96, respectively.

It has to be pointed out that the different 'crops' obtained in such an experimental design do not grow under equal conditions with respect to light intensity, temperature, precipitation, etc., although the growing periods overlap for the greater part. In the two years the climatical conditions differed to such an extent that the results are discussed separately.

To determine the dry matter weights and the green area, there were five intermediate harvests from heading onwards, viz:

H₁: when 50 % of the culms were heading (F_{10.3})

H₂: at flowering (F_{10.5.2})

H₃: two weeks after flowering

H₄: four weeks after flowering

H₅: at a grain moisture content of about 35 % (1967) or six weeks after flowering (1968).

At the final harvest in 1967 5.4 m² was available and 3.7 m² in 1967. Per intermediate harvest a sample of 0.25 m² was harvested from each plot, of which the total dry-matter weight and the number of culms were determined. In counting, the last culm of each ten was used to make a sub-sample of 10 culms. Of these culms the following green parts were measured:

- of each leaf lamina separately, its length (cm) and the greatest width (mm);
- length (cm) and diameter (mm) of the internodes, including the leaf sheaths;
- the dimensions of the stem and the ear.

After this, the ten culms were separated in leaves, stems and ears for dry-matter determination of the separate parts.

The leaf area in 1967 was obtained by multiplying the product of length and width with a correction factor (Table 1). This factor was determined at each intermediate harvest, because the shape of the green leaf area is not constant during ripening. This was done by means of photographic prints which gave the actual areas.

The date of 1967 showed a good correlation between the length and the area of the flag leaf and leaf 2, a correlation coefficient of 0.94 and 0.97, respectively (n = 288). Based on this, in 1968 leaf length was used as an index for the leaf area; the leaf coefficient in this case is the quotient of the photographical area and leaf length.

The green area of the internodes (including leaf sheaths) was calculated as the area of a cylinder with the formula: height × circumference. The green area of the ear was calculated in 1967 as length × width of the separate sides; in 1968 the perpendicular projections of the sides on the horizontal plane were measured photo-electrically.

Table 1. Average leaf coefficients of flag leaf, leaf 2 and leaf 3; calculated as the quotient of the photographical area and the product of length and width (1967 trial).

	Flag leaf	Leaf 2 *	Leaf 3 *
Harvest 1	0.80	0.88	0.93
Harvest 2	0.86	0.92	0.94
Harvest 3	0.92	0.96	1.01

* Leaves and internodes were numbered from top to bottom.

Results

In both years there was a significant varietal as well as sowing date effect on the grain yields and on the size of almost all the green areas. In addition there was a great deal of interaction between the varieties and the sowing dates. The chlormequat (CCC) treatment in 1968 had significant effects on the grain yield and the green areas of some organs; this did not apply to the factor seed rate (1967) and the late top dressing of nitrogen in 1968.

Green area

The green areas of the organs are not constant during the post-floral period: the green leaf area decreases more rapidly as the leaves on the culm are older, whereas the green area of the top internodes and ear continues to increase until 14 days after flowering, when they decrease rapidly (Table 2).

The size of the green area of the various assimilating parts of the plants has also been calculated as green area index = I (Fig. 1), by multiplying the green areas per culm with the number of culms per m^2 . The differences in green area indices (I) between the treatments were smaller than the differences in green area per culm, because a greater number of culms was accompanied by a smaller area per culm.

The size and the duration of the green parts can be expressed in one parameter, green area duration (D). This is calculated as the integral of the green area index against time. In the calculations the green area index was assumed to be linear and the green area duration can be found with the following formula:

$$D = \sum_{n=2}^e \frac{I(n-1) + I(n)}{2} \times \frac{\text{number of day}}{7} \quad (\text{dimension: weeks})$$

The D values in 1967 were calculated from heading to ripening as well as from flowering to ripening; in 1968 the D values were also calculated for each interval between two harvests.

Of the D_F value mentioned in Table 3 of flag leaf + peduncle + ear about 20 % were realized before flowering and about 80 % after; the latter percentage was divided as follows: 35 % in the first 14 days after flowering, 30 % in the next 14-day period and 15 % in the remaining period.

In all the D values there was a distinct varietal and sowing date effect, either as a major effect or as an interaction effect. The D values of the late-sown treatments were

Table 2. Average green area (cm^2) of the different parts of the culm at five intermediate harvests (1967 trial).

	H_1	H_2	H_3	H_4	H_5
Flag leaf	29.1	29.5	26.7	15.7	—
Leaf 2	27.8	26.5	23.5	3.5	—
Leaf 3	19.9	17.9	10.3	0.3	—
Leaf 4	7.7	6.1	—	—	—
Leaf total	85.4	80.3	61.7	19.5	—
Peduncle	13.7	28.4	30.8	23.0	1.5
Internode	24.8	24.8	25.1	20.8	1.8
Ear	20.1	25.7	33.7	27.8	?

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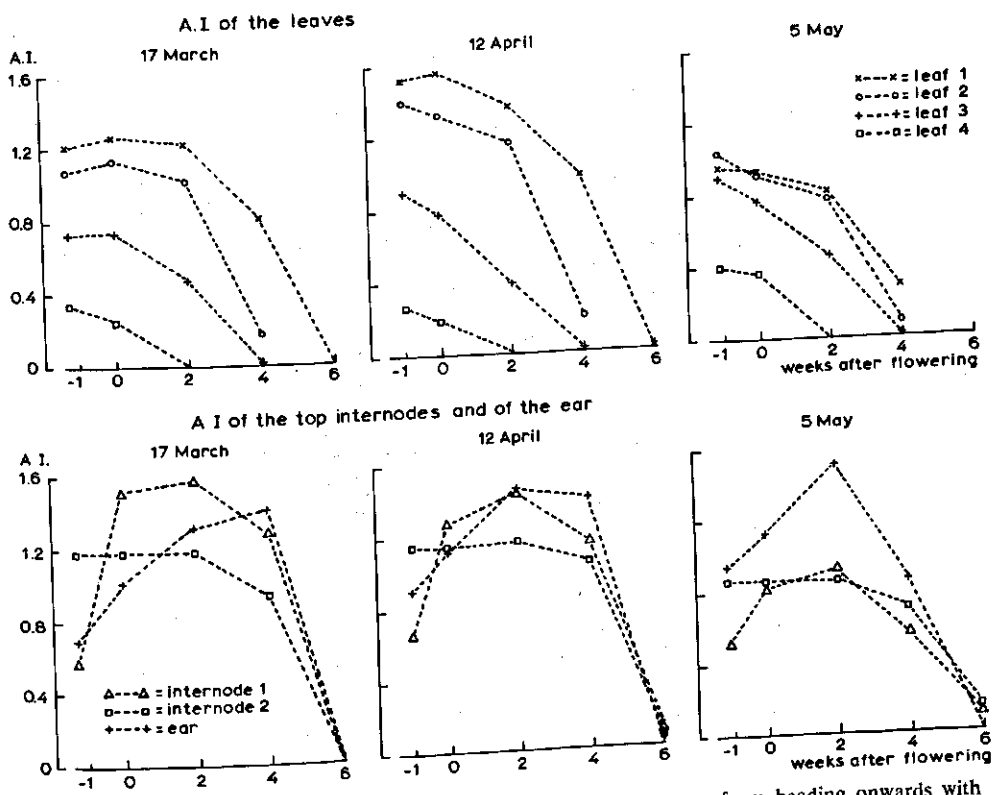


Fig. 1. Trend in the green area index (A.I.) of the separate culm parts from heading onwards with three different sowing dates.

distinctly lower than those of the early sown. This decrease was mainly due to a lower number of culms, as the result of less tillering, the sooner ripening of the late-sown treatments also affecting the D values. Of the remaining treatments chlormequat (CCC) gave a significant ($\alpha < 0.001$) decrease in the D_F value; for untreated and treated plots 19.2 and 16.5 weeks, respectively. This difference was caused by the decline in green area by chlormequat, especially of the peduncle. These data show that due to varietal characters and cultivation methods, the 'crops' differ in duration and size of the green area.

Grain yield

The grain yields were very much affected by the sowing date; especially the late-sown treatments had a much lower yield, e.g. in 'Orca' (Fig. 2). As is shown in Table 4 the sowing date effect was not identical in the two years on equal sowing dates; this was due to the differing climatical conditions.

The grain yield is composed of the following components: number of ears/m², number of grains/ear and the 1000-grain weight. In 1967 the 1000-grain weight was the main determinant of the grain yield ($r = 0.85$). In addition the number of ears per m² was important ($r = 0.59$), whereas the number of grains per ear did not show a

Table 3. Green area duration (weeks) in the period from heading to ripening.

1967 trial											
Variety (V) →	'Opal'			'Orca'			mean	σ	V ¹	S ¹	VS ¹
Sowing date (S) →	17/3	12/4	5/5	17/3	12/4	5/5					
Flag leaf (F)	6.4	7.7	4.2	7.6	7.4	4.1	6.2	0.6	ns	***	***
Leaf 2	5.0	4.9	3.8	5.0	5.6	3.6	4.7	0.5	ns	***	**
Leaf 3	2.2	1.4	2.1	3.1	3.2	3.1	2.5	0.4	***	**	***
Leaf total	14.0	14.0	10.4	16.7	17.0	12.4	14.1	1.4	***	***	ns
Peduncle (P)	8.2	7.6	4.8	9.6	7.2	4.4	7.0	0.8	ns	***	***
Internode 2	6.4	6.2	4.6	7.8	6.8	5.4	6.2	0.6	***	***	ns
Ear (E)	6.3	6.2	5.9	9.2	9.0	7.9	7.4	0.6	***	***	*
D _F = F + P + E	20.9	21.5	14.9	26.4	23.6	16.4	20.6	1.7	***	***	*

1968 trial											
Variety (V) →	'Opal'		'Gaby'		'Orca'		mean	σ	V ¹	S ¹	VS ¹
Sowing date (S) →	4/3	16/4	4/3	16/4	4/3	16/4					
D _F = F + P + E	23.5	16.5	20.2	12.9	21.9	12.2	17.9	1.6	***	***	***

¹ ns: non-significant ($\alpha > 0.05$); *: $0.05 \geq \alpha > 0.01$; **: $0.01 \geq \alpha > 0.001$; ***: $\alpha \leq 0.001$.

Table 4. Dry matter yields (kg. ha⁻¹) and the relevant yield components.

1967 trial											
Variety (V) →	'Opal'			'Orca'			mean	σ	V ¹	S ¹	VS ¹
Sowing date (S) →	17/3	12/4	5/5	17/3	12/4	5/5					
Yield (kg. ha⁻¹):											
Grain	4510	4527	3335	5106	4703	2943	4188	243	*	***	***
Straw	5661	5747	4354	6764	6495	5324	5724	360	***	***	—
Total	10171	10274	7689	11870	11198	8267	9912	—	—	—	—
Components:											
Ears/m ²	404	412	328	502	474	420	423	20	***	***	**
Grains/ear	37.8	42.3	43.2	33.6	33.2	34.2	37.4	3.4	***	*	*
1000-grain weight (g)	38.3	35.9	33.3	38.7	38.3	33.4	36.3	1.0	***	***	***

1968 trial											
Variety (V) →	'Opal'		'Gaby'		'Orca'		mean	σ	V ¹	S ¹	VS ¹
Sowing date (S) →	4/3	16/4	4/3	16/4	4/3	16/4					
Yield (kg. ha⁻¹):											
Grain	4440	3005	4155	2917	4025	2375	3486	420	***	**	ns
Straw	4960	3470	4390	3430	4360	3790	4068	—	***	***	***
Total	9400	6475	8545	6347	8385	6165	7552	—	***	***	*
Components:											
Ears/m ²	550	482	550	514	558	521	529	—	***	***	**
Grains/ear	30.1	—	28.1	—	23.5	—	27.2	—	***	—	—
1000-grain weight (g)	33.8	30.6	32.0	29.3	35.0	29.2	31.7	—	***	***	***

¹ ns: non-significant ($\alpha > 0.05$); *: $0.05 \geq \alpha > 0.01$; **: $0.01 \geq \alpha > 0.001$; ***: $\alpha \leq 0.001$.

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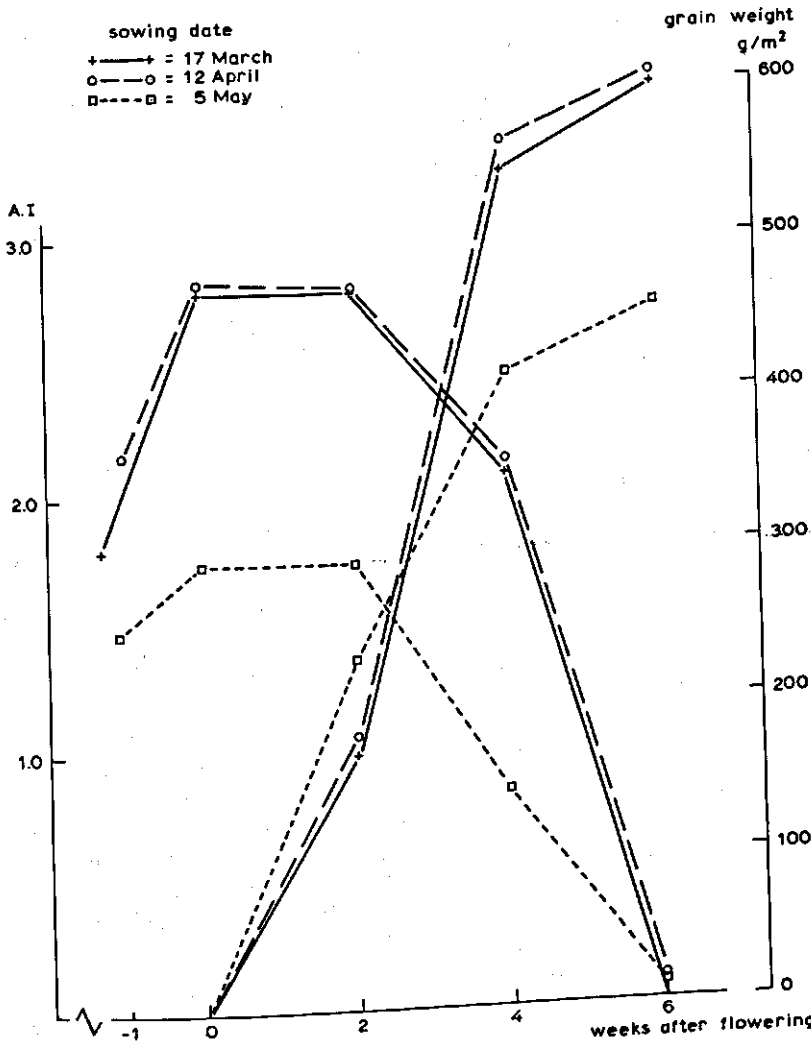


Fig. 2. Trend in green area index (A.I.) of the flag leaf + peduncle in relation to grain production with three sowing dates (1967).

significant correlation to the grain yield ($r = 0.17$).

In 1968 there were also appreciable differences in number of grains per ear between the varieties. The number of ears per m² and the 1000-grain weight were distinctly affected by an interaction of variety and sowing date.

Attention is called to the fact that the product of the number of ears per m², the number of grains per ear and the 1000-grain weight is higher than the actual yield. This is due to systematic over-estimation of the 1000-grain weight or the number of grains per ear and an underestimation of the actual yield due to sampling errors and threshing losses, respectively.

In the further calculations this level difference between actual and calculated yields will not be essential, because calculated and actual yields were found to be very closely correlated.

Table 5. Estimated proportion (R^2) of the variance in grain yield that can be attributed to its linear regression on the green area duration of the different green organs.

	1967 trial		1968 trial
	period from heading on-wards (n=72)	period from flowering on-wards (n=72)	period from heading on-wards (n=96)
Flag leaf	0.72	0.67	0.41
Leaf 2	0.53	0.45	0.38
Leaf 3	0	0	0.05
Leaf total	0.47	0.36	—
Peduncle	0.79	0.73	0.57
Internode 2	0.56	0.13	0.27
Ear	0.13	0.16	0.52
Flag leaf + peduncle	0.81	0.79	0.61
Flag leaf + leaf 2	0.70	0.63	0.44
Peduncle + internode 2	0.75	0.60	—
Flag leaf + peduncle + ear	0.68	0.62	0.63
Flag leaf + leaf 2 + peduncle + internode 2 + ear	0.68	0.60	0.55

—: correlation not calculated.

Relation between grain yield and green area duration

In the quantitative determination of the relation between grain yield and green area duration (D) regression and correlation calculations were applied. The squares of the correlation coefficients indicate which part of the total variance in the grain yield (y) is statistically explained by the concerning D values (x). These coefficients were calculated between the grain yield and the D values of the separate green organs during the period from heading and from flowering to ripening. Table 5 shows that the D values during the former period are closer correlated to the grain yield than the D values during the latter period. The D values of the flag leaf and the peduncle were very closely correlated with the grain yield in both years. By adding the separate D values, mainly the combination flag leaf + peduncle gave a higher correlation coefficient in the two years.

No correlation was found between the D values of leaf 3 and the grain yield which suggests that there is no direct contribution of leaf 3 to the ear filling. This is in accordance with the mentioned results of the ^{14}C experiments. The relation between the D value of the ear and the grain yield differed between the years, which was probably due to differences in the method of determining the green ear area.

The correlations between the grain yield and the green area duration were higher in 'Orca' than in 'Opal', 'Gaby' being intermediate. The regression line of 'Orca' had a somewhat steeper trend than that of 'Opal', which was due to the differing response of the varieties to the sowing date. In 'Orca' the grain yield was more than proportionally lower than the D value, as the sowing date was later, in 'Opal' the grain yield and the D value showed a similar response to late sowing.

The trends resulting from the simple regression and correlation calculations are reflected more distinctly by multiple regression calculations. In the 1967 trial the greater part of the variance in grain yield could be determined by the linear equations:

$Y = 17.3 D \text{ flag leaf} + 25.0 D \text{ peduncle} + 141.9$ $R^2 = 0.83$ $n = 72$
In the separate varieties:

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Table 6. Correlation matrix ($r \times 100$) of the D values (1967 trial).

	1	2	3	4	5	6
1. D flag leaf	100	86	0	84	79	43
2. D leaf 2		100	27	70	75	50
3. D leaf 3			100	2	32	79
4. D peduncle				100	85	38
5. D internode 2					100	64
6. D ear						100

Opal: $Y = 13.3 \text{ D flag leaf} + 20.5 \text{ D peduncle} + 194.3$ $R^2 = 0.74$ $n = 36$
Orca: $Y = 23.9 \text{ D flag leaf} + 24.8 \text{ D peduncle} + 102.7$ $R^2 = 0.89$ $n = 36$

$Y = \text{grain yield in g.m}^{-2}$; $D = \text{green area duration in weeks}$.

These equations indicate that flag leaf and peduncle are essential in ear filling. The partial regression coefficients, however, are not of absolute significance, because the D values of flag leaf peduncle are not only closely interrelated, but also correlated with the D values of other plant organs (see Table 6).

The D values of flag leaf and peduncle represent in the preceding therefore, a photosynthetic system including more than only their own green areas.

Grain-leaf ratio

The efficiency of the plant organs with respect to ear filling, indicated in the British literature as grain-leaf ratio (G), is calculated as the quotient of grain yield and green area duration (D).

In 1967 the G value referred to the D values of flag leaf + peduncle and in 1968 to the D values of flag leaf + peduncle + ear (see Table 7), because these D values showed the better correlation with grain yield. The average G value in 1968 was $19.8 \text{ g.m}^{-2}.\text{week}^{-1}$, and in 1967, when the D value of the ear was included in the calculation, $20.1 \text{ g.m}^{-2}.\text{week}^{-1}$. When the very late sowing date (5 May) is not included,

Table 7. G values ($\text{g.m}^{-2}.\text{week}^{-1}$), calculated from the grain yield and the D value at the final harvest.

1967 trial		'Opal'			'Orca'			mean	σ	V ₁	S ₁	VS ₁
Variety (V) →	Sowing date (S) →	17/3	12/4	5/5	17/3	12/4	5/5					
G (flag leaf + peduncle)		31.4	30.2	37.9	30.2	32.8	35.1	32.9	3.2	ns	***	*
1968 trial		'Opal'		'Gaby'		'Orca'		mean	σ	V ₁	S ₁	VS ₁
Variety (V) →	Sowing date (S) →	4/3	16/4	4/3	16/4	4/3	16/4					
G (flag leaf + peduncle + ear)		18.9	18.3	20.6	22.6	18.4	19.5	19.8	2.8	***	ns	*

¹ ns = non-significant; * $0.05 \geq \alpha > 0.01$; *** $\alpha \leq 0.01$.

Table 8. The relation between the number of grains and the green area of flag leaf and peduncle.

Variety (V) →	'Opal'			'Orca'		
	17/3	12/4	5/5	17/3	12/4	5/5
Sowing date (S) →						
Number of grains per 10 cm ² green area	8.2	7.5	10.9	7.8	8.1	11.0

the difference in G value between 1967 and 1968 is greater still: a sunny year and a wet and dark growing season, respectively.

Within the varieties the G value of 'Gaby' was significantly higher than in 'Opal' and 'Orca'. Similar as with the late sowing date, this did not result in a higher grain yield, because the green area duration was proportionally more decreased than the increase in the G value.

The G value was not constant throughout the ear-filling period; in 1968 the G value in the three subsequent fortnight periods after flowering was 26.4, 43.0 and 18.1 g.m⁻².week⁻¹, respectively. In the first 14-day period the assimilating area was somewhat larger than in the second, but the rate of ear filling was much retarded, for the period 1 and 2 this was 120 and 170 kg.ha⁻¹.day⁻¹, respectively. Immediately after flowering more carbohydrates may have been available than could be utilized by the growing grains. In the third post-floral period the lower G value was probably caused by aging of the assimilating organs.

Discussion

Various workers state that the grain yield is determined by the quantity of carbohydrates formed by the photosynthetically active green organs for the benefit of the ear filling after flowering. As a measure for the production capacity of carbohydrates the green area duration of special organs is used, viz the flag leaf (lamina and sheath), the peduncle and the ear. Direct ¹⁴C analyses of the plant have shown that the greater part of the assimilates produced in the post-floral period in these organs is translocated to the ear. Within this framework two experiments were conducted to study the correlation of the green area duration of special organs of the culm and the grain yield.

The results show (see Table 5) that green area duration calculated of the period from heading to ripening is more closely correlated to the grain yield than the green area duration in the period from flowering to ripening. On the other hand, Welbank et al. (1966) found that the green area duration from flowering to ripening was more closely correlated to the grain yield. However, it is not impossible, though ear filling only starts after flowering, that the photosynthesis in the period between heading and flowering affects the ultimate grain yield. This may be by:

- re-distribution of the assimilates being temporarily reserved in the peduncle, forming a contribution to ear filling;
- the effect of the assimilates available before and during flowering on the potential number of fertile grains per ear (Bremner, 1967; Ruckebauer, 1970) which determine the sink strength of the ear for assimilates.

The calculations further showed that in 1967 the green area duration of the flag leaf + peduncle gave the better correlation to the grain yield and that in 1968 an essential improvement in the correlation was obtained by also including the D value of the ear in the calculations. The D values of leaf 2 and internode 2 were less closely correlated to the grain yield, the D value of leaf 3 showing no correlation at all.

Since the D values of the various green parts of the culm were closely interrelated as well (Table 6), it was not possible to calculate the exact contribution of the separate organs in ear filling by regression calculations. The degree of correlation between grain yield and green area duration did indicate which organs were important in ear filling; these were, especially the peduncle (including the sheath of the flag leaf) and the flag leaf, followed by the ear, the last leaf and internode, but one. These also are the organs which to a more or less extent were found to be important as production centres of carbohydrates for ear filling in the literature mentioned in the introduction. The estimated contribution of the separate organs in ear filling was also found to vary with the ^{14}C method depending on the variety, experimental conditions and techniques applied. The older clipping and shading experiments had already shown that in a wheat culm the lost function of an eliminated organ is compensated to a considerable extent by the other green organs. Compensation effects are the greater as the effect of the treatment lasts longer.

For a better understanding of the importance of the crops structure in ear filling the rate of photosynthesis and translocation should be measured in addition to the green area of the organs (Lupton, 1969).

An idea of the average photosynthetic efficiency of the green parts is obtained by the grain-leaf ratio (G). The G value of the late sown treatment in 1967 was strikingly high. One of the reasons for this could be:

- a. a higher photosynthetic rate of the relatively young organs accompanied by a higher light intensity in the crop due to the lower density;
- b. a greater requirement for assimilates due to the great number of grains per ear.

The effect of the number of grains per ear on the G value can be inferred from the relation between the number of grains and the green area of the flag leaf and peduncle during the first two weeks of the post-floral period.

The parallelism in these figures with the G values (Table 7) shows that the sink strength might influence the G value.

In general it may be assumed that the correlation between green area duration and grain yield will be important, when the green area present cannot yet provide in the carbohydrate requirement of the ear. When sufficient carbohydrates are provided the grain yield is increasingly determined by the sink strength of the ear, i.e. the number of grains.

The efficiency of the green organs, in addition to the internal sink source relation will be influenced by climatical factors, in particular, the light regime in the crop and by the growing conditions, especially the availability of water and nitrogen.

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Effects of successive applications of maneb and benomyl on growth and yield of five wheat varieties of different heights

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Summary

The effect of some fungicide treatments on the production pattern of five wheat varieties with different culm lengths was investigated in a field experiment. The fungicide treatments consisted of: a sequence of 2 pre-floral sprayings with 2 kg maneb per ha and 2 post-floral sprayings with 1 kg benlate per ha. The varieties were Juliana (117 cm culm length), Manella (82 cm), Lely, (80 cm), Mex.-cross (69 cm) and Gaines (79 cm). There was hardly any mildew in the crop but *Septoria tritici* and *Septoria nodorum* were very much in evidence in all the varieties. Of the group of ripening diseases, black moulds and *Fusarium* were found to a lesser degree.

The combined application of maneb and benomyl greatly delayed the spread of *Septoria* in the crop, as a result of which the flag leaf in particular remained green for a longer period and the grain filling period was lengthened. The growth rate of the grains during the phase from the milk-ripe stage to the dough-ripe stage was raised from 204 kg ha⁻¹ day⁻¹ to 230 kg ha⁻¹ day⁻¹. The effect of the application was greater in the varieties most susceptible to *Septoria* (Lely and Gaines) than in the other varieties. The increases in grain yield of the varieties Juliana, Manella, Lely, Mex.-cross and Gaines were 14 %, 23 %, 32 %, 16 % and 42 %, respectively. By statistical analysis 85 % of the variance in the grain yield within the varieties could be attributed to the green area of the flag leaf. Thus, the main effect of *Septoria* seems to be a reduction of the photosynthetic area, causing a decreased supply of assimilates to reach the grain, and in this way lowering the 1000-grain weight.

The degree of disease infection was not significantly correlated with culm length or the amount of leaf area, so the tolerance and resistance characteristics of the varieties were not immediately due to differences in crop structure. Specific variety differences were still present, even after reduction of the disease infection with the fungicides.

Introduction

Cereal growers have always relied on breeding for resistance and on such methods as crop rotation, seed dressing, etc. for minimizing damage due to diseases. Owing to the increased disease intensity, which apparently is a consequence of narrower crop rotation and more intensive cultivation by using higher seed rates and more nitrogen fertilizer, the resistance of present-day wheat varieties to fungal diseases has in many cases proved inadequate (Dilz, 1970). Inadequate resistance is particularly evident in

periods in which climatic conditions encourage the spread of moulds. Under such conditions the application of fungicides would seem worthwhile, particularly since, with the present high level of yields, a small effect will increase the yield enough to compensate for the cost of a fungicide dressing (de Jong, 1970).

Besides the effects of climate on the incidence of disease, it has been found (Feekes, 1967) that there is a great difference between the varieties with regard to their resistance to and tolerance of such diseases as *Erysiphe graminis*, *Puccinia striiformis* and *Septoria nodorum*. It is also assumed that culm length is an important feature for susceptibility to diseases; in this view varieties with short culms are more readily and seriously infected than those with longer culms (Brönnimann, 1969a). In the case of *Septoria nodorum*, this is supposed to be due to the shorter infection path from the soil via stem and leaf to the ear, or to the microclimate in crops with short culms being more favourable for fungi. Therefore the question arises whether varieties with greatly differing morphology differ in production owing to their variety-dependent susceptibility to diseases or owing to factors attributable to the physiology of growth. This should be tested by comparing crops with and without disease control by fungicides.

A field experiment was undertaken with five varieties of winter wheat to study the effect of fungal diseases on the production pattern of varieties with different crop morphologies. The crop was treated with two fungicides at different times before and after anthesis. The effect of leaf diseases, in particular on the size of the leaf area and on the grain filling process are studied in the light of the findings.

Methods

The experiment was carried out in 1972 on good clayey soil in the Flevo polder. The following varieties and crosses of winter wheat were used:

Dutch varieties:

Juliana - Wilhelmina × Essex gladkaf; crossed in 1903, 1921 accepted in Dutch variety list;

Manella - Alba × Heine's 7; crossed in 1950, 1964 variety list;

Lely - Cebeco 30 × Flevina; crossed in 1960, 1970 variety list.

Semidwarfs:

Mex.-cross - (Nord × Heine's 7)₁₀₈ × Mex. dwarf; made available by Dr W. Feekes of Geertsema's Nurseries at Groningen;

Gaines - (Norin 10 × Brevor, sel 14) × Brevor × Oro × Turkey × Florence × Oro × Fortyfold × Federation; crossed in Washington, USA, CI No 13448.

Sowing date: 15 October 1971; seed rate: 120 kg per ha. Fertilized in autumn with 60 kg P₂O₅ superphosphate per ha. Potassium is abundant in this young marine clay, so no additional fertilizing was required. Two nitrogen dressings were given, viz 30 kg N per ha, as Ca (NO₃)₂ on 20 March, followed by a second dose of 30 kg N per ha on 4 May 1972.

Owing to the mild winter there was a good deal of chick-weed (*Stellaria media*) in April; this was controlled by spraying with 4 litres of MCPP and 4 litres MCPA per ha on 19 April. At the same time 3 litres of chlormequat per ha was sprayed on the crop.

Fungicides were-applied according to the following scheme:

Date	Stage on Feekes scale (Large, 1954)	Preparation			
		name of agent	concentration	quantity of product	
15 May F _{7 to 8}	}	maneb	manganous ethylene- bis[dithiocarbamate]	80 % sol.	2 kg/ha
29 May F _{9 to 10}					
20 June F _{10.3-10.5}	}	benlate	benomyl: methyl-butyl carbamoyl benzidiazolyl carbamate	50 % sol.	1 kg/ha
11 July idem + 3 weeks					

Number of plots: 5 (varieties) \times 2 (Maneb + Benlate) \times 6 (replicates) = 60.

The following intermediate harvests (H) were carried out to determine the dry matter weights, the number of tillers and the green areas:

H₁₋₄: 10 March, 17 April, 2 May, 16 May; 0.25 m² per variety;
 H₅₋₉: 30 May, 13 June, 27 June, 10 July, 25 July; 0.25 m² of each plot;
 H₁₀: 9 August; 1 m² of each plot;
 H₁₁: 21 August; 60 m² harvested with the combine harvester.

The degree of disease infection in the field crop was estimated by rating on the harvesting dates H₁₋₄; systematic estimates per leaf layer were made on 30 May, 7 June, 25 June and 10 July. On 20 July the leaf necrosis due to disease could no longer be clearly distinguished from normal dying off; therefore, only the percentage of green area of the flag leaf was ascertained on that date.

On 14 July the light interception at 3 heights in the crops was ascertained in all plots with the aid of an integrating photometer 1 metre long.

Results

Degree of infection

In 1972 the growing season was mainly dull, cold and wet, except for the second half of July, when there was a dry, sunny and extremely hot spell. Coming as it did after a mild winter, these weather conditions caused great disease intensity in the crop. Symptoms of the following diseases were determined:

at the base of culm :	<i>Cercospora herpotrichoides</i>	- eyespot
on leaf and ear :	<i>Septoria tritici</i>	- leaf blotch
	<i>Septoria nodorum</i>	- glume blotch
on the ear :	<i>Fusarium sp.</i>	- fusarium

Cercospora. On 15 June a test for soil-borne pathogens was carried out on 50 culms per plot. The degree of infection was calculated according to Fehrmann (1972) with the formula:

(% slightly infected + 2 \times % severely infected)/100
 The indices (scale: 0-2) thus calculated for Juliana, Manella, Lely, Mex.-cross and Gaines were 1.11, 1.23, 1.29, 1.16 and 0.95, respectively. It is evident from these figures that all varieties were moderately infected with soil-borne pathogens, thus causing an

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increased risk of lodging. Lodging in all varieties with the exception of Juliana was presumably prevented by a relatively low nitrogen dressing and an early application of chlormequat.

Septoria. The severest leaf infection was by *Septoria* (*S. tritici* and *S. nodorum*). By mid-May it was found that in all the varieties *Septoria* had covered the entire 5th leaf from the top and approximately 40 % of the 4th leaf. The first symptoms after anthesis were seen in the flag leaves in the untreated plots, whereas they did not appear in the plots treated with maneb and benomyl until a fortnight later. Early maneb sprayings followed by benomyl sprayings before and after anthesis did not eradicate *Septoria* but did largely inhibit its spread (Table 1). This is most evident from the green area of the flag leaf on 20 July, viz during grain growth.

Table 1. Infection in leaves and ears on 10 July and green area of flag leaves and two topmost internodes on 20 July.

		% of area covered with <i>Septoria</i> symptoms on 10/7				% of area green on 20/7	
		flag leaf	2nd leaf	3rd leaf	ear ¹	flag leaf	1st and 2nd internodes
Juliana	+	0.0	12.5	69.0	2.1	90.0	39.2
	—	1.0	40.8	95.0	4.9	77.5	44.2
Manella	+	0.7	7.5	72.5	11.8	93.3	17.5
	—	5.0	60.9	99.2	23.6	32.5	27.5
Lely	+	1.3	22.5	91.5	9.0	90.8	35.0
	—	9.2	95.0	100.0	15.8	12.5	31.7
Mex.-cross	+	0.0	1.5	24.2	22.9	84.2	20.0
	—	1.8	10.8	74.2	34.1	40.0	13.3
Gaines	+	1.2	68.2	100.0	17.9	64.2	15.8
	—	55.0	100.0	100.0	25.2	5.0	12.5
Average	+	0.6	22.4	71.4	12.7	84.5	21.3
	—	14.4	61.3	93.7	20.7	33.3	21.5

¹ In the ear *Septoria* and *Fusarium* symptoms.
+ = 2 × maneb + 2 × benlate; — = untreated.

Fusarium. On 10 July a test for ear diseases was carried out on 20 ears per plot. The degree of infection by *Septoria nodorum* and *S. tritici* and by *Fusarium culmorum* is represented by one figure for both diseases (Table 1). Manella, Mex.-cross and Gaines were most susceptible to ear diseases. On average the ear infection was decreased by fungicides from 20.7 to 12.7 %.

The effect of the fungicide on green leaf area was found to be greatest in the varieties that were most severely infected with *Septoria*; the sequence from high to low was: Gaines, Lely, Manella, Mex.-cross and Juliana.

A point that should be noted is that the shortest and tallest variety were the least infected by *Septoria*; consequently, other variety characteristics besides the length of the culm must have affected resistance.

The following diseases were also observed to a lesser degree of infection:
 at the base of the culm : *Gäummanomyces graminis* – take-all
 on the leaf : *Erysiphe graminis* – mildew
 : *Puccinia recondita* – brown rust
 in the ear (and on some other parts of the culm) : *Cladosporium* sp. – black moulds
 : *Alternaria* sp.

Effect of fungicides on production pattern

From anthesis onwards, the areas of the separate leaves were measured. Significant ($\alpha < 0.05$) positive effects of maneb and benomyl on leaf area were observed in leaf (4) on 13 June, in leaf (4) and leaf (3) on 27 June, in leaf (3), leaf (2) and flag leaf on 10 July, and in the flag leaf on 25 July. The differences in leaf area observed on 13 and 27 June were the results of the two treatments with maneb on 15 and 29 May; they had no effect on the number of grains per ear (Table 2). In this experiment the indirect effect of maneb on grain filling by the longer protection of the two topmost leaves from *Septoria* could not be distinguished from the fungicidal action of benomyl sprayed on 20 June and 11 July. The observation that maneb only protects the leaf against fungal diseases for a limited time (approximately a fortnight), would imply that it was due to

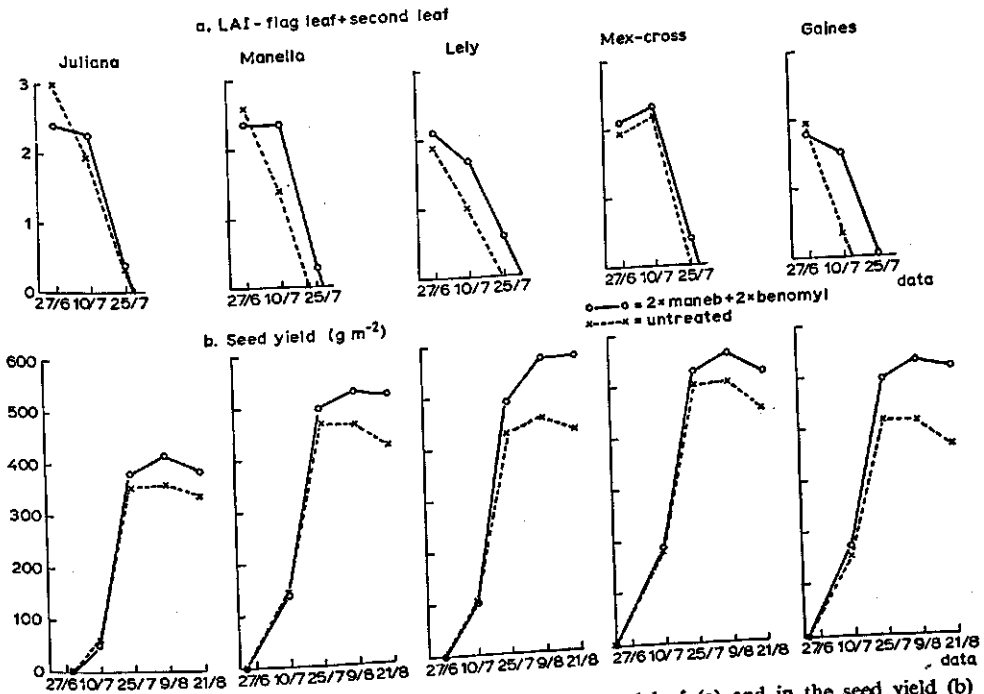


Fig. 1. Trend in the leaf area index of the flag leaf and second leaf (a) and in the seed yield (b) from flowering onwards with five varieties of wheat.

Table 2. Effect of two benomyl sprayings, preceded by two of maneb, on final yield and yield components.

	Juliana		Manella		Lely		Mex.-cross		Gaines		Mean	c.v.	Significances ¹		
	+	-	+	-	+	-	+	-	+	-			R (var.)	F (fung.)	RF
Seed ² (g/m ²)	389	342	520	422	573	432	532	452	521	366	454	4.3	****	****	****
Straw ³ (g/m ²)	872	834	669	661	670	643	648	599	628	629	685	7.4	****	*	n.s.
Chaff ³ (g/m ²)	114	107	129	127	145	137	130	131	190	182	139	6.6	****	*	n.s.
Total dry matter ³ (g/m ²)	1396	1287	1325	1249	1381	1253	1328	1228	1348	1223	1278	6.6	**	***	n.s.
Harvest index ⁴	0.32	0.29	0.42	0.39	0.44	0.40	0.44	0.44	0.42	0.36	0.39	3.3	****	****	***
Number of culms ³ per m ²	543	577	551	550	462	491	488	485	752	764	566	5.3	****	*	n.s.
Grain weight ³ (g/1000)	30.3	26.4	37.9	33.5	36.0	30.0	36.7	33.8	29.0	23.8	31.7	3.2	****	****	**
Number of grains per ear ⁴	26.3	25.0	25.9	26.4	34.0	33.7	30.6	30.8	25.3	24.4	28.3	8.5	****	****	n.s.

¹ n.s.: $\alpha > 0.10$; * $0.10 \geq \alpha > 0.05$; ** $0.05 \geq \alpha > 0.01$; *** $0.01 \geq \alpha > 0.001$; **** $\alpha \leq 0.001$.

² Harvest 22 August.

³ Harvest 9 August.

⁴ Harvest 25 July.

+ = 2 × maneb + 2 × benlate; -- = untreated.

benomyl that the topmost leaves in the treated plots remained healthier during the grain filling period.

The curves in Fig. 1 show that the differences in leaf area index of the two topmost leaves correspond in magnitude to the differences between the grain yields of the treated and untreated plots. As the differences in grain weight did not occur until after 10 July, the size of the green area of the flag leaf in particular would appear to have been the determining factor, the more so since there were hardly any significant differences between the treated and untreated varieties in the green area of the leaf-sheath and the peduncle. The varieties with the greatest differences in area indices, viz Gaines, Lely and Manella, also show the greatest differences in grain yield.

The differences in grain yield came about in three phases:

1. Owing to be noticeable accelerated growth in the treated plots during the steep part of the growth curve in the period between 10 and 25 July (Table 3), the growth rate increased on average over the five varieties from 204 to 230 kg per ha per day.
2. During ripening, from 25 July to 9 August, the grain growth in the untreated plots came practically to a standstill, whereas in all the treated plots there was a further increase in grain weights.
3. A decrease of kernel weight in the untreated plots from 9 to 22 August, after the morphological maturity stage, owing perhaps to greater respiration losses in the untreated than in the treated plots. The differences between the colour of untreated crops and those treated with fungicides showed that there were great differences in infection with black moulds.

Statistical calculations (Table 2) showed that there were significant differences in the increase of grain yield of the five varieties owing to the application of maneb and benomyl. The absolute differences in seed yield for Juliana, Manella, Lely, Mex.-cross and Gaines were +470, +980, +1410, +800 and +1550 kg of dry matter per ha, respectively. The straw yields were only noticeable higher in the Juliana, Lely and Mex.-cross varieties, viz +380, +270 and +490 kg of dry matter per ha, respectively. The relatively disproportionate increase in grain weight compared with straw weight was clearly expressed by the higher harvest indices for the Gaines and Lely varieties, which are very susceptible to Septoria; the increases due to maneb and benlate were from 0.36 to 0.42 and from 0.40 to 0.44, respectively. Striking was that despite great differences in grain weight and straw weight there were only slight differences (< 5%) between the varieties with regard to their total dry matter yield above ground in both treated and untreated plots. These differences, in fact, are mainly the result of differences between the varieties with respect to distribution of the assimilates over grain and straw; this is particularly true of the Juliana variety.

On the yield components, i.e. number of culms per m², 1000-grain weight and number of grains per ear, the 1000-grain weight was the most determinative for the differences in grain yield per ha. There was a slight negative fungicide effect on the number

Table 3. Growth rates of grain (kg ha⁻¹ day⁻¹) in the period from 10 to 25 July.

	Juliana	Manella	Lely	Mex.-cross	Gaines
Maneb + benomyl	217	233	254	229	217
Untreated	198	215	215	214	176
Difference	+19	+18	+39	+15	+41

of culms per m², resulting possibly from a phytotoxic action of maneb; there was no fungicide effect on the number of grains per ear. A very interesting point is that in the case of Lely and Mex.-cross a large number of grains per ear is accompanied by a high 1000-grain weight, whereas in that of Juliana and Gaines the opposite is observed; Manella occupies an intermediate position with a low number of grains and a high 1000-grain weight.

Correlation and regression analysis

To analyse the differences observed in grain yield, linear correlations between the grain yield in g per m² and a number of crop parameters such as yield components, green area, degree of infection and light profile have been worked out.

Owing to the great differences between the varieties, the simple correlation have been calculated in three ways (see Table 4):

- a) from the variance in y and x per variety;
- b) from the variance in y and x within the five varieties;
- c) from the variance in y and x between the five varieties.

The variance in y and x per variety and within the five varieties is mainly attributable to the effects of fungicides, whereas the variance between the five varieties is caused by varietal differences.

After elimination of the varietal differences, the grain yield showed a highly positive correlation with the 1000-grain weight ($r = 0.92$); there was a high negative correlation with the degree of *Septoria* infection ($r = -0.88$) in the topmost leaves, and with the *Septoria* and *Fusarium* infection in the ear ($r = -0.50$).

The effects of the *Septoria* infection were particularly evident from a reduction in the green area of the leaves, which resulted in a negative correlation ($r = -0.86$) between the degree of *Septoria* infection in the period between 26 June and 10 July and the flag leaf green area percentage on 20 July. The relation between leaf infection and ear diseases was fairly weak ($r = 0.36$); this was due to an occurrence of *Fusarium* in the ear not directly associated with *Septoria*.

Correlations between grain yield and green leaf area were positive within the varieties and negative between them (see variables 5 to 9 in Table 4). The negative correlation is due to the combination of much leaf and a low grain yield in Juliana and of little leaf and a relatively high grain yield in Gaines, the other varieties occupying an intermediate position. Except in the case of Juliana, the correlation between grain yield and the leaf area of the topmost leaves was most significantly positive within the varieties and within each variety individually. The extreme differences between the Juliana and Gaines varieties also explain the negative correlation between grain yield and the green area of the internodes (see variable 10 in Table 4). A positive correlation within the varieties was expected for this interrelationship, but it did not come about, since in a few varieties the leaf sheaths remained green for a longer period in the plots in which the leaves died first because of the damage of *Septoria*.

Measuring the light interception at various heights in the crop, which was done only once on 14 July, gave a good picture of the differences between the varieties, but was too inaccurate to give a reliable explanation of differences due to *Septoria* infection (variables 13 and 14). A better idea of the effect of leaf diseases on the light distribution in the crop could be obtained by the erectness scores of the plants (variable 15); it should be noted that only Juliana lodged completely; the other varieties only drooped slightly during ripening. Within the varieties as well as between them the correlations

Table 4. Correlation coefficients ($r \times 100$) between grain yield and crop characteristics for the five varieties individually, within varieties and between varieties. Dependent variable: seed weight on 22 August.

Independent variables	Juliana (n = 12)	Manella (n = 12)	Lely (n = 12)	Mex.-cross (n = 12)	Gaines (n = 12)	Within varieties (n = 55)	Between varieties (n = 5)
<i>a. yield components</i>							
1. 1000-grain weight on 9/8	64.2*	89.1***	89.3***	97.0***	79.3**	83.1***	66.7
2. Number of grains per ear on 25/7	20.8	-13.7	3.7	-20.0	28.9	4.2	69.4
3. Number of culms/m ² (average)	-66.1*	-3.0	-42.7	12.4	-7.0	-18.0	-35.3
<i>b. green area</i>							
4. LAI leaf 1 + 2 on 27/6	-50.1	-39.3	-18.5	42.3	-11.6	-10.9	-66.1
5. LAI leaf 1 + 2 on 10/7	2.6	72.8**	93.7***	-0.1	88.2***	73.4***	-32.8
6. LAI leaf 1 + 2 on 25/7	29.1	81.8***	90.6***	81.3***	8.2	55.2***	-45.7
7. LAD leaf 1 + 2 from 10/7 to end	24.4	82.0***	94.8***	74.1**	84.9***	72.9***	-41.3
8. LAD all leaves from 27/ to end	33.2	69.5**	72.4**	53.9	73.1**	45.5***	-38.5
9. % green area of flag leaf on 20/7	33.0	98.0***	98.8***	94.6***	98.3***	92.1***	-54.7
10. AI internodes 1 + 2 on 10/7	-74.9**	10.9	-26.8	24.4	14.5	-12.2	-95.6**
<i>c. disease infection</i>							
11. Septoria on top-leaves on 10/7	-59.7*	-92.2***	-98.2***	-75.6**	-90.4***	-87.5***	4.5
12. Sept. + Fus. in ear on 10/7	-61.1*	-82.2***	-69.8**	-78.6**	-23.7	-49.8***	69.2
<i>d. light profile</i>							
13. Light interception height of flag leaf on 14/7	-22.3	31.5	10.7	-28.3	1.9	4.1	94.9**
14. Light interception at 40 cm height on 14/7	-27.5	27.0	11.1	57.4*	-24.9	3.1	70.2
15. Degree of erectness on 8/8	0.0	44.9	8.0	30.9	56.9*	36.8**	95.3**

* 0.05 $\geq \alpha > 0.01$; ** 0.01 $\geq \alpha > 0.001$; *** $\alpha \leq 0.001$.

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Table 5. Simple and multiple regression equations calculated from variance within the five varieties (n = 55).

Variable ¹	Mean	b	σ_b	Student - t	Constant	100 R ²	c.v. - y
y = kernel yield	453.8						13.2
<i>Simple regressions with R² being > 0.50</i>							
x ₁ = 1000-kernel weight	31.7	17.9	± 1.6	11.0	-115.9	69.1	7.4
x ₅ = LAI leaf 1 + 2 on 10/7	2.0	103.0	±13.0	7.9	246.4	53.9	9.1
x ₇ = LAD leaf 1 + 2 from 10/7 to end	2.7	50.7	± 9.2	5.5	136.9	53.1	9.2
x ₉ = % green area flag on 20/7	59.0	1.9	± 0.1	17.4	343.1	84.8	5.2
x ₁₁ = % <i>Septoria</i> on leaves 1 + 2 on 10/7	33.2	- 1.5	± 0.1	14.9	503.6	76.6	6.3
<i>Multiple regression, with 9 x-variables in the sequence: x₉, x₇, x₁₀, x₁₁, x₁₂, x₁₅, x₁₃, x₃ and x₂. The only x-variables included in the equation are those whose t 0.05 value of the regression coefficient was greater than 1.96.</i>							
$y = ax_9 + bx_{10} + cx_{11} + dx_3 + C$							
x ₉ = % green flag leaf on 20/7	59.0	1.2	± 0.2	7.3		(84.8)	
x ₁₀ = AI internodes 1 + 2 on 10/7	0.4	-317.2	±85.0	3.7		(86.7)	
x ₁₁ = % <i>Septoria</i> on leaves 1 + 2 on 10/7	33.2	- 1.2	± 0.2	5.5		(90.8)	
x ₃ = number of culms per m ²	566.2	0.2	± 0.1	2.6	420.2	91.9	3.9

¹ The coding of the x-variables tallies with the coding of Table 4.

between grain yield and a high erectness score were significantly positive, the correlation being 36.8 and 95.3, respectively.

The correlations between 1000-grain weight and the variables in Table 4 were of the same order of magnitude as for grain yield.

Quantification of the correlations between grain yield and crop parameters by means of simple and multiple regression calculations is of relatively little value because the explanatory variables are not all independent and the causality of the correlations is only partly known. For these reasons only the most reliable and informative regression equations are given in Table 5.

The simple linear regression equations bring out once again the close correlation between grain yield and the parameters for the green area of the flag leaf. To illustrate this, Fig. 2 sets out the correlation between grain yield and green area, both expressed in relative values so as to eliminate differences in the levels of varieties.

The multiple regression analysis with the yield components as variables left 30 % of the variance in grain yield unaccounted for; the number of grains per ear and the number of ears per m² did not help to clarify the position. A regression analysis with 9 variables, including yield components, morphological characteristics and crop traits,

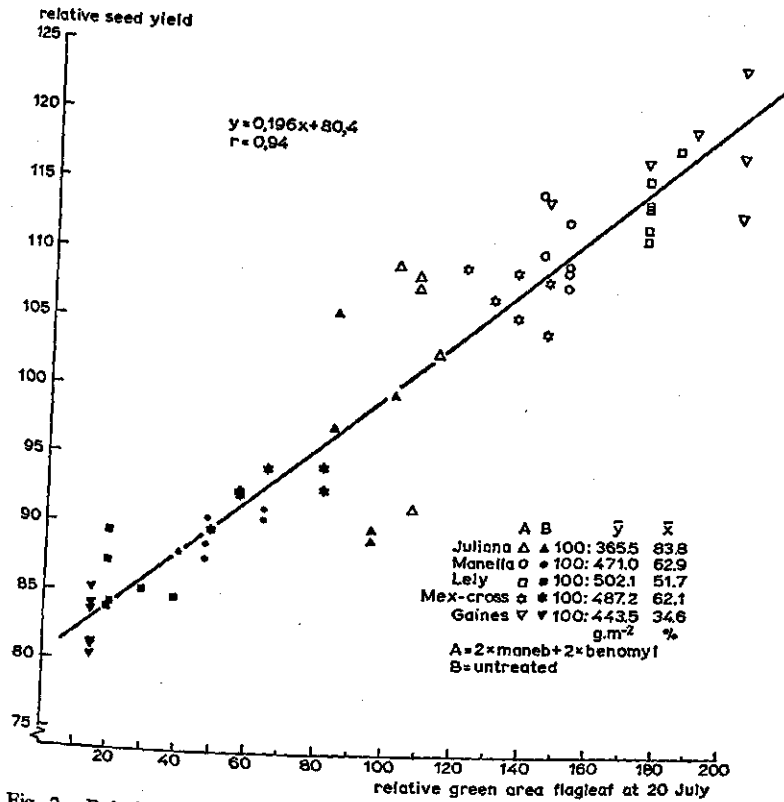


Fig. 2. Relation between the relative seed yield at harvest and the relative green area of the flag leaf at 20 July. For each variety the means of the x and y variables are fixed at 100.

resulted in a formula with 4 variables which together accounted for approximately 92 % of the original variance in grain yields (Table 5). The green area of the flag leaf constituted the major proportion (85 %). This parameter also largely represents the remaining green area of the second leaf and the ear. The *Septoria* infection mainly affected the grain weight and grain yield by reducing the photosynthetic leaf area, in addition it had an effect of its own of approximately 4 %.

Nitrogen metabolism

The nitrogen content of the seed on 25 July (dough-ripe) was clearly lower in the plots treated with fungicides (1.68 % as against 1.84 %) but in the total culm the differences were slighter (0.91 % as against 0.97 %). The differences must be the result of a more rapid grain growth in the plots treated with fungicides, as the quantities of nitrogen taken up in the culm did not differ. The content therefore declines as a result of a diluent effect.

In the period between 25 July and the final harvest on 22 August the nitrogen content of the seed was found to have increased in both untreated and treated plots; the content was 1.86 % and 1.95 % nitrogen, respectively. The quantity of nitrogen in the

EFFECT OF MANEB AND BENOMYL ON GROWTH AND YIELD OF WHEAT VARIETIES

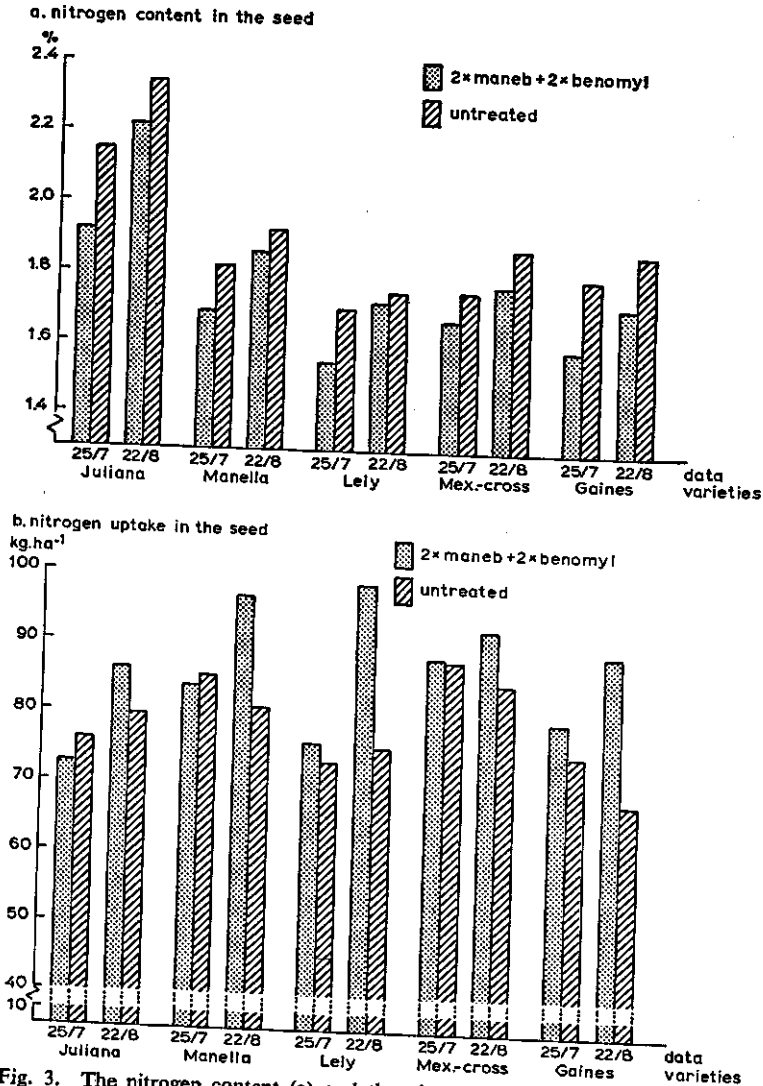


Fig. 3. The nitrogen content (a) and the nitrogen uptake (b) in the seed by five wheat varieties at two harvest data, 25 July and 22 August, for the untreated and the fungicides plots.

treated plots had risen noticeably owing to the increased nitrogen content of the seed and the increased grain weight, resulting in differences of +7.6%, +19.7%, +32.0%, +9.5% and +30.5% for the Juliana, Manella, Lely, Mex.-cross and Gaines varieties, respectively, compared with the untreated plots. The nitrogen content and the quantity of nitrogen taken up in the seed also varied greatly from variety to variety (Fig. 3A and 3B). A high N content in the Juliana variety did not correspond with a high uptake whereas the highest yield of nitrogen was found in the seed of Lely, which had a relatively low nitrogen content. It was impossible to establish whether the increase in

the quantity of nitrogen in the seed in the plots treated with fungicides was the result of retranslocation from leaf and stem or direct uptake from the soil via the roots. because no analysis were carried out on the straw at the final harvest.

Discussion

The incidence of fungal diseases is dependent to a high degree on climatic conditions. According to Brönnimann (1968) the principal disease in this experiment, *Septoria nodorum* and *S. tritici* occur regularly in regions with high precipitation. Van der Wal (pers. commun. 1972) states that a relatively low temperature and a long wet-leaf period in particular promote the spread of *Septoria*. The weather factors in the 1972 growing season provided these conditions.

The differences observed between the five varieties with regard to disease occurrence are not the direct consequence of morphological differences, because the shortest and the tallest variety were the least diseased and the varieties with the lowest leaf area index were most heavily infected. It cannot be denied, however, that the morphology of a crop can affect the microclimate and consequently also the amount of infection within a variety.

To control as wide a spectrum of fungal diseases as possible, one systematic preparation (benomyl) and one non-systematic (maneb) were used. Bouchet et al. (1972) obtained better results with a combination of fungicides than with single fungicides. In their experiments the extra yields of winter wheat ranged from 4% to 21.7% in 1970 and from 3.7% to 56.3% in 1971. The results depended very much indeed on the combination used and the moment at which the dressing is applied.

Although *Septoria* does not usually occur in the grain-producing organs until late in the growing season, it can do considerably damage. Shipton (1968) quotes from the relevant literature yield losses of 28% and extreme values up to 95% for *S. tritici* and *S. nodorum*, respectively, after natural infection; the damage done by *S. tritici* might increase to 45% by artificial inoculation. Although the plots treated with benomyl and maneb in our own experiment were not free from disease, there were extra yields of 13.8%, 23.4%, 32.3%, 15.6% and 42.1% for Juliana, Manella, Lely, Mex.-cross and Gaines, respectively, compared with the untreated plots. It should be noted that even after treatment with fungicides the yield this year fell far short of the potential level in the Netherlands.

By statistical analysis 69% of the variance in grain yield was attributable to the 1000-grain weight; the number of grains per ear was scarcely affected by fungicide treatment. Similar results were obtained by Brönnimann (1972) and Dilz & Schepers (1972).

Brönnimann (1969) noted yield losses after the infection of separate organs with *S. nodorum*, 40.6%, 45.7%, 14.8% and 1.1% of which were caused by the ear, the flag leaf, leaf 2 and leaf 3, respectively. He suggested that besides damage to the assimilative tissue there is also disturbance of the translocation of the assimilates to the grains. Our own findings concerning the relationship between the green area of the flag leaf and the kernel yield ($R^2 = 0.85$) stress the importance of keeping the flag leaf and function of supplying assimilates to the growing grain was also confirmed repeatedly by ^{14}C tests (Rawson & Hofstra, 1969, and others). The multiple correlation and regression calculation showed that all but 4% of the total effect of *Septoria* on the variance in grain yield was attributable to a change in the assimilative area.

Fusarium and black moulds as well as *Septoria* occurred in the ear during ripening. The latter group in particular appeared to be considerably inhibited by benomyl. The very slight weight losses in the treated compared with the untreated plots in the period from 9 to 22 August were possibly due to benomyl.

It is known that benomyl is also active against *Cercospora herpotrichoides* (Fehrmann, 1972). There are one or two indications that even late applications of benomyl (before and after anthesis) reduced somewhat the fairly high degree of infection by soil-borne pathogens, since the culms in the treated plots, with the exception of Juliana, drooped less than in the untreated ones. At the same time the uptake of nitrogen by the seed in the period from 25 July to 22 August averaged 14% in the plots treated with fungicide, whereas there was no further uptake in the untreated plots. This indicates greater root activity in the treated plots, since in the Lely variety in particular the 25 kg increase of nitrogen in the seed is to great to have become available merely from the 49 kg store in the straw at 25 July.

It may be concluded that the control of fungal diseases in wheat varieties with maneb and benomyl in crops with differing crop structure and disease susceptibility in each case resulted in an increase in the grain yield or straw yield. The higher grain yield in this experiment was brought about mainly by the flag leaf and other assimilative organs remaining green for a longer period, so that in the last fortnight of grain filling there were marked differences between the treated and the untreated plots. Quantitatively, the effect of treatment was greatest in the varieties most sensitive to *Septoria*, viz Lely and Gaines. Characteristic differences between the varieties even remained after the inhibition of several fungal diseases, particularly with regard to their dry matter distribution (harvest index) and the uptake of nitrogen in the above-ground parts.

Acknowledgments

This study was carried out in consultation with Ir L. J. P. Kupers and various colleagues, to whom I wish to express my gratitude for their interest. Thanks are especially due to Mr J. Ellen for skilful assistance and to Mr J. B. Lettinga and co-workers for careful execution of the various treatments.

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Grain growth and distribution of dry matter in the wheat plant as influenced by temperature, light energy and ear size

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Summary

An experiment was carried out under controlled growing conditions to study the plant response during the postfloral stage to temperature, light intensity and ear size. Within the range of 15 to 25 °C a raise in temperature increased the growth rate of the grains but the duration of the post-floral development of the plant was very much shortened. The final result was that higher temperatures caused lower grain yields. An increase of light intensity from 92 to 147 cal cm⁻² day⁻¹ has shown a more positive effect on grain weight than an increase from 147 to 175 cal cm⁻² day⁻¹. The artificial reduction of ear size by removing spikelets from the ear increased the thousand-grain weight but not enough to compensate for the reduction in number of kernels per ear. The effects of the main factors – temperature, light intensity and ear size – and of the combined treatments on the supply and storage of carbohydrate are discussed within the framework of a sink-source model.

Introduction

Grain yield in a wheat plant is partly determined in the pre-floral period, for instance by the size of the photosynthetic area and the potential number of kernels per ear, but mainly in the post-floral period by the rate and the duration of grain growth. Before ear initiation, tillering and leaf production are affected by temperature and light intensity (Friend, 1965); during the booting stage temperature has a strong influence on the developmental rate (Friend, 1966), while light intensity determines the number of ears per plant and the development of the spikelets (Puckridge, 1968; Willey, 1965). The supply of assimilates to the growing organs depends on the activity and the duration of photosynthesis in the green organs of the plant, mainly the leaves. A rather complete description of the contribution by each leaf to the total pool of assimilates available for growth and the translocation at different stages is presented by Rawson & Hofstra (1969). They concluded that the lower leaves mainly contribute their assimilates to the roots and the side tillers, while the top leaves provide the assimilate requirements of stem and ear. Much research has been done on the source function of the flag leaf, the peduncle and the ear (Stoy, 1965; Carr & Wardlaw, 1965; Lupton, 1972; Evans & Rawson, 1970, and many others) in relation to the sink demand of the grains. Often there was evidence that leaf area and the rate of photosynthesis did not limit the supply of assimilates in the early stages of grain growth.

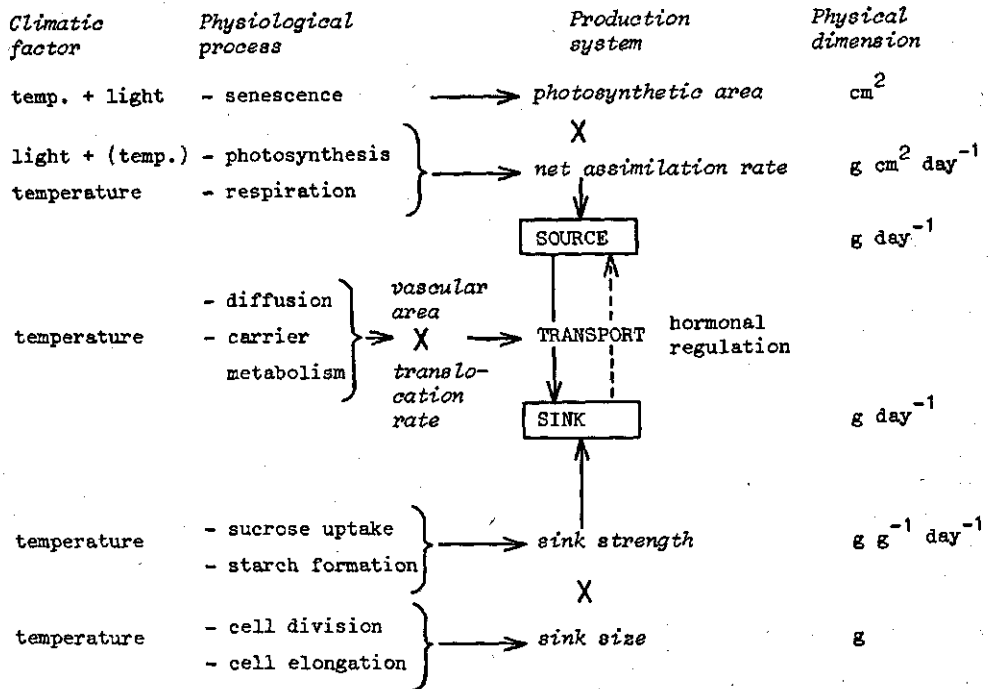


Fig. 1 Model for grain growth.

For that reason more attention has been paid to other possible limiting factors in grain growth, in particular:

- the transport through the vascular system (Evans et al., 1970; Hanif & Langer, 1972);
- all the processes involved in converting sucrose to starch in the endosperm cells (Jenner & Rathjen, 1972);
- the pattern of the grain growth within the ear (Rawson & Evans, 1970; Walpole & Morgan, 1970; Bremner, 1972).

There is evidence, too, that a hormonal mechanism regulates the attraction and the competition for assimilates within the ear (Michaël et al., 1970).

The rate of grain growth in wheat is related to various physiological processes. The connections between these processes can be illustrated within a sink-source model (Fig. 1). As the model shows, assimilate supply (source) is determined by light energy and temperature, while transport and sink capacity are influenced by temperature in many ways. In the single plant situation, temperature has a key function in grain growth; in the crop situation, light may be more important due to mutual shading. At present knowledge about the influence of temperature is rather scarce. To study the effect of temperature on the relationship between sink and source during the post-floral period, an experiment was carried out in a controlled environment with four temperature treatments, combined with three levels of light intensity and three ear sizes.

Material and methods

The experiments were done in the phytotron of the Department of Field Crops and Grassland Husbandry of the Agricultural University, Wageningen.

Seeds of the *spring wheat variety Orca* with a diameter of 3.0–3.4 mm were used for the experiments. In 240 pots filled with 5 kg soil consisting of 50 % sand and 50 % marine clay, 20 seeds were sown at random; two weeks after germination the number of seedlings was reduced to 15 per pot (area = 300 cm²). To prevent seed-borne diseases and mildew the seeds were dressed with Aatisan and Milstem; during the growing period insecticides and fungicides were applied regularly. The plants grew under natural daylength and a temperature regime of 15 °C during the day and 10 °C at night.

From flowering onwards the following treatments were applied:

Group A	T ₁	T ₂	T ₃	T ₄
I – 4 temperatures: day	15 °C	15 °C	25 °C	25 °C (16 hours)
night	15 °C	25 °C	15 °C	25 °C (8 hours)
II – 3 light intensities:	L ₁	L ₂	L ₃	
	92	146	175	cal cm ⁻² day ⁻¹

III – 3 ear sizes: by artificially removing some spikelets at flowering the number of kernels was reduced. In 120 pots each with 15 main culms, five ears were kept at normal length, from five ears the top spikelets and from another five ears the top and the central spikelets were removed. This interference resulted in three groups of five ears each with a different number of kernels (as a mean for the light and temperature treatments): S₀ : 47.0 kernels per ear (control); S₁ : 36.6 kernels per ear; S₂ : 24.3 kernels per ear.

Group B

The same treatments as A₁ and A₂, however, with an additional cold treatment (2 °C) of soaked seeds at germination. This resulted in a one week delay of flowering and in an additional 1.3 spikelet per ear.

The pots were fertilized weekly or fortnightly with a mineral solution of NH₄NO₃, Ca(NO₃)₂, KNO₃, KH₂PO₄ and MgSO₄. The total amount of minerals for the whole growing period was (in meq per pot): 27.5 NH₄⁺; 95 NO₃⁻; 70 K⁺; 12.5 Ca²⁺; 25 Mg²⁺; 32.5 H₂PO₄⁻; and 22.5 SO₄²⁻. The micro-elements were applied once at the beginning of the growing period.

Observations were made on the following dates:

	H ₀	H ₁	H ₂	H ₃	H ₄	H ₅	H ₆
T ₁ = 15/15 °C	20/8	9/9	–	22/9	–	6/10	13/10
T ₂ = 15/25 °C	20/8	9/9	–	22/9	–	6/10	13/10
T ₃ = 25/15 °C	20/8	9/9	17/9	22/9	29/9	–	–
T ₄ = 25/25 °C	20/8	9/9	17/9	22/9	29/9	–	–

At the intermediate and at the final harvest the measurements were carried out on the main culms. To determine dry matter weights and leaf area the culms were separated into:

a) flag leaf, other green leaves and dead leaves;

b) peduncle and remaining internodes;

c) ear; in some cases divided into the top, the central and the basal part.

The side culms were separated into ears and straw. Stubble and root weights were determined together for all culms per pot.

After 18 hours drying at 70 °C the individual samples were weighed and the ears were treshed. The anthrone method (Yemm & Willis, 1954) was used to determine the content of water-soluble carbohydrate by an auto-analyser.

The measurements of photosynthesis and respiration with the Gilson respirometer were carried out on small parts, about 200 mg fresh weight, of the flag leaf, the peduncle and the ear (one or two spikelets); under steady state conditions photosynthesis and respiration were measured during 4 intervals of 15 minutes.

Results

Analysis of variance

In the first analysis of the effects of the four temperature treatments, the main effects of 15 and 25 °C during day-time and at night were calculated. The effect of temperature during day-time was mostly twice as large as that of the night temperature, but

Table 1. The effects of various treatments on the weight of the components of the main culm (Group A).

Component	Date	Mean	c.v.	Ear size (S)	Temperature (T)	Light (L)	S × L	S × T	L × T
1. weight per ear (mg)	20/8	473	—	—	—	—	—	—	—
	9/9	1289	6.1	***	***	***	***	n.s.	n.s.
	22/9	1874	5.7	***	***	***	*	**	n.s.
ripeness		2248	4.4	***	***	***	n.s.	**	*
2. seed weight per main ear (mg)	9/9	897	14.3	***	***	***	n.s.	n.s.	n.s.
	22/9	1456	7.0	***	***	***	*	*	n.s.
	ripeness	1603	6.4	***	***	***	n.s.	*	*
3. kernel weight (mg)	9/9	25.3	5.9	***	***	***	n.s.	n.s.	*
	22/9	43.6	3.6	***	***	***	*	n.s.	*
	ripeness	44.3	6.4	***	***	n.s.	n.s.	n.s.	n.s.
4. number of kernels (mg)	9/9	36.0	13.1	***	n.s.	n.s.	n.s.	n.s.	n.s.
	22/9	33.4	5.3	***	*	*	n.s.	n.s.	n.s.
5. weight of peduncle (mg)	9/9	556	6.5	**	***	***	n.s.	n.s.	n.s.
	22/9	479	4.8	***	***	n.s.	n.s.	n.s.	n.s.
	ripeness	462	4.6	***	***	n.s.	n.s.	n.s.	n.s.
6. weight of the other internodes (mg)	9/9	1134	8.3	**	***	***	n.s.	n.s.	n.s.
	22/9	961	5.2	***	***	*	n.s.	n.s.	n.s.
	ripeness	906	3.5	***	***	n.s.	n.s.	n.s.	n.s.
7. weight of the leaves (mg)	9/9	540	9.3	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	22/9	502	8.4	n.s.	**	n.s.	n.s.	n.s.	n.s.
	ripeness	436	8.8	n.s.	***	n.s.	n.s.	n.s.	*
8. total aerial weight of main culm (mg)	9/9	3520	3.8	***	***	***	*	n.s.	n.s.
	22/9	3816	3.7	***	***	***	n.s.	*	n.s.
	ripeness	3792	3.7	***	***	***	n.s.	*	*

n.s.: $\alpha > 0.05$; x: $0.05 \geq \alpha > 0.01$; xx: $0.01 \geq \alpha > 0.001$; xxx $\alpha \leq 0.001$.

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Table 2. The analysis of variance by means of a multiple regression with real variables.

Variable	Level	b	δb	Student -t	Degrees of freedom	Constant	100 R ²	c.v.
y = seed yield main culm (mg/ear)	1,810	-	-	-	35	-	100	39.0
x ₁ = mean temp. (°C)	20	-145.2	20.2	7.2	34	4,715	39.6	24.9
x ₁ = mean temp. (°C)	20	-145.2	19.9	7.3	33	4,238	37.4	24.6
x ₂ = light intensity (cal cm ⁻² day ⁻¹)	138.2	3.5	2.5	1.4				
x ₁ = mean temp. (°C)	20	-94.3	9.0	10.5	32	2,099	6.0	10.0
x ₂ = light intensity (cal cm ⁻² day ⁻¹)	138.2	2.1	1.0	2.1				
x ₃ = ear size (kernels/ear)	40	32.5	2.5	13.0				

also the day-length (16 hours) was twice the night period (8 hours). For that reason the four temperature treatments - 15/15 °C, 15/25 °C, 25/15 °C and 25/25 °C - will be considered as mean daily temperatures of 15, 18.3, 21.7 and 25 °C.

The experiment was carried out as a split-plot design with the factor temperature in the main split and light in the sub-split. The results of the analysis of variance for the components of the main culm (Group A) are presented in Table 1. All the parameters which are related with grain growth, were strongly influenced by the main factors: ear size, light intensity and temperature.

The first-order interactions were of minor importance. The results of Group B were of the same magnitude.

By means of a multiple regression analysis with all main factors and first-order interactions as dummy variables, the coefficient of variation for the seed yield of the main culm was decreased from 39.0 to 8.9 %. Thereby temperature, light intensity and ear size accounted for 74.0, 2.1 and 18.8 % of the variance in seed yield respectively. The calculations with real variables gave about the same results (Table 2).

A change in temperature caused a decrease of 94.3 mg seed/culm per °C and a change in light intensity or ear size gave an increase of 2.1 and 32.5 mg seed/culm, per calorie and per kernel, respectively. So the total response of seed yield to temperature is negative mainly due to the earlier senescence of the plants. An increase in light intensity or in number of kernels per ear resulted in a higher seed yield per culm.

Influence of temperature

During the post-floral period the growth rate of the kernels increased with rising temperature, but the senescence of the leaves and other green parts of the plant also increased. The resultant of these opposite processes was an initially higher growth rate during a relatively short period at 25 °C and a slower growth rate during a long period at 15 °C; 18.3 ° and 21.7 °C were intermediate in their effect upon growth rate and senescence (Fig. 2). The acceleration of leaf senescence and ripening of the kernels by higher temperatures was more important for the ultimate grain yield than the increase of the growth rate. The period between flowering and a dry matter content in the ear of 65 % has lasted 52, 40, 31 and 26 days for 15, 18.3, 21.7 and

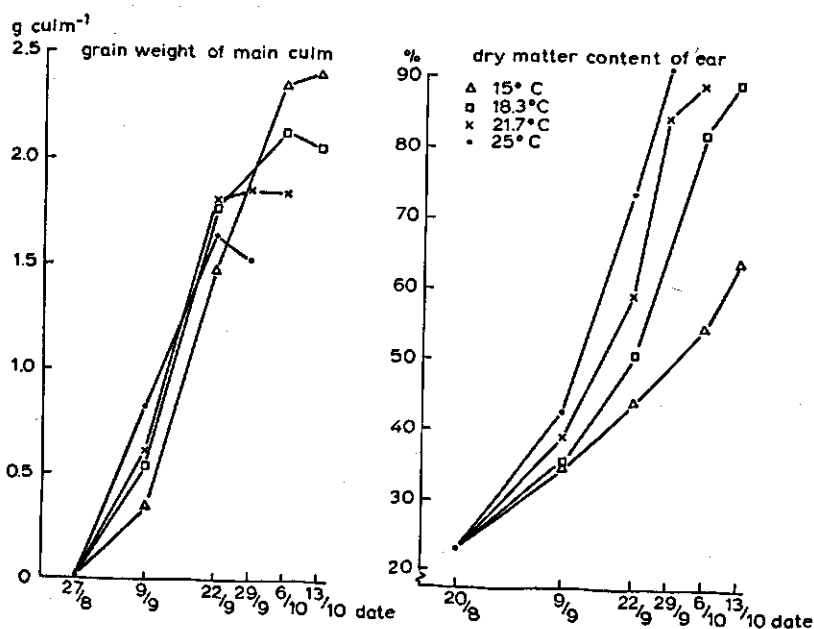


Fig. 2. The influence of temperature on grain growth and dry matter content of the ear (data of Group B).

25 °C, respectively. Thus the kernel filling period was doubled by a decrease in temperature of 10 °C.

The influence of temperature on leaf area duration is demonstrated by the leaf area at three weeks after flowering; a decrease from 63, 47, 34 to 21 cm² per culm within the temperature range 15–25 °C. Which factor first stops grain growth is not clear; there is some evidence that it might be the supply of assimilates, because at the highest temperature grain growth stopped at a dry matter content in the ear of about 40 %, while at 15 °C grain growth continued up to 65 % dry matter. There are many literature sources, which report a physiological limit for grain growth at 35 % moisture content. This percentage will be somewhat lower for the ears, because the rachilla and the glumes contain less moisture than the kernels.

The distribution of the assimilates was also influenced by temperature (Fig. 3). With higher temperatures more assimilates were used for grain growth at the expense of the weight of the internodes and perhaps also of the roots. The weight of the peduncle increased during the first two weeks after flowering and from that time onwards the peduncle weight decreased slowly, whereas the weight of the other internodes dropped sharply after flowering, especially at higher temperatures.

This decrease in dry matter weight of the stem was greater than the gain in kernel weight. Therefore the supply of assimilates to the grains by remobilization out of the stem may only have been a part of the loss in weight. Much more of the weight loss was caused by the increase of respiration at higher temperatures. This can be illustrated by a few measurements of photosynthesis and respiration with a Gilson respirometer, taken at 15 and 25 °C (Table 3) for the four temperature treatments.

The increase of temperature gave a Q_{10} value for the respiration of more than 2 as a

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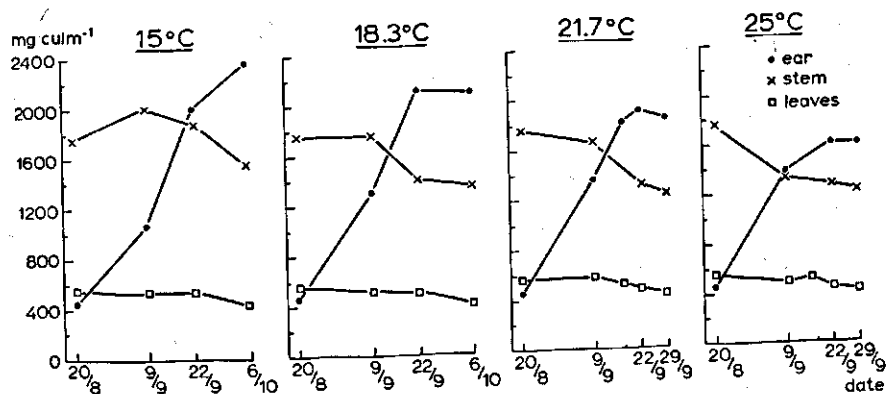


Fig. 3. The influence of temperature on dry matter distribution after flowering (data of Group A).

Table 3. The magnitude of photosynthesis in flag leaf and of respiration in flag leaf, peduncle and ear at the milk to dough ripe stage ($\mu\text{l O}_2/\text{g fresh weight/minute}$).

	Flag leaf		Peduncle		Ear		
	photosynthesis	dark respiration	dark respiration		dark respiration		
	15 °C	15 °C	25 °C	15 °C	25 °C	15 °C	25 °C
T _r : 15/15	44.0	7.6	19.2	3.1	14.7	5.6	12.4
T _r : 15/25	49.5	4.9	10.2	4.5	9.3	4.4	9.4
T _r : 25/15	51.2	-	-	-	-	5.8	11.0
T _r : 25/25	58.9	-	-	-	-	3.4	9.4

(1 g fresh weight = 55 cm² flag leaf.)

mean. To compare the organs, attention should be paid to the fresh weight ratio of these organs per plant; here the ratio for flag leaf, peduncle and ear was 1 : 4 : 15. So per plant the respiration of the ear is much higher than that of the leaf.

Influence of light intensity

Seed yield and growth rate of the grains gave a higher response to an increase of light intensity from 92 to 142 cal cm⁻² day⁻¹ than to an increase from 147 to 175 cal cm⁻² day⁻¹ (Fig. 4).

During the first two weeks after flowering the weight of the peduncle as well as the weight of the other internodes was significantly increased by a higher light intensity. This means that shortly after flowering there is some basipetal transport of assimilates in the plant. The amount of downward transport, however, will depend on the supply and on the storage of assimilates in the ear; the remainder of assimilates will be stored mainly in the stem.

The advantage of a higher light intensity for grain growth was partly reduced by the more rapid leaf senescence. With 92, 147 and 175 cal cm⁻² day⁻¹ the leaf area per culm three weeks after flowering amounted to 45.7, 41.5 and 36.5 cm² culm⁻¹, respectively.

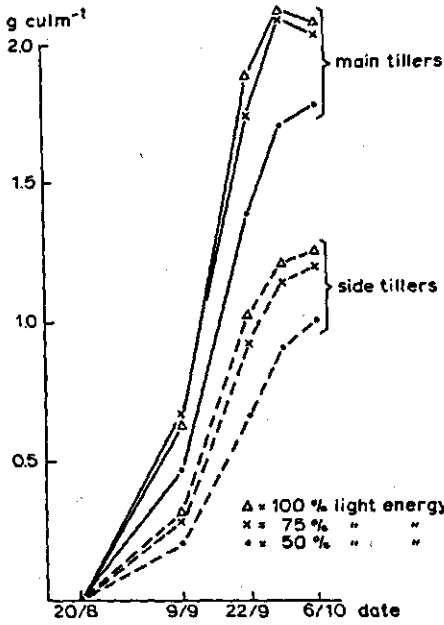


Fig. 4. The influenced of light intensity on grain growth of main and side tillers (data of Group B).

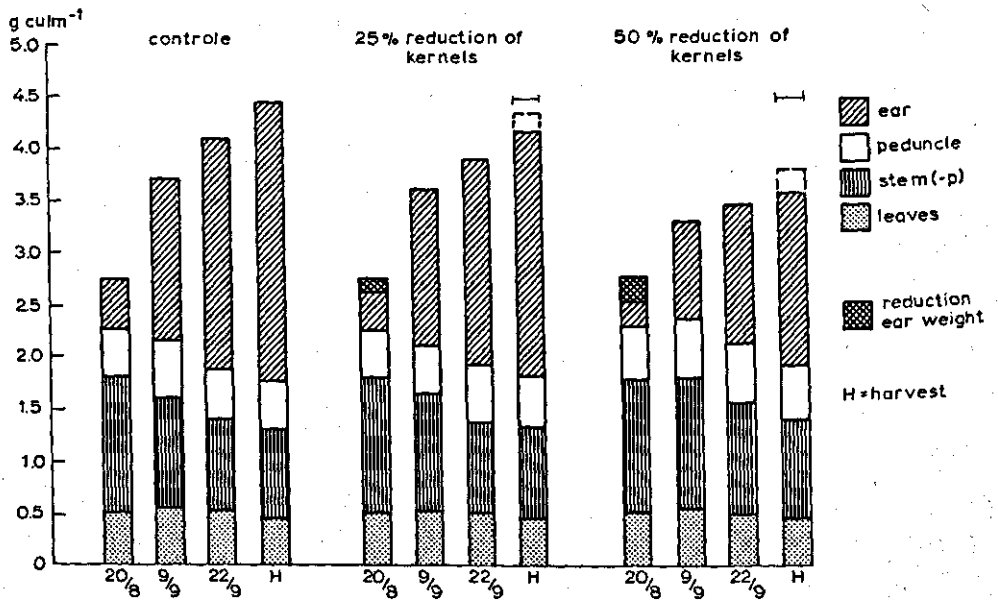


Fig. 5. The influence of ear size on dry matter distribution after flowering (data of Group A).

GRAIN GROWTH AND DISTRIBUTION OF DRY MATTER IN WHEAT

Table 4. Grain weight of main culm and side culm with three different numbers of kernels per main ear (g ear⁻¹).

Dates	Number of kernels on main culm	Main culm			Side culm		
		S ₀ (control)	S ₁ (-25 %)	S ₂ (-50 %)	S ₀ (control)	S ₁ (-25 %)	S ₂ (-50 %)
3 weeks after flowering		1.13	0.92	0.64	0.82	0.93	0.97
5 weeks after flowering		1.72	1.56	1.09	1.29	1.35	1.46
7 weeks after flowering		1.97	1.68	1.18	1.37	1.51	1.59

Influence of the ear size

The storage capacity in the ear was reduced by removing some of the top and central spikelets. This interference resulted in three storage capacities with 47.0, 36.6 and 24.3 kernels per ear, respectively.

Because of the reduced storage capacity there was initially an increase in the dry weight of the peduncle and the other internodes; this increase was, however, not sufficient to compensate for the decrease of the ear weight (Fig. 5).

The differences in dry weight of the internodes diminished during ripening, those of the ear remained up to the mature stage. Striking was the fact that the removal of spikelets on the main culm resulted in a significant increase of the seed yield of the side culms (Table 4). This indicates that when the storage capacity of the main ear

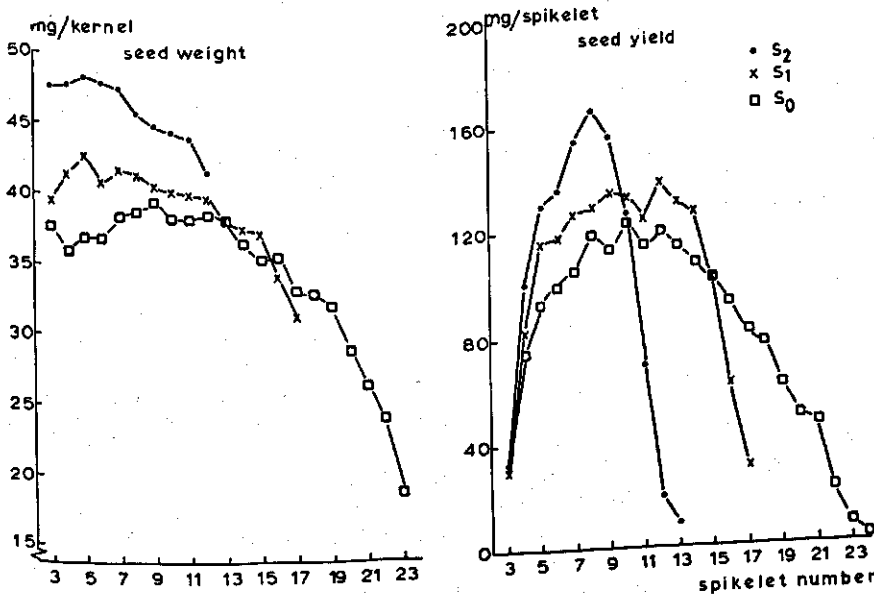


Fig. 6. The influence of the number of kernels per spikelets on individual grain weight and grain yield per spikelet (data of Group A: averaged for T₂ and T₁).

Table 5. The absolute growth rate (AGR) and the relative growth rate (RGR) of ear and kernels.

	Ear			Kernel		
	S ₀ (control)	S ₁ (-25 %)	S ₂ (-50 %)	S ₀ (control)	S ₁ (-25 %)	S ₂ (-50 %)
<i>AGR (mg day⁻¹)</i>						
20/8 - 9/9	88.8	90.3	64.6	1.88	2.12	2.34
9/9 - 22/9	51.5	43.5	30.6	1.11	1.27	1.56
22/9 - 6/10	29.1	25.2	21.7	0.43	0.52	0.42
<i>RGR (mg g⁻¹ day⁻¹)</i>						
20/8 - 9/9	98	124	148	259	304	370
9/9 - 22/9	25	25	27	38	38	41
22/9 - 6/10	13	12	14	5	6	4

is very limited there is a downward flow of assimilates, which probably indirectly (e.g. by means of a better root activity) favours the grain growth in the side culms.

The most important compensation for the reduction in number of kernels per ear was a considerable increase of the individual kernel weight. So the initial 50 % reduction in kernel number resulted in a 25 % increase of the kernel weight. By removing the top spikelets, the kernel weights of the spikelets on the basal part of the ear were favoured by the additional supply of assimilates (Fig. 6).

To analyse the effect of different ear sizes on the physiological activity of the ear and the kernels as a storage organ the absolute and the relative growth rate have to be compared (Table 5).

The absolute growth rate of the total ear was decreased by reducing the ear size, whereas the growth rate of the individual kernel was increased up to the ripening stage. Difference in ear size affected the relative growth rate only a fortnight after flowering in such a way that the growth rate of both the total ear and the individual kernel were increased corresponding to the reduction in ear size. During the remainder of the kernel filling period there were hardly any differences in relative growth rate. Obviously in that phase there is a factor other than carbohydrate supply which is limiting the growth rate.

The content of water-soluble carbohydrates (wsc)

Before anthesis water-soluble carbohydrates accumulate in the stem. The contribution of these stem reserves to grain growth depends on the growing conditions. However, in the wheat plant the stem acts as a pool of available carbohydrates which increases with a surplus of photosynthates and decreases with consumption of carbohydrates, either by respiration or by retranslocation. The extent to which this pool was affected by temperature and light intensity is presented in Table 6.

From flowering onwards the content of water-soluble carbohydrates of the stem was strongly affected by temperature as well as by light intensity. The lower wsc content at higher temperatures might be caused by a more rapid retranslocation to the kernels, by a higher respiration rate of the stem or a greater carbohydrate consumption by the roots. Especially at lower temperatures higher light intensities resulted in an increased wsc content; so under low temperature conditions there is a greater surplus of carbohydrates than at higher temperatures.

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Table 6. The content of water-soluble carbohydrates of the peduncle and the remaining internodes of the stem (Group B) at different temperatures (T₁ etc.) and light intensities (L₁ etc).

	T ₁			T ₂			T ₃			T ₄		
	L ₁	L ₂	L ₃	L ₁	L ₂	L ₃	L ₁	L ₂	L ₃	L ₁	L ₂	L ₃
<i>Peduncle</i>												
9/9	15.3	18.8	22.4	8.4	20.2	20.9	6.7	10.5	15.6	7.2	8.5	13.4
22/9	15.0	21.4	24.4	3.1	9.1	11.0	1.4	1.7	3.5	1.0	1.2	1.3
29/9	-	-	-	-	-	-	1.4	1.4	?	0	0.9	0.9
6/10	11.3	12.6	10.4	0.8	0.8	1.9	-	-	-	-	-	-
<i>Lower internodes</i>												
9/9	28.2	29.9	35.1	24.9	25.1	30.2	20.8	21.7	23.4	10.2	11.7	15.1
22/9	24.5	28.1	29.2	8.9	12.2	14.2	2.4	2.8	3.0	2.3	2.8	2.8
29/9	-	-	-	-	-	-	1.0	1.5	2.4	0.7	1.0	1.1
6/10	11.7	13.4	18.0	1.1	2.5	1.5	-	-	-	-	-	-

The reduction of the ear had a smaller effect on the wsc content: a reduction of the kernels per ear with 50 % caused an increase in wsc content of about 15 %.

Discussion

It was stressed earlier that grain growth was determined by the supply of carbohydrate and the sink capacity of the ear. In this experiment the surplus of carbohydrates was varied by light intensity and temperature. It was found that reducing the light intensity from 175 to 92 cal cm⁻² day (400-700 nm) did not decrease the grain yield proportionally. Also Willey (1965) found relatively small reductions in yield with shading experiments in the field during the grain filling period. Of course the magnitude of the mutual shading of the plants will depend on the number of culms and on the leaf area per culm. Generally, light competition during the pre-flowering phase has turned out to be more critical for grain yield than competition at a later stage (Willey, 1965; Puckridge, 1968; Fischer, 1972).

Temperature has influenced the supply of assimilates in various ways. First the senescence of the leaves was accelerated by raised temperatures and secondly the respiration of leaves, stem and ear was increased. Despite this increase of respiration, the growth rate of the kernels did not decrease, but was even greater. This indicates that there was up to 3 weeks after flowering no absolute shortage of assimilates at higher temperatures; only the content of wsc in the stem decreased rapidly. It is unknown whether a lower carbohydrate level in the plant causes a much faster rate of senescence; there is some evidence that with higher temperatures the movement of nitrogen from the leaves into the grain is greater. This may be an important factor affecting the leaf area duration. Studying the duration of post-anthesis development under field conditions, Marcellos & Single (1971) found that an increase of the mean daily temperature from 17.5 to 22.5 °C during the post-flowering period reduced the duration of this phase by about 30 %. In this phytotron experiment the effect of the temperature was greater, which might be explained by the additional influence of the environmental temperature on the roots of the plants grown in pots. Under field

conditions soil temperature is affected less by the aerial temperature and by diurnal variations in temperature.

The storage capacity of the ear depends on the potential size of the grains and on the number of grains (Bingham, 1967). The latter of these two components was artificially varied in this experiment after flowering; normally in a field crop the number of grains is predominantly affected by the growing conditions before flowering (Fischer, 1972). The potential size of the grains seems to be partly genetically controlled, but also temperature and light intensity affect the number of endosperm cells (Wardlaw, 1970). From recent work (Jenner & Rathjen, 1972) it may be concluded that also the rate at which carbohydrate can accumulate in the ear is determined by the flow rate of sucrose into the grain. Jenner (1970) showed that the concentration of sucrose in the endosperm was closely related to the rate at which starch was deposited. However, the level of sucrose in the endosperm was not linearly related to the amounts of sucrose in the other parts of the ear. It was concluded that the transport of sucrose into the grains is in some way very restricted on the final stages of its passage into the endosperm.

In this experiment the sink capacity of the ear was determined by temperature and ear size; during the early phase of kernel filling temperature predominated over the effect of ear size by affecting the growth rate of the kernels (Fig. 7). The effect of ear size on the growth rate of the kernels was greater with higher temperatures; at 25 °C there was a decrease in the weight of individual grains with an increasing number of kernels per ear, while at 15 °C there was hardly any differences. Thus under circumstances with a fast growth rate of the kernels the supply of carbohydrates will be limiting. That is why the positive effect of a higher light intensity also was greater with raised temperatures. This phenomenon was confirmed by the effects of temperature and light intensity on the changes in thousand-grain weight during the kernel filling period (Fig. 8) and on the content of water soluble carbohydrates in the stem. At low temperatures the effect of a relative shortage of carbohydrates on the thousand-grain weight came about at a later stage of kernel filling.

The quantity of wsc in the stem may be considered as a balance between the production (photosynthesis of green tissues) and the consumption (respiration, starch formation, etc.) of assimilates. The data of Table 6 show very clearly that at low

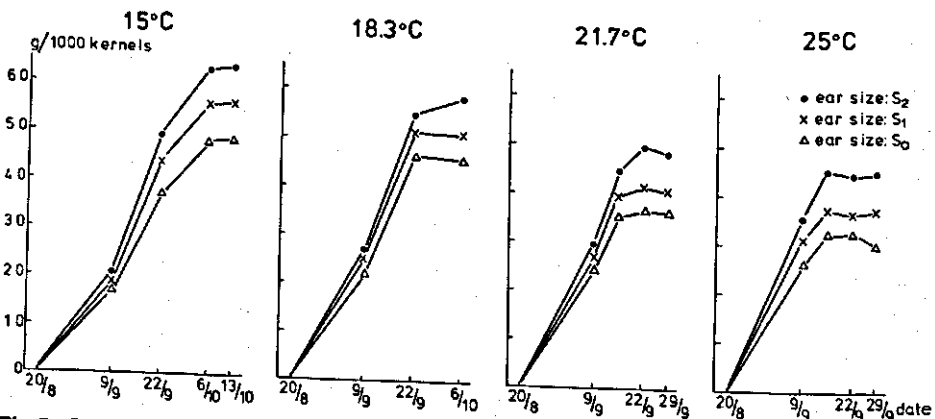


Fig. 7. The influence of temperature and ear size on thousand-grain weight (data of Group A) .

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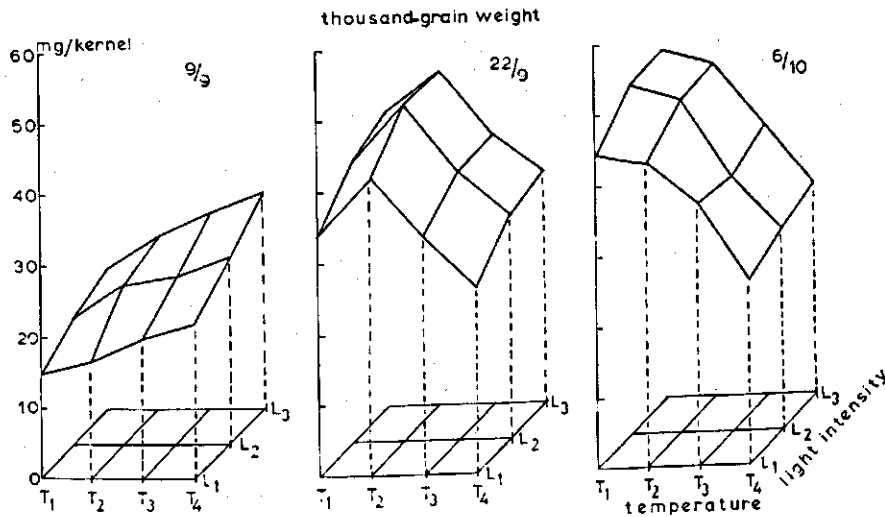


Fig. 8. The change in thousand-grain weight after flowering, as affected by temperature and light intensity (data of Group A: alone S_0 data).

temperatures there were initially higher contents of wsc in the stem, which decreased rather slowly during kernel filling. At high temperatures the wsc content in the stem decreased even in the early stage of kernel filling. This decrease of the wsc content will be caused mainly by increased respiration (Table 3) and by more retranslocation to the grains. The increased loss of stem sugars at higher temperatures is in agreement with the results of Asana & Saini (1962).

The conclusion might be that the final grain yield depends on the balance between carbohydrate supply and ear capacity. The carbohydrate supply was determined by temperature and light intensity, because both climatic factors affected the net assimilation rate and the leaf area duration. Low temperatures together with high light intensity resulted in a surplus of available carbohydrates. Under such circumstances there must be a favourable effect of a greater ear capacity on grain yield; or one might also conclude, that with low temperatures during the kernel filling period a high light intensity is not necessary to achieve a normal grain weight. The storage capacity of the ear is more limited by removing the kernels from the central spikelets than from the top of the ear. The reduction in number of kernels per ear could only partly be compensated by an increase in thousand-grain weight. Temperature affected ear capacity by influencing the rate at which carbohydrate can accumulate in the ear. There is some evidence that various processes are involved, such as the translocation rate of assimilates, the passage of sucrose into the grain, the rate of converting sucrose into starch. To what extent these processes are important for grain growth and final grain size would be worthwhile for further research.

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The influence of temperature and light intensity on grain growth in relation to the carbohydrate and nitrogen economy of the wheat plant

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Summary

The response of grain growth to temperature and light intensity was studied under controlled conditions within the ranges from 10 to 25 °C and from 64 to 188 W m⁻², respectively. Warmth hastened the senescence of the wheat plant and enhanced the initial growth rate of the grains. Additional light promoted the rate of grain growth more at high than at low temperatures; under the latter conditions there was a considerable accumulation of carbohydrates in the stem (up to 40 %) from anthesis onwards. The rate of grain growth ranged from 0.70 to 1.64 mg day⁻¹ kernel⁻¹. The duration of grain growth was prolonged by decreasing the temperature from 25 to 10 °C; the increase in growth duration from about 30 to 80 days corresponded with a relatively stable temperature sum. Temperature and light also affected the redistribution of assimilates and the chemical composition of the grain. The rate of protein synthesis was promoted more by warmth than the rate of starch synthesis. This resulted in an increased nitrogen content of the grain. The final content of total non-structural carbohydrates (starch and sugars) was slightly decreased by warmth. Additional light raised the carbohydrate content of all parts of the plant and so decreased the nitrogen content of these parts. However, light intensity had less effect on nitrogen distribution and yield than temperature had.

Introduction

From site to site and from year to year great variations in light energy and temperature occur during the grain-filling period of wheat. Lower radiation during this period affects grain growth by decreasing photosynthesis and the supply of assi-

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milates (Willey & Holliday, 1971; Fischer, 1975). The effect of temperature on grain growth is more complex than the effect of light intensity: there are effects on 'source' processes (e.g. earlier senescence of the leaves) and on 'sink' processes (e.g. faster initial growth rate of the kernels). Usually a rise in temperature shortens the kernel-filling period and decreases the final grain yield (Thorne, 1973; Sofield et al., 1974; Spiertz, 1974; Ford & Thorne, 1975; Meredith & Jenkins, 1976). The importance of the various components and aspects involved in the physiology of grain growth has been extensively reviewed by Evans & Wardlaw (1976).

This paper presents the results of an experiment in which the main objectives were to investigate the influence of light energy and temperature on grain growth and on the distribution of assimilates, in relation to the carbohydrate and nitrogen economy of the wheat plant during the grain-filling period.

Materials and methods

The experiment was carried out in the phytotron of the Department of Field Crops and Grassland Husbandry of the Agricultural University, Wageningen.

Plant material and growth conditions

Seeds of the spring wheat variety Orca with a diameter of at least 2.6 mm were used for the experiment. To prevent seedborne diseases, the seeds were dressed with Quinolate V-4. Twenty seeds were sown at random per pot; about two weeks after emergence the number of seedlings was reduced to 15 per pot of 300 cm².

Each pot contained 5 kg of sandy soil. Chemical analysis of this soil gave the following data: pH_{KCl} 5.7; K-value 6.0; P-value 25; organic matter content 4.1%. The pots were fertilized weekly or fortnightly with a mineral solution of NH₄NO₃, Ca(NO₃)₂, KNO₃, KH₂PO₄ and MgSO₄. The total amount of minerals (in meq per pot) for the whole growing period was: 210 N (ratio NH₄⁺+NO₃⁻ was 1:2.5), 60 P, 120 K, 30 Ca, 30 Mg, and 30 S. The micro-elements were applied twice.

During the growing period, insecticides and fungicides were applied regularly to keep the plants healthy.

Arrangement of experiments

From sowing to ear emergence (12 March to 15 June) the plants were grown in a greenhouse with natural daylength and temperature controlled at 12 and 8 °C for day and night, respectively.

Just before ear emergence the plants were transferred to growth rooms. The temperature was kept at 15 °C and the daylength at 16 hours.

From flowering (29 June) onwards, 12 temperature/light intensity combinations were imposed as follows:

- 4 temperatures (°C): 10 (t₁), 15 (t₂), 20 (t₃) and 25 (t₄)
- 3 light intensities (W m⁻²; 0.4-0.7 nm): 188 (L₁), 118 (L₂) and 64 (L₃).

The daily quantities of light energy (MJ m⁻²) intercepted on different heights during a 16-hour light period 3 weeks after flowering were:

		L_1	L_2	L_3
level just above the plants	(\pm 2.00 m)	10.80	6.82	3.68
level of the ears	(\pm 1.80 m)	8.58	5.02	2.80
level of the flag leaves	(\pm 1.60 m)	4.81	2.68	1.39
level of the second leaves	(\pm 1.40 m)	1.93	0.96	0.42
level of the plant base	(\pm 1.00 m)	1.05	0.46	0.13

The relative humidity was kept between 80 and 90 % with the higher values for the 10 and 15 °C treatments and the lower values for the 20 and 25 °C treatments.

Sampling and observations

Plants were sampled at various times by harvesting 4 pots per treatment; most of the observations were made on the main culms. To determine dry matter weights and leaf area the culms were separated into

- a) flag leaf, penultimate leaf, other green leaves and dead leaves;
- b) peduncle, penultimate and remaining internodes;
- c) ear (chaff and grains).

The side culms were separated into ears and straw. Stubble and root weights were determined together for all culms per pot.

The coefficients of variation ranged from 2.7 to 14.4 % for the various dry weight observations.

Determining the photosynthesis and respiration rates

Photosynthetic and respiratory rates were determined with an infrared gas analyser (URAS, Hartmann Brown Co., Frankfurt am Main) by enclosing leaves and ears in an assimilation chamber. The tube-shaped chamber was 40 cm long and 25 mm wide. The measurements were made under the light conditions in the growth room. The temperature of the air in the chamber was adjusted to 20 °C when determining the photosynthetic rate and adjusted to the temperature of the different treatments for determining the respiratory rates.

The air passed through the chamber at a rate of 3.8 l min⁻¹ and a CO₂ concentration of about 325 μ l l⁻¹. The rates of photosynthesis and respiration were calculated from the difference in CO₂ concentration in the air between inlet and outlet of the chamber.

Determining nitrogen and sugar content

The samples of the different parts of the plant were dried at 70 °C to a constant weight. The dried material was ground through a 1-mm sieve and stored in air-tight plastic bags. To determine total nitrogen, a modified Kjeldahl method was used.

To determine water-soluble carbohydrates, 500 mg of dried material was boiled in 50 ml water for 10 minutes. After cooling, 5 ml of a mixed solution of 238 g zinc acetate + 30 g acetic acid, dissolved in 1000 ml of water were added. One minute later, 5 ml of a solution of 106 g K₄Fe(CN)₆ · 3 H₂O, dissolved in 1000 ml of water were added. This mixture was made up to 100 ml with water and filtered; 5 ml of filtrate were diluted with water and used for the determination of the total soluble

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carbohydrates with anthrone by means of an auto-analyser.

To determine the starch content, 250 mg of dried material were used; after being boiled in water the samples were treated for 2 hours in an autoclave at 120 °C and 149 cm water pressure. After cooling, 2.5 ml of acetate buffer and 10 mg amyloglucosidase per 100 mg (expected) starch were added. This solution was made up to 50 ml with water and placed in a waterbath at 60 °C for one hour. After cooling, the samples were treated similarly to the analysis of the water-soluble carbohydrates.

Total soluble carbohydrate and starch content were expressed in glucose units.

Results

Influence of light intensity and temperature after anthesis on the area of green parts of the plants, photosynthetic activity and respiration

The total green area of the main culm at anthesis was composed of 152 cm² of leaf area, 80 cm² of stem area and an undetermined area of the ear. Both flag leaf and penultimate leaf had an area of 54 cm², whilst the dry weights amounted to 163 and 145 mg per leaf, respectively. The green area of the two side culms per plant was not determined. It was found that warmth hastened the senescence of the leaves and the yellowing of the other green organs (Table 1). At 25 °C the senescence was almost completed after 4 weeks, whilst at 10 °C there remained some green leaf area even after 11 weeks.

Light intensity also had a slight influence; the green coloration lasted longer at low light intensities.

The rate of uptake of CO₂ (apparent photosynthesis) of the flag leaf was about 23.5 mg dm⁻²h⁻¹ at ear emergence; at anthesis this value had decreased to about

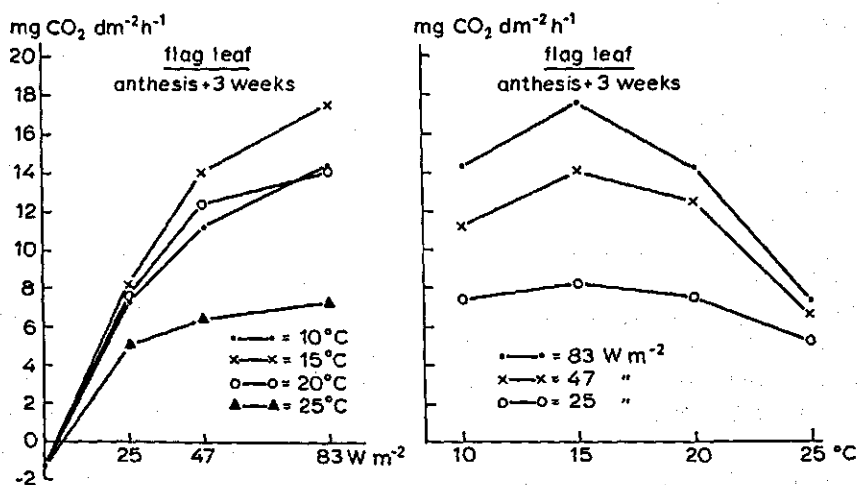


Fig. 1. The rate of apparent photosynthesis of the flag leaf at 3 weeks after anthesis in relation to the post-floral temperature and light treatments.

Table 1. Amount of green area of the flag leaves expressed as percentage of the leaf area at anthesis.

Temperature (°C)	Anthesis + 2 weeks	Anthesis + 4 weeks	Anthesis + 6 weeks
10	100	85	42
15	100	69	36
20	100	31	0
25	100	2	0

21.5 mg. During the first few weeks after anthesis the rate of photosynthesis remained constant per unit green area at all temperatures except 25 °C. At 3 weeks after anthesis the 15 °C treatment showed the highest rate of photosynthesis (Fig. 1). The decrease in photosynthetic rate at higher temperatures may have been caused by faster ageing of the leaves, whilst the photosynthetic rate at 10 °C may have been limited by the slow-down of metabolic processes and the very high carbohydrate content of the vegetative organs.

The rate of dark respiration of the flag leaf at ear emergence and anthesis amounted to 6.0 % and 4.8 % of the rate of apparent photosynthesis, respectively. Soon after anthesis the rate of respiration of the ear and the flag leaf increased in response to warmth. However, at 3 weeks after anthesis the rate of respiration of the ear decreased with a rise in temperature. The respiration rate of the ear was 1.11, 1.49, 1.17 and 0.63 mg CO₂ per g dry weight per hour with 10, 15, 20 and 25 °C, respectively.

In this experiment the production of assimilates depended mainly on:

- light intensity: fixed at 3 levels;
- rate of photosynthesis per unit green area;
- amount and duration of the green area per culm.

Although the few measurements of photosynthesis and respiration do not allow a complete carbohydrate balance to be made, we might conclude from the data of Table 1 and Fig. 1, that temperature affected the duration of green area per culm more than net photosynthesis. Therefore the total production of assimilates after anthesis is favoured by low temperatures, combined with high light intensities.

Influence of light intensity and temperature after anthesis on grain growth and dry matter distribution

After anthesis, warmth reduced the duration of stem and grain growth (Fig. 2). The stem weight increased more at lower temperatures, so there was a surplus of assimilates for grain growth. After the mid kernel-filling stage the senescence of the leaves had already proceeded to a large extent, decreasing the production of assimilates. The reduced supply of assimilates from photosynthesis was partly compensated by a retranslocation of assimilates from the stem to the grains. The average decrease in stem weight was 30 % of the final kernel weight.

The weight of the leaves decreased only slightly after anthesis. However, warmth reduced the weight of the roots considerably during the kernel-filling period.

There were significant interaction effects of light and temperatures on grain

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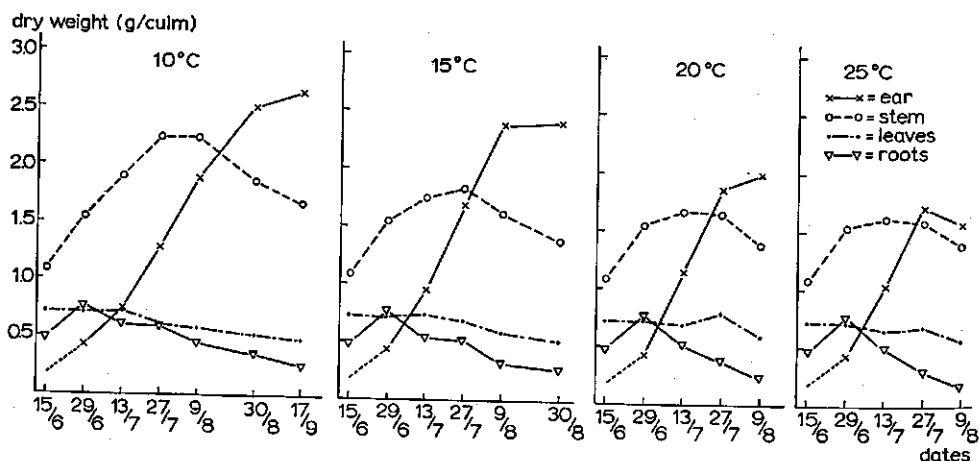


Fig. 2. Dry matter weights of the various parts of the main culm from heading onwards.

growth. The growth rate of the kernels during the apparently linear phase of grain-filling varied within a range from 30 to 74 mg per ear per day. Differences in grain growth due to the reduction of light intensity were less at lower than at higher temperatures (Table 2).

Faster grain growth due to warmth was set off by accelerated senescence of the plants and resulted in a decrease of grain yields (Fig. 3). The post-floral period was shortened from about 80 to 30 days. However, the sum of daily temperatures during the kernel-filling proved to be relatively constant. At ripeness it seemed that the temperature sum was somewhat lower at high temperatures. This may have been caused by shortage of water or assimilates.

Grain growth per degree-day was about the same during the initial phase of kernel filling. After 300 degree-days the growth curves deviated from the 10 °C curve in the sequence 25, 20 and 15 °C. From the point of deviation until maximum kernel weight was attained, the growth rate was not determined by temperature, but predominantly by the supply of assimilates.

Grain yields per ear ranged from 0.79 to 2.56 g because of the effects of temperature and light intensity on the rate and the duration of grain growth. Differences in grain yield per ear were not only attributable to the effects of light and temper-

Table 2. The rate of grain growth (mg day⁻¹) during the linear phase of grain filling, at different light intensities.

Temperature (°C)	188 W m ⁻²		118 W m ⁻²		64 W m ⁻²	
	per ear	per kernel	per ear	per kernel	per ear	per kernel
10	43	0.86	41	0.82	30	0.70
15	52	1.04	43	0.91	34	0.80
20	64	1.31	47	1.04	38	0.93
25	74	1.64	54	1.29	48	1.23

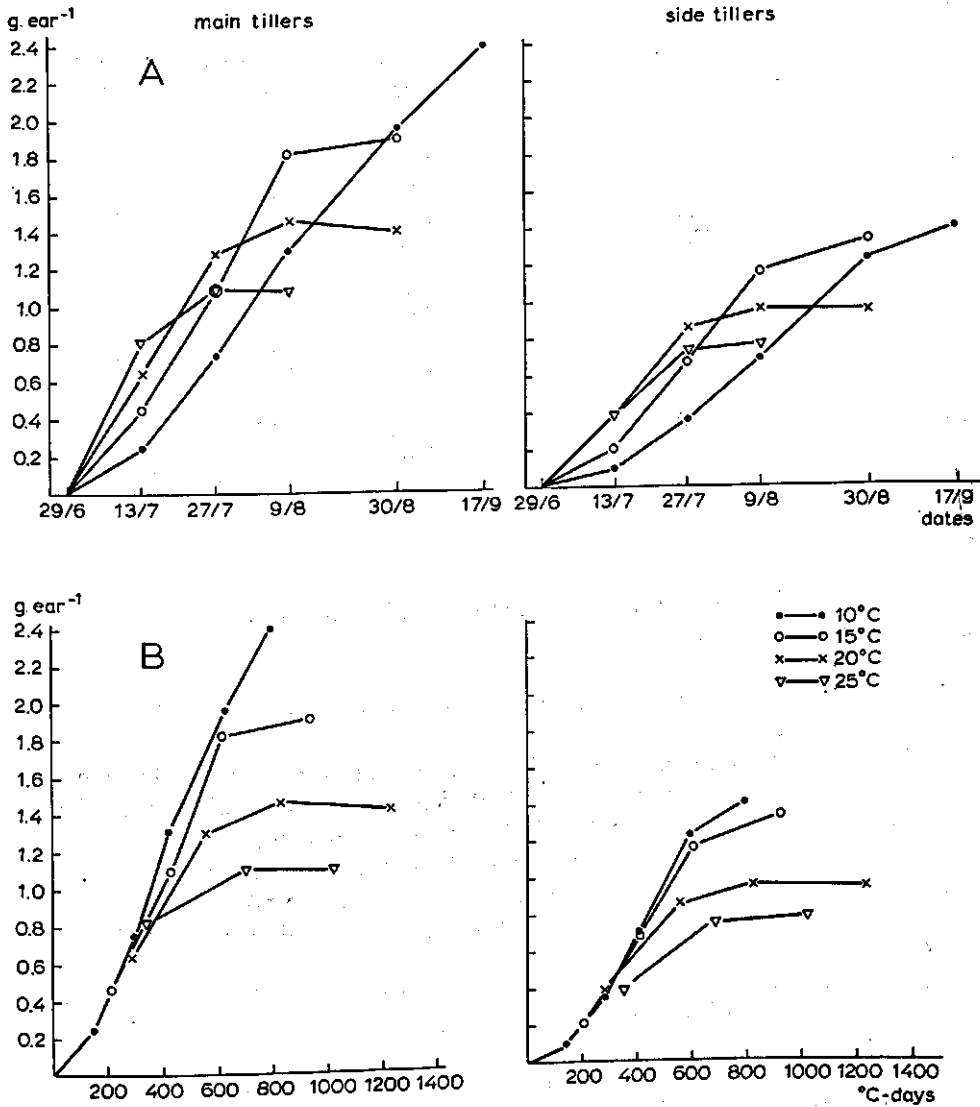


Fig. 3. Grain growth at 4 temperatures, expressed as g dry matter per ear against time (A) and against the sum of daily temperatures after anthesis (B).

ature on the grain weight per kernel, but also to the number of kernels per ear. Obviously, reduced light intensity and warmth after anthesis caused many embryos to be aborted, thereby decreasing the number of kernels per ear (Table 3). Thus the effects of temperature and light were more pronounced on grain yield per ear than on kernel weight. Harvest index increased, when growing conditions (a relatively low temperature combined with a high light intensity) were more favourable

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Table 3. Grain yield and yield components of main culms.

Light intensity (W m ⁻²)	Temperature (°C)	Weight/kernel (mg)	Kernels/ear	Grain weight/ear (g)	Dry matter/culm (g)	Harvest index (%)
188	10	48.9	52.3	2.56	5.23	48.9
	15	43.6	49.3	2.15	4.62	46.5
	20	37.5	49.0	1.83	4.34	42.2
	25	32.0	44.5	1.42	3.81	37.3
118	10	49.7	49.3	2.44	5.15	47.6
	15	45.8	44.9	2.06	4.46	46.2
	20	31.9	44.0	1.40	3.94	35.6
	25	26.6	42.5	1.13	3.56	31.7
64	10	38.0	46.8	1.78	4.04	44.6
	15	31.9	42.8	1.36	3.86	35.4
	20	26.1	41.3	1.08	3.37	32.0
	25	20.3	39.0	0.79	3.15	25.1

for a long period of photosynthetic activity. In this experiment the harvest index ranged from 0.25 to 0.49.

Influence of light intensity and temperature after anthesis on water-soluble carbohydrates (w.s.c.) and starch

Carbohydrates are the main substrate for starch synthesis in the grain. The amount of available carbohydrates in the wheat plant after flowering depends on the balance between photosynthetic production and utilization of assimilates.

In this phytotron experiment the carbohydrate economy was more affected by temperature (range 10-25 °C) than by light intensity (range 64-188 W m⁻²). The changes in starch and w.s.c. contents during the post-floral period are shown in Fig. 4.

The rate of starch synthesis was strongly enhanced by warmth and less by light intensity. The effect of light intensity on starch synthesis was greater at high than at low temperatures.

Although the percentage of w.s.c. in the kernels differed considerably because of temperature, the amount of w.s.c. was about equal for all temperature treatments during the first two weeks after anthesis. A high percentage of w.s.c. in the grain resulted from a lower rate of grain growth. Conversely, a high starch content in the grain was associated with increased grain growth due to warmth. Where the growth rate of the grains was accelerated by a higher light intensity, the starch content was hardly affected. Thus the rate at which sugars were converted into starch was determined by temperature.

The final contents of total non-structural carbohydrates were 21.3, 20.4, 16.2 and 16.5 % sugar and 65.1, 62.2, 58.5 and 53.5 % starch at temperatures of 10, 15, 20 and 25 °C, respectively.

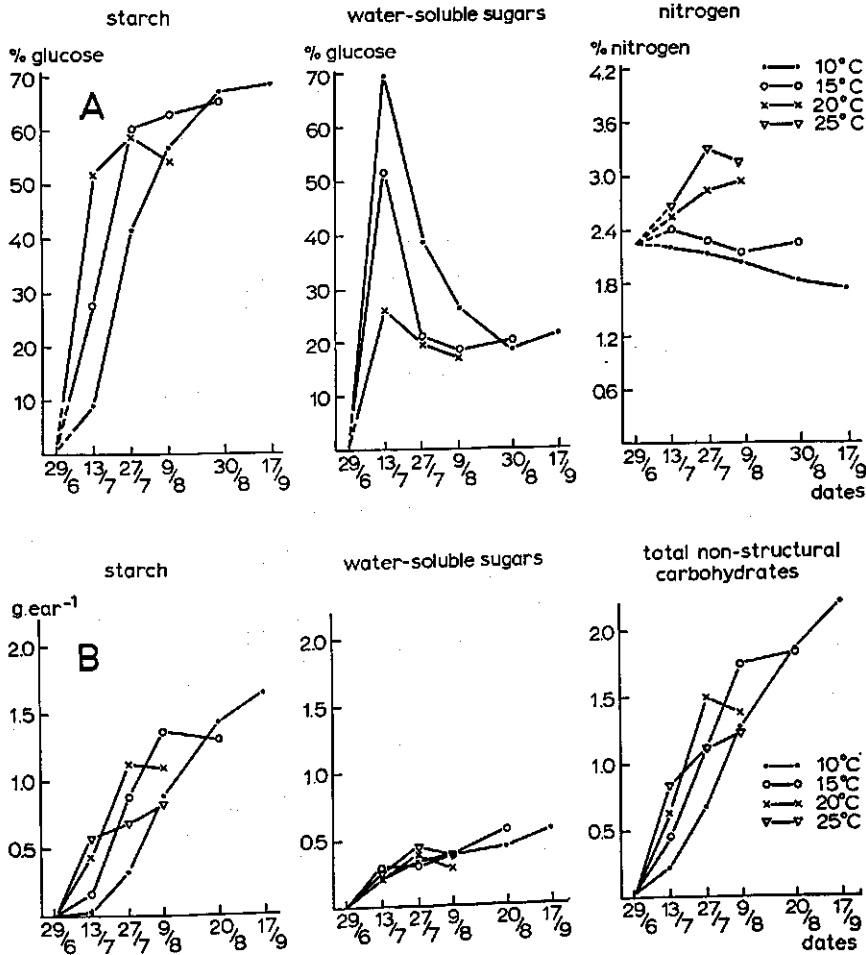


Fig. 4A. The percentage of non-structural carbohydrates in the grain at three temperature treatments (the 25 °C treatment is omitted, because samples were missing) and the percentage of nitrogen in the grain at four temperature treatments.

Fig. 4B. The accumulation of non-structural carbohydrates in the grain.

The w.s.c. content in the various vegetative organs of the wheat plant was also strongly affected by temperature (Fig. 6). At lower temperatures the w.s.c. content of the stem increased considerably after flowering. There was also a marked increase of the w.s.c. content of the upper leaves after flowering. The w.s.c. content of the roots and stubbles likewise responded to lower temperatures by increasing markedly.

The influences of temperature and light intensity on the storage capacity of the grains and on the amount of w.s.c. reserves available for grain growth in stem and leaves are shown in Fig. 5. As there was a considerable accumulation of carbo-

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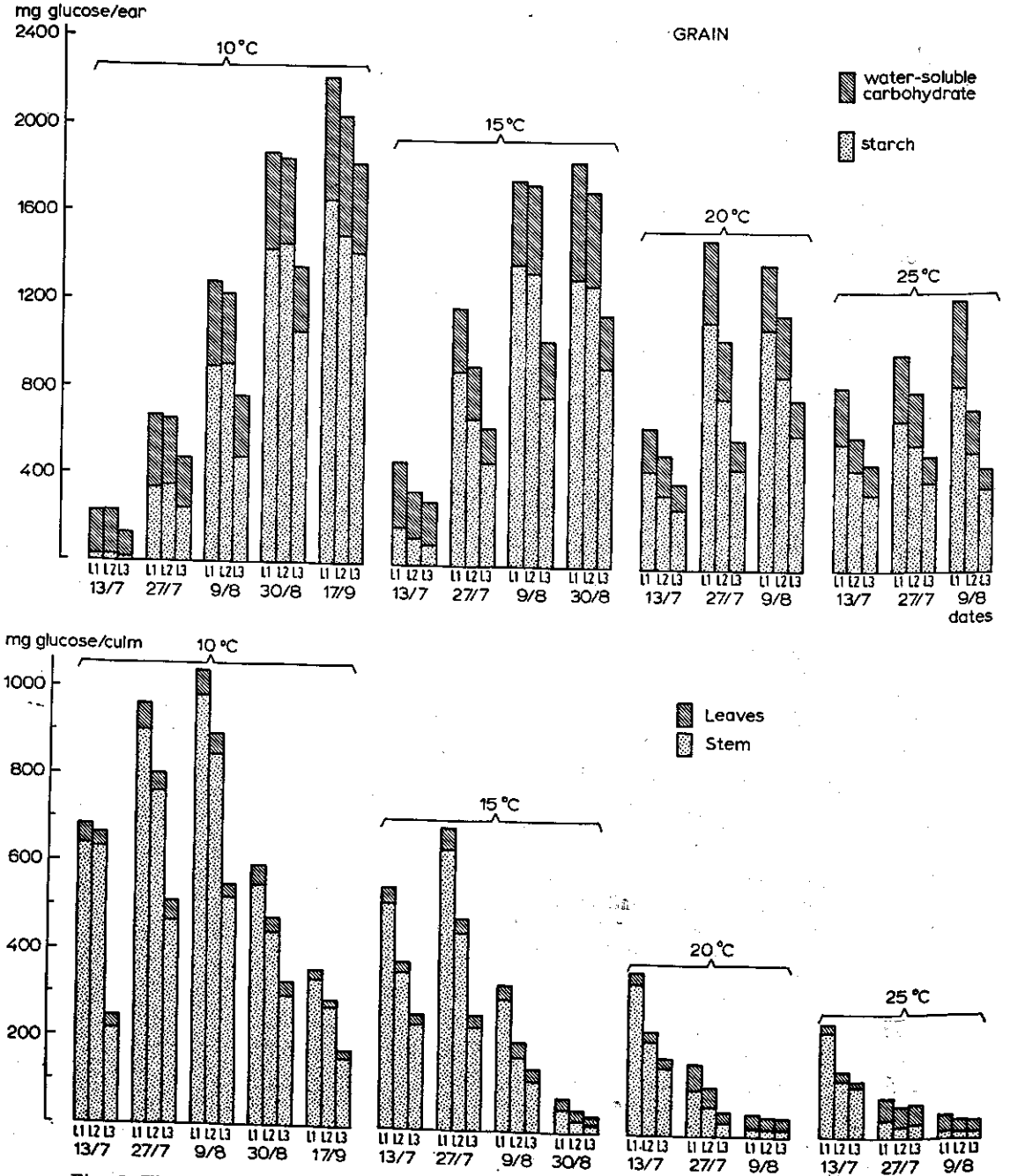


Fig. 5. The amount of non-structural carbohydrates in the stem and the leaves and in the grain of the main culm during the post-floral period at four temperature and three light treatments.

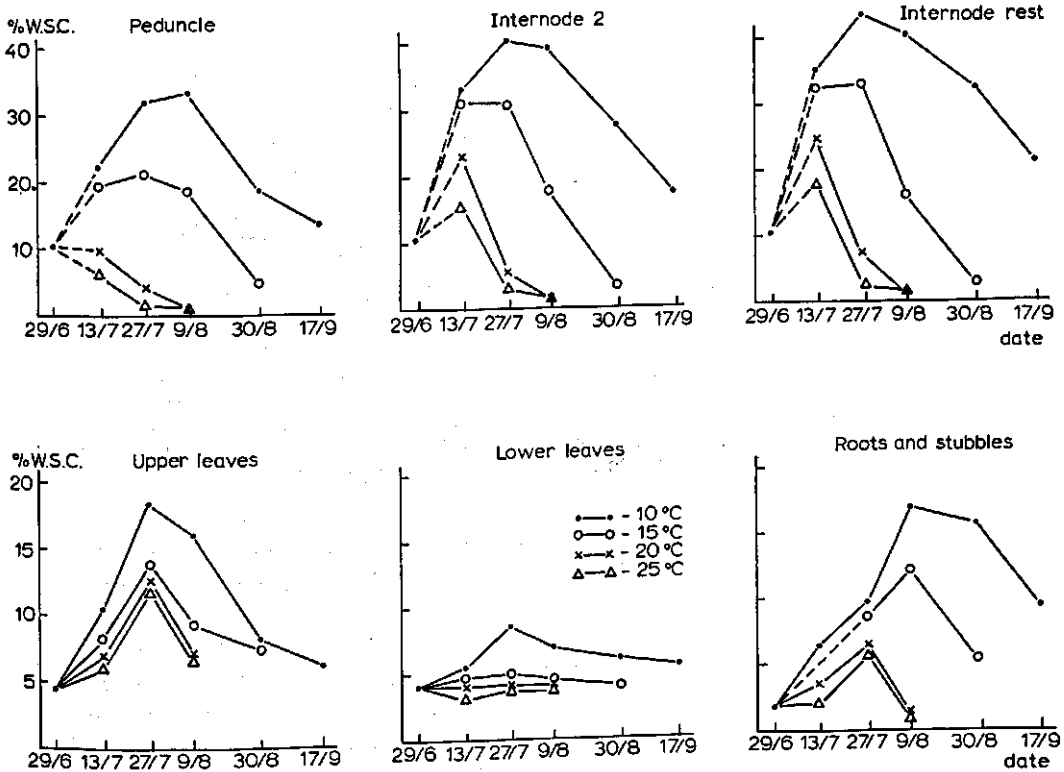


Fig. 6. The percentages of water-soluble carbohydrates in the vegetative organs of the main culm during the post-floral period.

hydrates in the stem at lower temperatures, it may be inferred that the growth rate of the grains was affected more by temperature than by the supply of assimilates. The leaves were of minor importance as an alternative sink for carbohydrates.

High light intensities and low temperatures both increased the amount of w.s.c. in the grains.

Influence of light intensity and temperature after anthesis on nitrogen uptake and distribution

Samples of plant parts, viz leaf blades, internodes (including leaf sheaths) and ears (grains and chaff), were taken at regular intervals from anthesis onwards. There was only a slight influence of light intensity on the nitrogen content of the leaves and stem. The nitrogen percentage of the leaves decreased during the post-floral period: on average from 3.8 to 0.8 % for the flag leaf and from 2.0 to 0.9 % for the lower leaves. Temperature affected the rate at which the nitrogen content of the leaves declined. The average decrease of the nitrogen percentages of the peduncle, internode 2 and lower internodes was from 1.50 to 0.35 %, from 0.65 to

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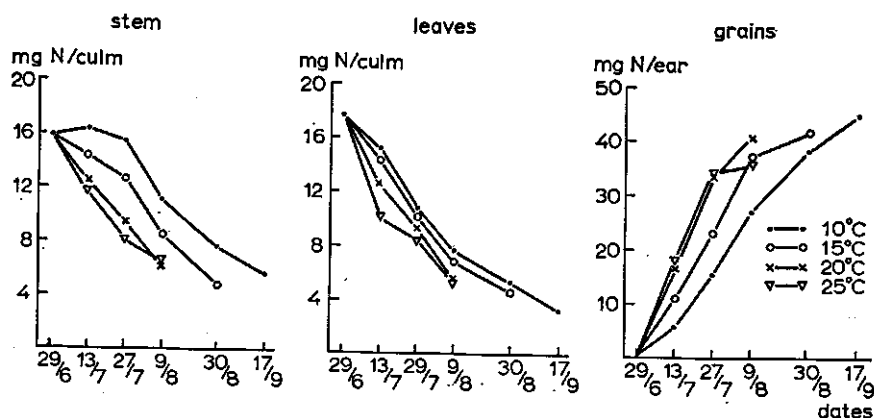


Fig. 7. The amount of nitrogen compounds in the leaves, stem and grain of the main culm during the post-floral period in relation to the four temperature treatments.

0.25 % and from 0.50 to 0.25 %, respectively. The rate of decline was accelerated by warmth; a reduced light intensity gave a slightly higher nitrogen percentage of all internodes.

Warmth enhanced the rate of uptake of nitrogen in the grain from 0.6 to 1.2 mg N per ear per day within the range from 10 to 20 °C. A further increase of temperature did not raise the nitrogen uptake. Enhanced uptake of nitrogen by the grains was associated with accelerated depletion of the nitrogen reserves in the stem and the leaves (Fig. 7). The contribution of the nitrogen reserves in stem and leaves

Table 4. Nitrogen content of the grain and nitrogen uptake and distribution within the main culm.

Light intensity (W m ⁻²)	Temp-erature (°C)	mg N per culm one week after anthesis	mg N per culm at harvest	mg N in straw	mg N in grain	Nitrogen index	% N in grain
188	10	40.7	53.5	11.3	42.2	0.79	1.65
	15	37.2	50.8	12.5	38.3	0.75	1.78
	20	37.1	53.4	13.1	40.3	0.75	2.20
	25	33.8	51.8	13.7	38.1	0.74	2.68
118	10	40.7	56.5	11.1	45.4	0.80	1.86
	15	39.6	53.1	12.3	40.8	0.77	1.98
	20	34.0	52.1	13.7	38.4	0.74	2.74
	25	34.1	49.3	14.7	34.6	0.70	3.06
64	10	41.1	51.5	13.1	38.4	0.75	2.16
	15	41.3	51.0	14.4	36.6	0.72	2.69
	20	37.5	54.0	15.1	38.9	0.72	3.60
	25	29.5	48.1	16.9	31.2	0.65	3.95

accounted for no more than about 60 % of the nitrogen yield of the grains, so there must have been an additional supply of nitrogen to the grains from nitrogen uptake by the plant after anthesis (Table 4). The nitrogen yields of the grains differed only slightly, as did the nitrogen quantities left in the straw. This was all the more striking because of the great effect of temperature on the dry matter yield of the grains.

Discussion

The results of this experiment confirm the more general finding that high post-anthesis temperatures hasten senescence of the wheat plant, shorten the growth period and decrease total dry matter weight as well as grain yield (Thorne et al., 1968; Sofield et al., 1974; Spiertz, 1974; Ford & Thorne, 1975). This shorter growth period was associated with a faster initial growth rate of the grains and an accelerated movement of carbohydrates and proteins from the vegetative organs to the developing grains. Ford et al. (1976) demonstrated that the effects of warmth on processes related to grain growth were caused by the temperature of the ears themselves, rather than of the whole plant.

Although temperature is very important, light intensity also affects grain growth. Contrary to the conclusion reached by Ford & Thorne (1975), we found a considerable interaction between temperature and light intensity on the growth rate of the grains. During the linear phase of grain filling the growth rate was increased more by additional light at high than at low temperatures (from 0.70 to 0.86 per day per kernel at 10 °C and from 1.23 to 1.64 mg per day per kernel at 25 °C with an increase in light intensity from 64 to 188 W m⁻²). At high temperatures the demands of the grains required more assimilates than the amount produced under the conditions of reduced light intensity. At low temperatures there are ample carbohydrate reserves in the stem. Nevertheless the rate of grain growth increased with additional light. So one might conclude that assimilates from current photosynthesis are more readily available for grain growth than are assimilates stored in the stem.

The temperature and light treatments from anthesis onwards also affected seed setting. High light intensities and low temperatures (growing conditions favouring a high level of carbohydrates in the plant), increased the number of kernels per ear. The importance of supply of assimilates for seed setting was also found in a CO₂ enrichment experiment (Krenzer & Moss, 1975). They found that kernel number and size were more dependent on additional assimilates at high than at low temperatures. Our results confirm the effect of temperature on the rate of grain growth found by Sofield et al. (1974), but do not correspond to their conclusion that differences in rate of grain growth per ear are due almost entirely to grain number per ear and not to radiation. There are other stimulating effects of light on grain growth besides an additional supply of assimilates; e.g. Wardlaw (1970) found that reduced light energy decreased the number of endosperm cells. We found a positive effect of light intensity, even with ample carbohydrate reserves, at the low temperature treatments.

The faster initial growth rate did not result from an increased net photosynthesis, but was mainly an effect of temperature on processes involved in grain growth. The

actual growth of the kernels will be determined by the supply of assimilates and the rate at which low molecular substrates are converted to high molecular storage substances. In our experiment, starch and protein synthesis in the grains were considerably promoted by warmth up to 20 °C; a further rise in temperature to 25 °C was less effective. Protein synthesis was enhanced more by warmth than was starch synthesis (see Fig. 4 and 7). This resulted in a higher nitrogen content in the seed. Kolderup (1975) also found that a rise in temperature increased grain nitrogen content considerably. Similar effects of temperature in the range from 10 to 23 °C have been found for protein and starch synthesis in pea seeds (Robertson et al., 1962).

Initially, more assimilates were produced than used for grain growth; therefore the reserves in the vegetative organs increased during the first weeks after anthesis. Later on the increased utilization of assimilates for grain growth and respiration caused the carbohydrate reserves in the stem to deplete rapidly, especially at high temperatures.

On average, the losses of carbohydrates and nitrogen from the stem and leaves amounted to about 30 and 60 % of the ultimate quantities of carbon and nitrogen compounds in the grains respectively. However, the loss of carbohydrates cannot be completely attributable to retranslocation, it is partly caused by respiration. Rawson & Evans (1971) estimated the loss due to respiration to be one-third of the change in stem weight. However, the respiration rate will depend on temperature and available substrate. Spiertz (1974) found a Q_{10} value of about 2 for the respiration of different organs during the milk- to dough-ripe stage. This value was confirmed by more detailed studies of respiration by J. Vos (Dept. of Field Crops & Grassland Husbandry, Agricultural University, Wageningen; pers. comm., 1976) recently; he found a Q_{10} value of 2.0 one week after anthesis. Therefore the contribution of stem reserves to the starch accumulation in the grain must have been considerably lower than 30 % of the ultimate grain yield. The percentage of water-soluble carbohydrates in the stem at the final harvest provides some evidence that the redistribution of carbohydrates was greater at higher temperatures.

Early studies on carbohydrate translocation (Miller, 1939) showed that sugars move into the grain until the moisture content falls to about 40 %. Sugars continue to be converted to starch while the desiccation of the kernel occurs. Not all sugars are converted to starch in the grain. Escalada & Moss (1976) studied the changes in non-structural carbohydrate fractions of field-grown spring wheat. They found that the glucose, fructose and glucofructan contents reached maxima before the phase of rapid starch synthesis, but then decreased as the kernels matured. We found a similar pattern in w.s.c., but the percentage of w.s.c. attained relatively higher values (± 15 à 20 %). The quantity of sugars remained constant during kernel-filling: this corresponds to data published by Jennings & Morton (1963).

In contrast to the w.s.c. content, the starch content was relatively low, so a part of the polysaccharides was determined as 'water-soluble' carbohydrates instead of as starch. The percentage total non-structural carbohydrates (starch + w.s.c.) decreased with warmth. This was compensated for by an increase of the structural carbohydrates. However, the protein content also increased with warmth. Thus

warmth not only affected dry weight, but also the chemical composition of the grain.

In our experiment, water and sugar uptake were affected both by temperature and by light intensity. The rate of desiccation was determined by temperature. It is not clear whether the water content is a reflection of ripening or actively affects ripening processes. Radley (1976) found that the water loss of the grains is preceded by an increase in the abscisic acid content. This endogenous growth substance might be a regulating agent in changing the biochemical and physical attributes of the pericarp, which are related to water loss of the grain. Jenner & Rathjen (1975) stated that the onset of the decrease of starch accumulation in the grain is caused by a fall in the synthetic capacity of the endosperm and not by a reduction in the supply of sucrose to the sites of starch synthesis. They hypothesized that enzymic changes involved in converting sucrose to starch affect the duration of grain growth. We found that the kernel-filling period was longer as the levels of carbohydrates and proteins in the vegetative organs were higher and the grains had a higher water content. The high level of proteins might help prolong the photosynthetic activity of the leaves, and the available carbohydrates might promote the functioning of the roots.

The final grain yield depends both on the rate of dry matter accumulation and on the length of the grain-filling period. The duration of grain growth is determined by processes involved in the senescence of the vegetative organs and processes governing the ripening of the grain. The number of days between anthesis and maximum kernel weight, the so-called 'effective grain-filling period', amounted to 81, 63, 41 and 29 days corresponding to temperature treatments of 10, 15, 20 and 25 °C, respectively. Grain growth per unit of degree-day was the same with all temperature treatments until 300 degree-days. From that point onwards the decline in the growth curve occurred in the sequence 25, 20, 15 and 10 °C. One might conclude that at high temperatures the rapid senescence of the green tissue and the high respiration caused a shortage of carbohydrates, which reduced the growth rate towards the end of the kernel filling. At lower temperatures under more optimal growing conditions, we observed that the ripening of the ears preceded the senescence of the top leaves.

An analysis of yield differences of field-grown wheat crops in different seasons has shown positive effects of warmth on the rate of grain growth (Spiertz, in preparation). Positive effects of warmth on the efficiency, defined as grain-leaf ratio, were also found with a field-grown crop by Welbank et al. (1968). The importance of light intensity in a field crop was studied extensively by Willey & Holliday (1971) and Fischer (1975) in shading experiments. The significance of light intensity is over-estimated in this type of experiment because of the effect of shading on the temperature of the wheat plant. In spite of these difficulties, the results of field and phytotron experiments agree well.

Grain yields of wheat might be enhanced if wheat plants were better adapted to hot spells during the kernel-filling period. This would allow the wheat plant to benefit more from the higher light intensity that is mostly associated with warmth.

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Effects of nitrogen on crop development and grain growth of winter wheat in relation to assimilation and utilization of assimilates and nutrients

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Key words: nitrogen supply, leaf area, grain number, grain growth, carbohydrate reserves, uptake of nutrients, distribution of nutrients, harvest index, winter wheat

Summary

Grain growth and yield components of winter wheat (cv. Lely) were studied in a field experiment in 1976 with four regimes of nitrogen dressing (50, 100, 100 + 50 and 100 + 100 kg N ha⁻¹). Growing conditions were characterized by a high level of solar radiation, warmth, ample nutrient supply and no damage by diseases.

Nitrogen raised grain number per m² from 16 700 to 20 600 and grain yield from 640 to 821 g dry weight m⁻². Grain growth duration was short, due to warmth, but the rate of the grain filling was very high: from 24.0 to 29.2 g m⁻² day⁻¹ during the effective grain-filling period. A high grain yield was associated with a high nitrogen percentage of the grains, which resulted in a grain protein yield ranging from 63.8 to 107.1 g m⁻² with an increased nitrogen dressing from 50 to 200 kg ha⁻¹.

The carbohydrate demand of the grains was provided by current photosynthesis and relocation of stem reserves. The latter was reflected in a decline of the stem weight after the mid-kernel filling stage. Nitrogen and phosphorus demand of the grains were supplied by withdrawal from the vegetative organs (leaves, stem, chaff) and to a large extent by post-floral uptake and assimilation.

Under the prevailing growing conditions the grains turned out to be very strong sinks for carbohydrate, nitrogen and phosphorus as shown by the harvest-indices. Additional nitrogen dressings increased the harvest-indices of dry matter, nitrogen and phosphorus from 0.40 to 0.48, from 0.75 to 0.81 and from 0.91 to 0.93, respectively.

It was suggested that a more restricted vegetative crop development at high nitro-

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gen levels and a longer duration of root activity, photosynthesis and grain growth after anthesis would considerably favour grain yield.

Introduction

Grain yield of wheat is a function of the number and growth rate of kernels per unit ground area. The growth rate is the result of production of assimilates and storage of carbon and nitrogen compounds in the developing grains. The carbon supply depends mainly on the green area duration and the net photosynthesis of leaves, glumes and stem after anthesis (Evans & Wardlaw, 1976; Stoy, 1975). The nitrogen supply depends on the relocation of reserves in the vegetative organs to the grains and on the uptake and reduction of nitrate during the grain filling periode (Austin et al., 1976; Dalling et al., 1976; Campbell et al., 1977b).

The aim of this experiment was to study the effect of various levels of nitrogen dressing and disease control on plant growth and crop development (number of culms, grain number, leaf area), on the post-floral economy of carbohydrates and nutrients (N, P and K) and on the grain growth pattern of winter wheat under optimal growing conditions in the field.

Methods

The experiment was carried out on the experimental farm of the Agricultural University, located in the Flevopolder. The type of soil was marine clay of the following characteristics: clay content ($< 16 \mu\text{m}$) 45%; organic matter 2.8%; pH-KCl 7.3; CaCO_3 10.0%; K. value 22; K-HCl 24; Pw value 23. Before sowing 250 kg per ha of 43% superphosphate was applied; potassium was omitted since it was already abundant in the soil. Nitrate-nitrogen, available in the soil layer of 0.75 m depth, amounted to approximately 80 kg N per ha at the end of February 1976. The mineralization of nitrogen in the soil during the growing season of 1976 was relatively high. The wheat crop was grown in a nine-year rotation with seed potatoes as previous crop.

Sowing of the cultivar Lely was done on 23 October 1975 with a seed rate of 400 kernels per m^2 . Nitrogen was applied as split dressing with the following treatments (in kg N ha^{-1}):

	16 March	20 May	Total
N_1	50	0	50
N_2	100	0	100
N_3	100	50	150
N_4	100	100	200

The experiment consisted of a completely random block design with four nitrogen and four fungicide treatments and with four replicates. The fungicide sprayings were carried out at stage F5-6, at F10.3 and at both stages with 4 kg ha^{-1} of Bavistin M which contained 240 g carbendazim and 1700 g maneb as active substance.

NITROGEN SUPPLY, CROP DEVELOPMENT AND GRAIN GROWTH IN WHEAT

Table 1. Weather conditions during the growing season of 1976, compared to the mean data for the period 1931-1960.

	April			May			June			July		
	1	2	3 total or mean	1	2	3 total or mean	1	2	3 total or mean	1	2	3 total or mean
	Rainfall (mm)*	2.2	0	1.1 3.3	6.6	4.8	8.4 19.8	3.1	13.8	4.5 21.4	0	10.3
Radiation (MJ m ⁻² day ⁻¹)**	13.2	18.1	18.6 48.8	17.1	19.6	17.4 51.5	21.2	20.3	26.2 58.0	27.0	16.6	17.8 76.8
Daily temperature (°C)**	6.4	9.0	6.0 7.1	13.8	12.4	12.2 16.4	14.8	15.6	20.9 17.8	20.8	19.1	15.6 15.8
Max. temperature (°C)**	14.1	18.4	14.2 8.5	22.9	20.5	19.6 12.4	22.9	22.9	30.7 15.5	31.4	26.9	23.5 17.0
Min. temperature (°C)**	-1.8	-0.3	-1.6 13.3	4.0	2.5	4.1 17.7	4.9	6.7	10.7 20.7	9.9	10.2	8.4 21.9
			3.9			7.1			10.1			12.2

* Total; ** Mean.

Weeds were controlled by spraying with 4 litres MCPP per ha at the end of April. This spraying was combined with the application of 2 litres chlormequat (CCC) per ha.

The individual plots had an area of 6×20 m² with row widths of 15 cm. An inner strip of 3 m was reserved for the combine harvest. Sampling during the growth period were carried out in the inner rows of the border strips, each consisting of 10 rows of 20 m length.

Observations

Measurements of crop growth and plant development were carried out on 27 April, 18 May, 1 June and weekly from 15 June onwards. The area sampled at these intermediate harvests amounted to 0.30 m² (= 4 rows of 0.50 m) per plot. After determining fresh weight and tiller number the samples were sub-divided for measurements of leaf area per leaf layer and dry weight of the various parts of the culm. For the chemical analyses small samples were prepared. All samples were dried at 70 °C (for details, see Spiertz, 1977). Chemical analyses of nitrogen, phosphorus and potassium were done by the Department of Soils and Fertilizers of the Agricultural University.

The light interception by the crop was measured in all plots perpendicular to the rows with an integrating photometer (0.4-0.7 nm) of one metre length.

In 1976 the growing season started relatively cold, sunny and dry in April (see Table 1). After anthesis, on 12 June, the weather became much warmer and dryer than average, especially from a fortnight after anthesis onwards. The crop senesced very rapidly therefore and the grain filling period was comparatively short. In spite of this extreme weather conditions there was ample water available at 60 cm depth in this polder soil; thus the early ripening was obviously not caused by water shortage.

Disease infections were very limited during this growing season. Only during the early stages of crop development *Septoria tritici* could be observed. From the fungicide treatments it appeared that no damage of leaf and ear diseases had occurred.

Results

The data are presented without considering fungicide treatments. At intermediate harvests the number of replicates amounted to four, whilst at the harvests of 27 and 29 July a complete analysis of variance was computed (Table 2).

Canopy structure, yield and yield components

Plant density was quite high, about 344 plants per m², due to the high seed rate and the mild winter. Tillering amounted on average to about 2.5 and 4.1 tillers per plant on 6 and 27 April, respectively. The maximum tiller number was achieved at the end of April and amounted to 1410 per m². There was no significant difference in tiller density between the nitrogen treatments. The weather in May did not favour leaf and stem elongation of the wheat plant, so the crop remained

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Table 2. Influence of four levels of nitrogen dressing on dry matter yield, harvest index, yield components and other crop characteristics.

Characteristic	Nitrogen dressing (kg N ha ⁻¹)				Mean	c.v.	F test ¹
	50	100	100 + 50	100 + 100			
<i>Dry weight (g m⁻²)</i>							
- grain (from combine harvest of 60 m ² at 29/7)	640	732	799	821	748	4.7	****
- grain (intermediate harvest of 0.30 m ² at 27/7)	629	691	856	858	759	13.8	****
- chaff (ditto)	179	172	194	192	184	18.6	—
- straw (ditto)	775	701	768	739	746	8.2	***
- total minus roots (ditto)	1572	1571	1821	1787	1687	11.0	**
- harvest index (ditto)	0.40	0.44	0.47	0.48	0.45	3.3	****
- total minus roots (calculated from grain yield at 29/7)	1600	1664	1700	1710	1669	—	—
<i>Yield components (observations at 27/7)</i>							
- grain dry weight per ear (mg)	1.31	1.48	1.59	1.61	1.50	11.8	****
- dry weight per grain (mg)	40.0	41.3	42.1	42.1	41.4	2.6	****
- number of grains per ear	32.8	35.9	37.8	38.2	36.2	10.8	****
- number of ears per m ²	509	498	540	538	521	7.1	****
- number of grains per m ² (× 10 ⁵)	16.7	17.9	20.4	20.6	18.9	—	—
<i>Leaf area index</i>							
- LAI on 15 June	2.36	2.36	2.69	2.75	2.54	9.3	****
- LAI on 22 June	2.31	2.32	2.65	2.80	2.52	8.9	**
- LAI on 29 June	1.90	2.14	2.31	2.41	2.19	12.2	*
- LAI on 7 July	0.66	1.27	1.69	1.91	1.38	20.6	****
- LAI on 13 July	0	0.06	0.38	0.84	0.32	77.7	***
<i>Light interception</i>							
- % of incident radiation on 2 July	83.5	89.0	91.5	90.5	88.6	10.0	***

¹ Confidence limits: * = 0.10 > α > 0.05; ** = 0.05 > α > 0.01; *** = 0.01 > α > 0.001; **** = α < 0.001.

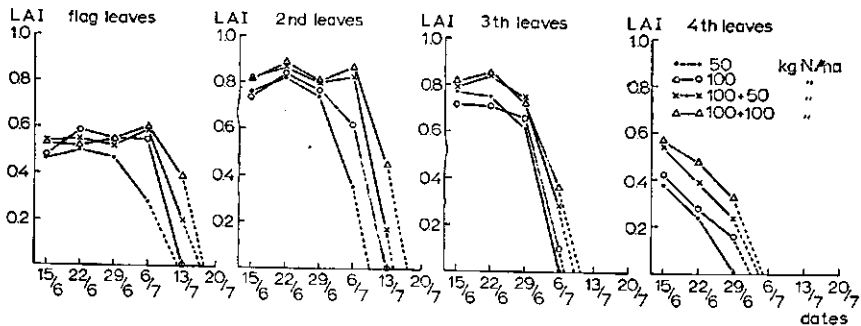


Fig. 1. Leaf area index per leaf layer after anthesis at four levels of nitrogen dressing.

short and stiff-stawed. The areas of the leaves were much smaller than is normally expected; the flag leaf in particular was very short (Fig. 1). The area of the upper leaves remained rather constant for two weeks after anthesis; from then on senescence proceeded very rapidly, especially with the lower nitrogen treatments. The difference in the duration of the green area between the plots with 50 and 200 kg N/ha was about seven days.

Despite the low leaf lamina area index, light interception by the crop 2 weeks after anthesis ranged from 83.5 to 91.5% of the incident visible radiation (Table 2). Stems and ears therefore must also have intercepted a large amount of radiation. The contribution of the leaf laminae to the total (one-sided) green area amounted to about 40%.

The positive response of grain yield to a rise in nitrogen supply must be attributed mainly to an increase in the number of kernels per ear (Table 2). This number raised from 32.8 to 35.9 kernels per ear by increasing the nitrogen dressing on 16 March from 50 to 100 kg ha⁻¹. An additional nitrogen dressing of 50 kg ha⁻¹ during the boot stage gave an extra response of about two kernels per ear. Dry weight per grain increased from 40.0 to 42.1 mg as nitrogen dressings were raised from 50 to 100 + 50 kg N ha⁻¹, respectively. The number of ears was also increased by extra nitrogen, but to a lesser extent than the number of kernels per ear. Grain yield was therefore mainly determined by the number of kernels per m². An increase in the number of kernels per m² from 16 700 to 20 600 corresponded with grain yields of 640 and 821 g dry weight per m² at the final harvest (29 July).

Dry weights of straw and chaff were determined on samples from an intermediate harvest of 0.30 m² on 27 July. The nitrogen treatments were only partly reflected in straw and total dry matter yield, in spite of a clear response of the grain yield to nitrogen. For this reason the total dry weight was also calculated from the grain yield of an area of 60 m² by means of the harvest index. The total dry matter yield then increased from 16.0 to 17.1 tons with nitrogen dressings of 50 and 100 + 100 kg ha⁻¹ respectively. This increase was less than the rise in the total grain weight, which indicates an improved translocation of assimilates from the vegetative parts of the wheat plant to the grains with increased nitrogen supply. Thus

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the range from 0.40 to 0.48 for the harvest index was mainly brought about by the differences in grain yield.

When individual treatments instead of the whole range of nitrogen dressings are compared, Student's test (confidence level of 50%) did not show any significant differences in grain yield and yield components between 100 + 50 and 100 + 100 kg N ha⁻¹. Thus the maximum grain yield, as far as nitrogen was concerned, was almost completely realized with a split dressing of 100 + 50 kg N ha⁻¹. A further increase of nitrogen did not raise the yield substantially. The effect of nitrogen on the uptake of nutrients and on the chemical composition of the various parts of the wheat plant are discussed further on in the paper.

Rate and duration of grain growth

Grain growth of this winter wheat crop was characterized by a short growth period. The effective grain-filling period lasted about 4 weeks, while the period from anthesis to maximum grain weight amounted to about 5 weeks. The period with a high rate of grain growth ended before mid-July, followed by only a small increase in grain weight later on.

Despite the very short kernel-filling period grain yields turned out to be quite high. So the rate of grain growth must have been exceptionally fast. From the end of anthesis (15/6) until the stage of maximum kernel weight (20/7) the daily grain growth ranged from 1.13 to 1.19 mg dry weight per kernel, from 33.4 to 41.1 mg dry weight per ear and from 19.0 to 24.0 g m⁻², due to an increased nitrogen dressing (Fig. 2).

From approximately 29 June to 6 July, the growth rate of individual grains was hardly affected by nitrogen and amounted on average to 2.5 mg kernel⁻¹ day⁻¹. After the midkernel filling stage late nitrogen treatments increased grain growth rate from 0.78 to 1.09 mg kernel⁻¹ day⁻¹.

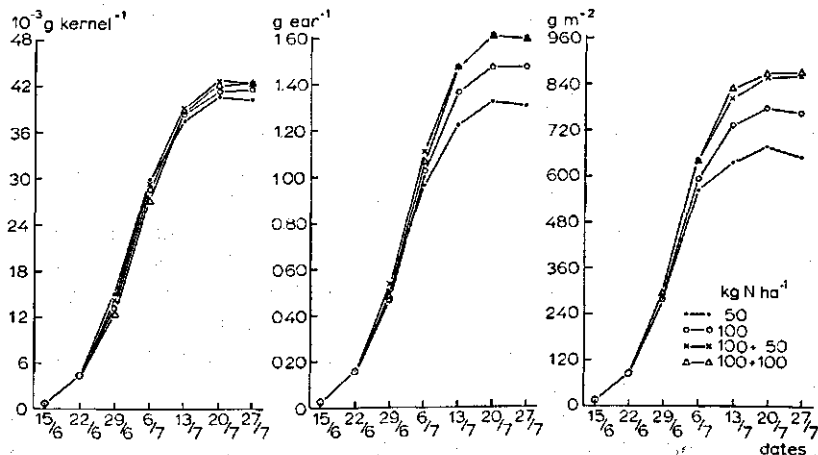


Fig. 2. Growth curves of grain dry weight per kernel, per ear and per m² at four levels of nitrogen dressing.

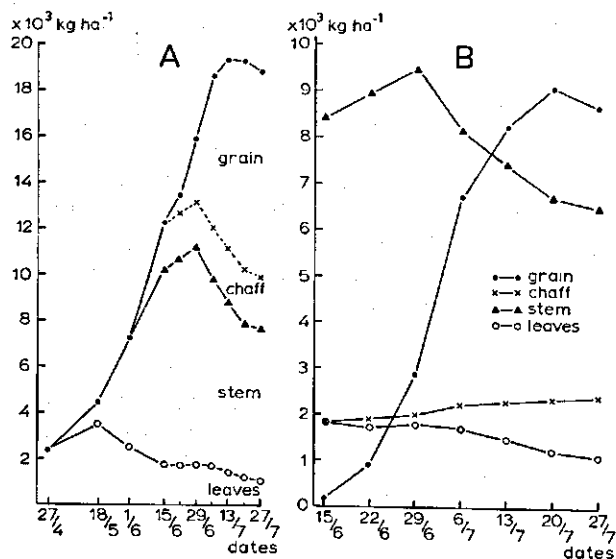


Fig. 3A. Distribution pattern of dry weight for the above-ground parts of the wheat plant at nitrogen dressing of 100 + 100 kg N ha⁻¹.

Fig. 3B. Course of dry weights of grain, chaff, stem and leaves after anthesis at a nitrogen dressing of 100 + 100 kg N ha⁻¹.

As additional nitrogen increased both the number of kernels per m² and the growth rate per kernel, more assimilates must have been made available from grain growth either by an increased photosynthetic production or by an improved utilization of stored assimilates in the stem. In fact, additional nitrogen promoted photosynthetic production, as shown by the increase in the total matter yield of the crop (Table 2). Nevertheless a gap in the dry weight balance for the grains existed, which can only have been filled up by an increased relocation of assimilates from the stem to the grains.

Dry matter distribution and carbohydrate reserves

There were only small changes in the dry weights of the leaf blades and the chaff from flowering onwards, but stem weight increased during the two weeks after anthesis, succeeded by a sharp decline (Fig. 3). Thus initially the production of assimilates by current photosynthesis was greater than the demand for grain growth. The decrease in stem weight took place simultaneously with the start of a hot spell, which obviously accelerated grain growth. The loss of stem weight amounted, within a 3-week period, to 3360 and 2760 kg ha⁻¹ with 50 and 200 kg N ha⁻¹, respectively (Table 3). It may be assumed, that a part of the loss in stem weight was caused by respiration, but relocation of assimilates to the grains and the roots may also have contributed to it. Especially during the latter part of the grain filling period, when grain growth coincides with a decline in current photosynthesis of senescing green organs, relocation of stem reserves may have been important source of assimilates.

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Table 3. Losses of dry weight and water-soluble carbohydrates (w.s.c.) from the stem during the grain-filling period.

Nitrogen dressing (kg N ha ⁻¹)	29 June		20 July		Loss from 29-6 to 20-7	
	mg per culm	g m ⁻²	mg per culm	g m ⁻²	mg per culm	g m ⁻²
<i>stem dry weight</i>						
50	1.91	972	1.25	636	0.66	336
100 + 100	1.75	928	1.23	652	0.52	276
<i>w.s.c. content</i>						
50	0.63	323	0.08	38	0.55	285
100 + 100	0.47	249	0.05	26	0.42	223

Changes in dry weight of the stems are mainly caused by changes in the non-structural carbohydrates. The influence of nitrogen on the percentage and amount of water-soluble carbohydrates in stem, leaves and grain is shown in Fig 4. Generally the carbohydrate percentages are lowered by an increased nitrogen supply. However, the pattern of accumulation and decrease of carbohydrate reserves in the vegetative organs during the post-floral period is more interesting. It gives more insight into the reserves available for energy-requiring processes (e.g. respiration) and for grain growth.

The water-soluble carbohydrates (w.s.c.) accumulated in the stem up to a fortnight after anthesis. The w.s.c. percentage at that stage ranged from 26.8 to 33.2

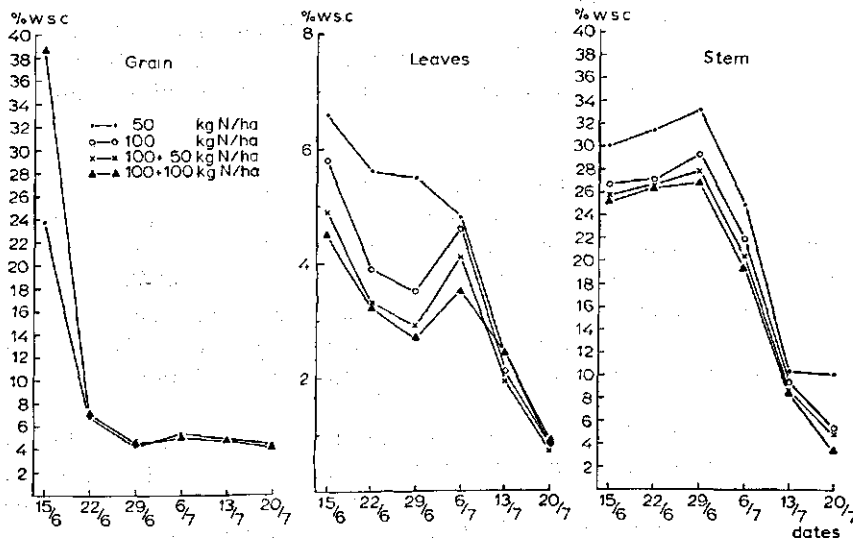


Fig. 4. The water-soluble carbohydrate content of grain, leaves and stem after anthesis at four levels of nitrogen dressing.

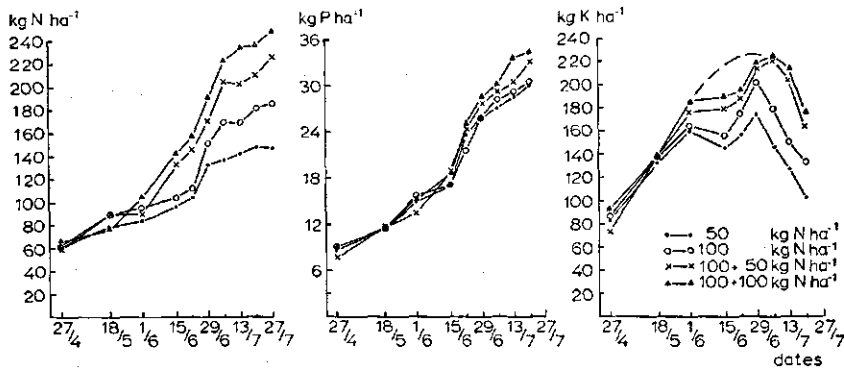


Fig. 5. Amounts of nitrogen (N), phosphorus (P) and potassium (K) in the wheat culm during the growing season at four levels of nitrogen dressing.

the stem, from 2.7 to 5.5 in the leaves and amounted to 5% in the grains for nitrogen dressings from 200 to 50 kg N ha⁻¹. The storage function of the stem is also strongly expressed by the quantity of w.s.c. available in it. This quantity increased for two weeks after anthesis from for two weeks after anthesis from about 250 to about 280 g m⁻², followed by a sharp decrease from 280 to 60 g m⁻² after the mid-kernel filling stage. The w.s.c. quantities in the other organs are on a lower level: at anthesis for leaves, chaff an grain about 9.5, 12.5 and 5.0 g m⁻², respectively. During the post-floral period the carbohydrate quantities of the leaves did not decrease linearly, but there was a second peak 3 weeks after anthesis. This peak coincided with a decline in the rate of grain growth. The amount of w.s.c. in the grains increased up to 35.0 g m⁻².

These data show that the w.s.c. reserves in the stem play an important role as a carbohydrate source for the grains, when the production of assimilates by current photosynthesis is reduced, due to progressive senescence of the photosynthetic tissues.

Uptake and distribution of nitrogen, phosphate and potassium

The uptake of nitrogen, phosphorus and potassium showed a peculiar pattern, which was characterized by a temporary slow-down of nitrogen and potassium uptake during the heading phase followed by an accelerated assimilation of nutrients during the post-floral period (Fig. 5). This phenomenon may be associated with the cool, dry weather during the pre-anthesis period, interrupted by a sharp rise in temperature after anthesis and a significant amount of rainfall (18.3 mm) one week after anthesis.

The maximum nitrogen (N) and phosphorus (P) yields of the above-ground parts of the plant were attained at ripening and ranged from 147 to 248 kg ha⁻¹ and from 30 to 35 kg ha⁻¹ with 50 and 200 kg nitrogen dressing, respectively. The potassium yield reached maximum levels at the mid-kernel filling stage and ranged from 175 to 223 kg ha⁻¹ (Fig. 5). The highest rates of uptake amounted to 4.6, 0.4 and 2.4 kg ha⁻¹ day⁻¹ of nitrogen, phosphorus and potassium, respectively,

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during the kernel-filling period. The assimilation of these nutrients by the grains amounted during the same period to 7.6, 1.4 and 1.1 kg ha⁻¹ day⁻¹, with the highest nitrogen dressing. Thus the demand of the grains, as far as nitrogen and

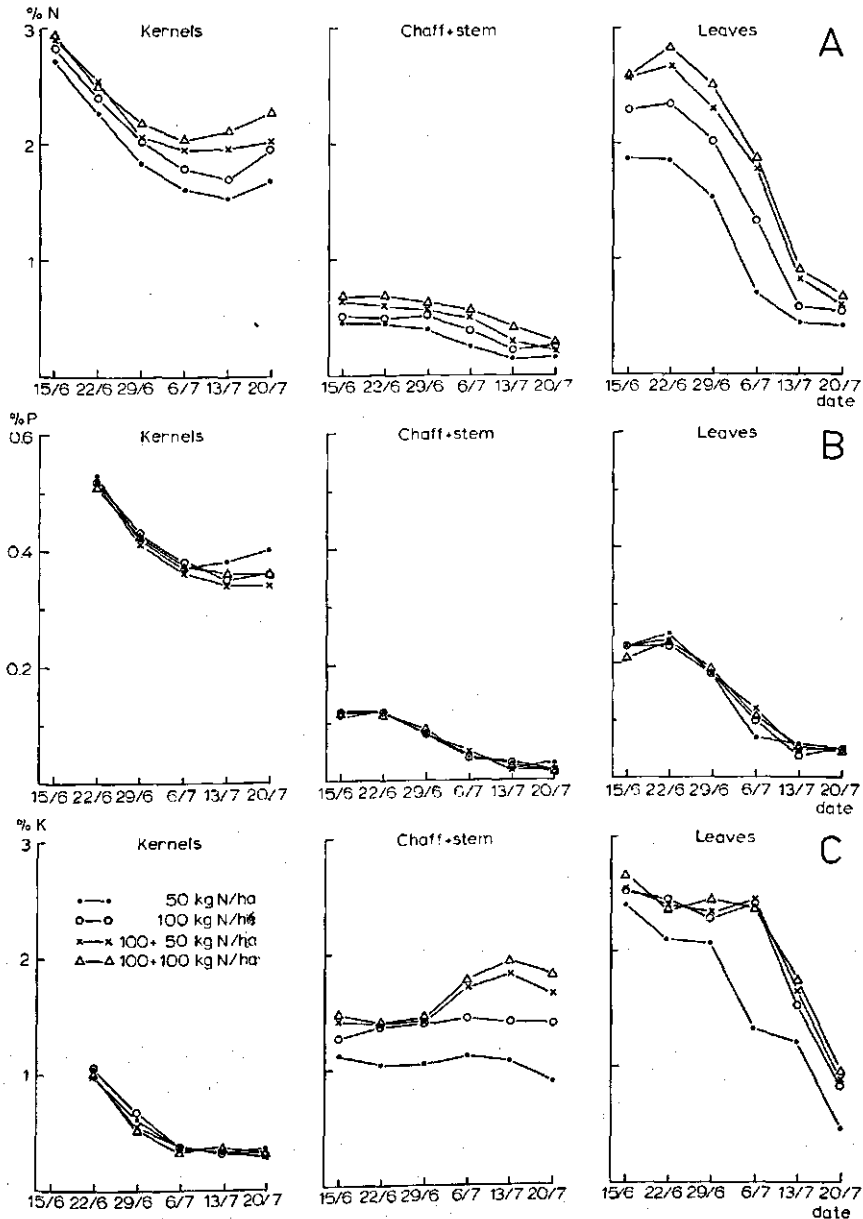


Fig. 6. Effects of the nitrogen dressings on nitrogen (A), phosphorus (B) and potassium (C) percentages of the grains, stem and leaves after anthesis.

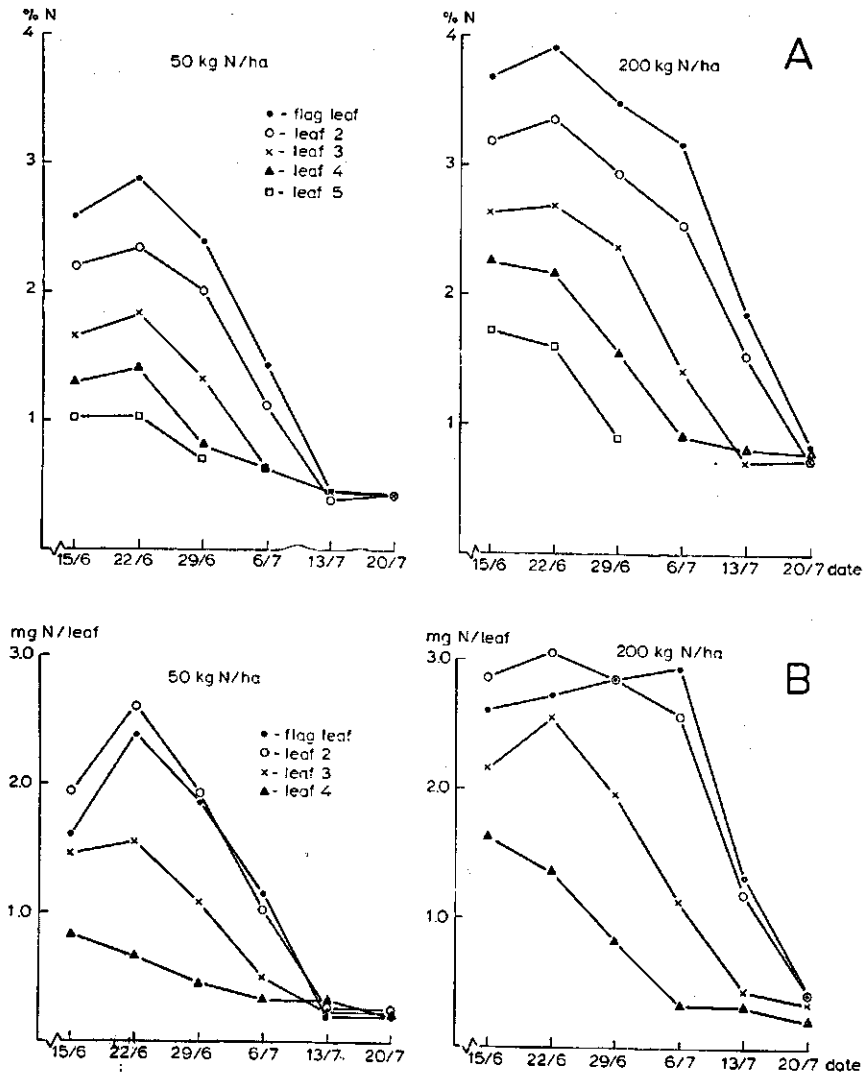


Fig. 7. Post-floral nitrogen percentages (A) and contents (B) of the various leaf layers at 50 and 200 kg N ha⁻¹.

phosphorus are concerned, was considerably higher than the post-floral uptake by the plant. From these figures it follows that a supply from the vegetative parts was made available to the grains.

The pattern of nitrogen, phosphorus and potassium contents, expressed as percentages of the dry weight of leaves, stem and grain, is shown in Fig. 6. On average the nitrogen percentages of the leaves decreased during the post-floral period from 2.4 to 0.6, but there were large differences due to nitrogen level and leaf layer.

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The nitrogen concentration of the other vegetative above-ground organs — stem, rachis and chaff — also increased with additional nitrogen supply. The nitrogen concentration of the stem increased from 0.45 to 0.70% and of the chaff (including the rachis) from 1.48 to 1.69%. These nitrogen percentages decreased linearly during the grain-filling period to levels of about 0.25% and 0.50% for the stem and chaff, respectively.

The nitrogen percentage of the grain decreased during the first three weeks after anthesis from about 2.80 to 1.80% and rose again at the end of the grain-filling period to about 2.09%. As a result of the nitrogen dressings the nitrogen contents of the grain at ripening ranged from 1.72 to 2.25%.

The nitrogen treatments hardly affected the phosphorus content of the various components, but increased the potassium content of the vegetative parts of the culm. Nitrogen applied at Feekes stage 8 raised the potassium content of the stem, but not of the leaves. The potassium content of the grains was not affected by nitrogen at all.

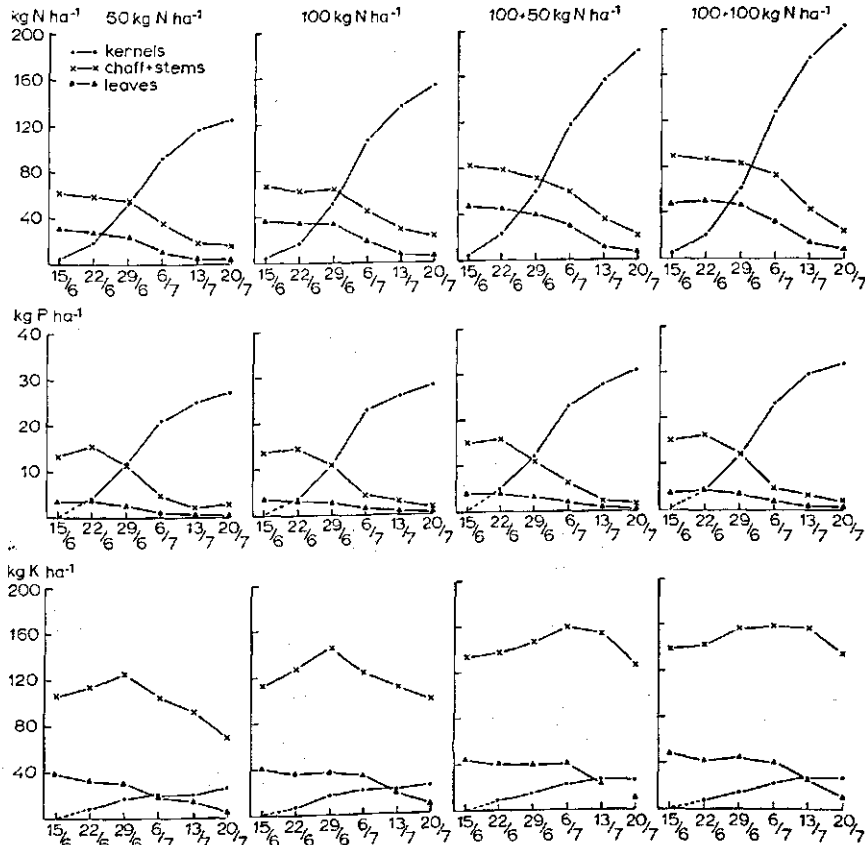


Fig. 8. Distribution pattern of nitrogen (A), phosphorus (B) and potassium (C) in the wheat culm after anthesis at four levels of nitrogen dressing.

Table 4. Uptake, distribution and yield of nitrogen, phosphorus and potassium in the above-ground parts of the wheat plant on 20 July (phosphorus and potassium) and 27 July (nitrogen).

Nitrogen dressing (kg N ha ⁻¹)	Net uptake of nitrogen after anthesis		Loss of nitrogen from the 'straw' (kg ha ⁻¹)	Nitrogen yield (kg ha ⁻¹)		Nitrogen harvest index
	kg ha ⁻¹	% of grain nitrogen		grain	'straw' total	
50	51	43.6	70	110	37	0.75
100	72	48.3	82	143	40	0.78
100 + 50	93	49.7	101	179	46	0.80
100 + 100	106	51.0	105	200	47	0.81
Phosphorus						
	Net uptake of phosphorus after anthesis		Loss of phosphorus from the 'straw' (kg ha ⁻¹)	Phosphorus yield (kg ha ⁻¹)		Phosphorus harvest index
	kg ha ⁻¹	% of grain phosphorus		grain	'straw' total	
50	12.8	46.7	15.6	27.4	2.6	0.91
100	12.9	45.9	16.6	28.1	2.4	0.92
100 + 50	13.7	44.8	17.3	30.6	2.4	0.93
100 + 100	14.3	44.7	18.3	32.0	2.5	0.93
Potassium						
	Net uptake of potassium after anthesis		Loss of potassium from the 'straw' (kg ha ⁻¹)	Potassium yield (kg ha ⁻¹)		Potassium harvest index
	kg ha ⁻¹	% of grain potassium		grain	'straw' total	
50	-43 (+30/-73)	-	73	22	80	0.22
100	-23 (+46/-69)	-	69	25	107	0.19
100 + 50	-17 (+41/-58)	-	58	26	136	0.16
100 + 100	-14 (+34/-48)	-	42	28	147	0.16

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A rise in the nitrogen dressing from 50 to 100 + 100 kg N ha⁻¹ increased the nitrogen percentages of the leaves: for the flag leaf from 2.87 to 3.90%, for the penultimate leaf from 2.34 to 3.35%, for the third leaf from 1.82 to 2.68% and for the fourth leaf from 1.40 to 2.16% at 10 days after anthesis (Fig. 7A). These differences in nitrogen percentages persisted during the grain filling period until the leaves senesced. Even then a small difference in nitrogen concentration remained. The pattern of nitrogen content of the leaves clearly shows that additional nitrogen delayed senescence of the top leaves by 8 to 10 days and considerably increased the amount of nitrogen available in the leaves for re-distribution to the grains (Fig. 7B).

The distribution patterns of nitrogen, phosphorus and potassium in the wheat culm are shown in Fig. 8 and Table 4. During the post-floral period the grains are a large sink for nitrogen and phosphorus. The supply from the reserves stored in the vegetative parts of the culm at anthesis did not fulfil the demand of the grains. Therefore, the nitrogen and phosphorus yields could not have been realized but for a substantial contribution through uptake during the grain-filling period. The amount of nitrogen uptake after anthesis corresponded on average to 48% of the nitrogen yield of the grains. Thus the reserves in the vegetative organs contributed only about 52% of the nitrogen stored in the grain. The same pattern was established with phosphorus: 45% was contributed by uptake after anthesis and 55% by relocation from the vegetative organs. The rachis and chaff contained relatively more phosphorus than nitrogen at anthesis and also acted as an important source of phosphorus for the grains. The distribution of the nutrients in the wheat culm expressed as harvest index is presented in Table 4; this parameter is calculated as the ratio of the nutrient amount in the grain and in the above-ground part of the culm. The harvest index of phosphorus ranged from 0.91 to 0.93 and of nitrogen from 0.75 to 0.81. Late nitrogen applications promoted the uptake of nutrients during the kernel-filling period and consequently raised these harvest indices.

The potassium economy of the wheat shoot was quite different from that of nitrogen and phosphorus. Although potassium uptake by the grain was small, potassium contents of the stem and the leaves dropped from about the mid-kernel filling stage onwards. The main storage centre for potassium was the stem (including the leaf sheaths); with lower nitrogen applications potassium accumulated in the stem for two weeks after anthesis, followed by a linear decrease until maturity. With additional late nitrogen applications the potassium accumulation in the stem continued for four weeks after anthesis, followed by a short period of potassium loss from the stem. Generally, the balance between uptake and loss of potassium in the vegetative parts of the culm after anthesis seemed to be more negative with lower nitrogen applications (Table 4). Thus an increased nitrogen dressing greatly promoted the potassium yield in the vegetative parts of the culm; the potassium content of the grain responded less to nitrogen. The potassium harvest index decreased therefore with a higher nitrogen supply.

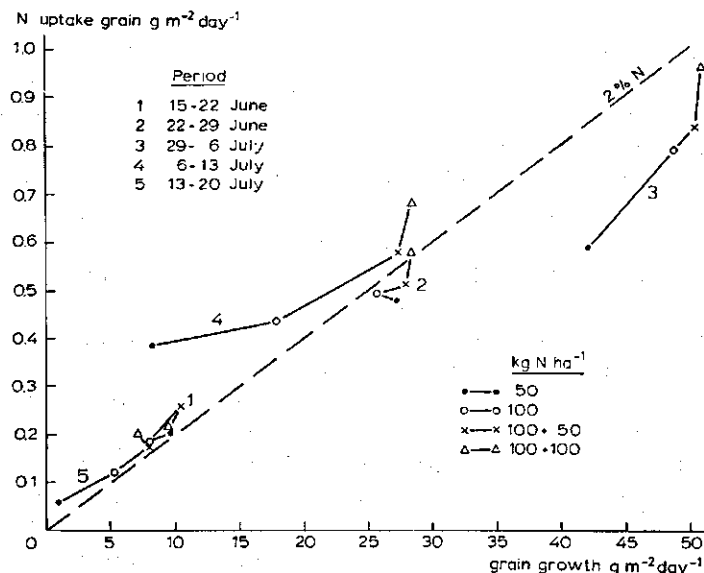


Fig. 9. The relation between grain growth and nitrogen uptake at weekly intervals with four nitrogen dressings.

Interrelationship between carbohydrate and nitrogen metabolism

Carbohydrate and nitrogen supply to the grain are partly interrelated because nitrogen translocated from the vegetative parts to the grains consist mainly of amino acids.

The relationship between the rate of grain growth and the rate of nitrogen uptake is shown in Fig. 9. Nitrogen dressings hardly affected the nitrogen uptake in the first two weeks after anthesis, but had a considerable effect during the third and fourth weeks. Thus the regulation of the nitrogen uptake by the grain was not under genetic control alone but also depended on the nitrogen supply, whether by transfer from the vegetative parts or by direct contribution from the roots. The greatest demand of the grains for nitrogen occurred during the mid-kernel filling phase. Then the nitrogen uptake ranged from 5.7 to 9.6 kg ha⁻¹ day⁻¹ with 50 and 200 kg N ha⁻¹ dressing, respectively.

Not only is the supply of carbon and nitrogen to the grain interrelated, but also the loss of these components from the vegetative organs: leaves, stem and chaff. Assuming that the nitrogen was translocated as amino acids containing 16% nitrogen (Austin et al., 1977), the losses of carbohydrate associated with the export of nitrogen can be calculated. The total loss of nitrogen from the vegetative parts of the plant ranged within the applied nitrogen dressings from 70 to 105 kg N ha⁻¹ (Table 4), which corresponded to a dry matter loss from 437 to 656 kg ha⁻¹. Stem and leaves contributed equally, each about 38%, to this loss of nitrogen; the remaining part, about 24%, came from the chaff. The dry weight loss of the stem by nitrogen compounds contributed only slightly (from 6 to 9%) to the total losses, but nitrogen compounds accounted for about 40% of the weight

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loss of the leaves.

When there is simultaneous import and export of nitrogen compounds in the vegetative organs, then the estimates are only related to the net differences in the amount of stored nitrogen. It is possible that more nitrogen passes through the vegetative parts (e.g. leaves) during grain filling, which implies a higher dry weight loss associated with nitrogen assimilation and relocation.

Discussion

The weather conditions during the growing season of 1976 were characterized by an exceptionally low rainfall and an exceptionally high level of radiation (Table 1). In April the cloudless sky caused frequent night frosts. Simulation studies of crop behaviour during April showed a negative water balance in the plants on many days (W. Dekkers, pers. commun., 1977). During May growing conditions were more favourable, although the relative humidity was low. Leaf growth and stem extension were relatively more reduced than dry weight increase. This resulted in short and stiff culms with small leaves, but also root growth may have been favoured.

The thorough study of interactions between soil moisture and fertilizer N by Campbell et al. (1977a) on wheat growth and grain production showed that the root distribution was affected by moisture and growth stage. They found that due to a hot and dry spell between booting and anthesis the crop depleted all available water in the soil region to 90 cm depth and from 45 to 75 cm depth with the dry and irrigated treatments, respectively. Thus even with an additional water supply there may be, under conditions of high evapotranspiration, soil moisture deficits in the regions with a high root density. Usually, more than half the root mass is located in the top 30 cm of the soil (Campbell et al., 1977). Under the conditions of 1976 the phenomenon of temporary water stress of the root system in the top layer of the soil might have occurred. This could also explain the reduction of nutrient uptake (and even loss) compared with dry matter increase during the dry period before anthesis.

The general response of the crop to warmth after anthesis, showed a pattern of grain filling similar to those found by various studies of temperature effects on grain growth in phytotron experiments (Sofield et al., 1974; Spiertz, 1974; Ford & Thorne, 1975; Warrington et al., 1977). This pattern is characterized by the apparent absence of a lag period, a high grain growth rate of short duration and premature senescence of the plant. There was one major difference with these indoor experiments; the final grain size was less affected by warmth. This might be explained by the better supply of assimilates to the fast growing grains in the field experiments, due to the higher level of radiation, as compared to the conditions in phytotron experiments. Nevertheless lower temperatures during the grain-filling period would certainly have favoured the dry weight of the grains. If lowering of the temperature by 5 degrees kelvin would have been possible without changing the level of solar radiation, then the corresponding increase of the kernel weight could be estimated to be 15 to 20% according to the response curve to

temperature in phytotron experiments (Spiertz, 1977; Warrington et al., 1977).

Analysis of nitrogen effects on the grain production pattern under these particular growing conditions showed that an increased nitrogen supply raised the number of kernels per ear. The effect of top dressings at the boot stage on grain number was striking. This positive response to a late nitrogen application was also found in previous experiments and is confirmed by long-term field experiments (Gliemeroth & Kübler, 1977) under conditions of a low level of nitrogen mineralization and only inorganic fertilization. A more detailed study of nitrogen effects on spike fertility was done by Langer & Lieuw (1973) with spring wheat grown in solution culture. They found that raising the nitrogen supply at the double-ridge stage increased the number of spikelets, and a high nitrogen level between floret initiation and ear emergence favoured the number of kernels per spikelet. In our experiment the number of spikelets per ear was not affected by raising the early dressing from 50 to 100 kg N ha⁻¹, this was obviously due to an adequate supply of soil nitrogen. The number of spikelets per ear amounted on average to 22 and the number of kernels per spikelet ranged from zero (the basal and top spikelet) to about three (spikelets 7 to 9 in the central part of the ear). Thus the major part of the positive effect of additional nitrogen on the number of kernels per spikelet was attributable to greater grain numbers in the lower and central part of the ear. The considerable increase in grain number per ear combined with the relatively small positive effect of nitrogen on the number of ears per m², resulted in an increase in grain number per m² from 16 700 to 20 600. The rise in grain yield was mainly attributable to the number of grains per m². This agrees with the general view that under very sunny conditions and high temperatures the number of grains per unit ground area is a major component of grain yield (Biscoe & Gallagher, 1977). Since final grain number was fixed soon after anthesis it may be concluded that the grain pattern of the individual kernels will be decisive for the grain yield.

Additional nitrogen affected both the growth duration and the growth rate of individual grains. However, with all nitrogen treatments the rate of grain growth was very high due to warmth. The growth rates during a seven-day period in the linear phase of grain filling amounted on average to 2.5 mg kernel⁻¹ day⁻¹. This value is higher than the maximum rate of 2 mg day⁻¹ quoted for wheat in a recent review of literature (Evans & Wardlaw, 1976). With the cultivar Maris Huntsman, however, Meredith & Jenkins (1976) found a grain growth rate of 2.6 mg day⁻¹ during 11 days and Gallagher et al. (1976) reported an increase in the rate of grain growth up to 2.11 mg day⁻¹ during 14 days under the hot and sunny conditions of 1976.

The proportionality between grain number and grain yield implies that the photosynthetic system of the plant has produced adequate amounts of assimilates to satisfy the demands of the grains. This assumption is supported by the storage of excess assimilates in the stem for two weeks after anthesis (Fig 3) and the high content of carbohydrates available in the stem for relocation to the grains (Fig. 4). Although additional nitrogen promoted leaf area development and duration and thereby the photosynthetic capacity, the content of water-soluble carbohydrates

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was decreased from 33 to 26% of the stem dry weight. The lower content of carbohydrate reserves may have been caused by a higher respiration rate and/or a greater demand of assimilates for grain growth (Höfner & Orlovius, 1977). Austin et al. (1977) found that losses of dry matter from the stems during the post-floral period ranged from 82 to 256 g m⁻² with various genotypes of winter wheat. The proportion of these losses caused by respiration was estimated to be about 62%. The rate of stem respiration ranged from 0.28 to 0.35 mg CO₂ g⁻¹ dry weight h⁻¹ at 15 °C. Assuming a Q₁₀ value of 2 for the data of Austin et al. and a mean temperature of 20 °C in our experiment, then the stem loss due to respiration can be estimated to be about 1500 kg ha⁻¹ for the period from 29 June to 20 July. Based on this average respiration loss and with a correction of 500 kg ha⁻¹ for translocation of carbohydrates to the roots, the contribution of stem reserves to the grains may have been in the order of 760 to 1360 kg ha⁻¹ or 9.0 to 21.3% of the final grain yield with 200 and 50 kg N ha⁻¹, respectively. It seems that when plants are grown at a high nitrogen level, stem reserves might be less important because of the availability of more assimilates produced by the prolonged photosynthetic activity of the green tissues.

The enormous decrease in stem weight was mainly (from 80 to 85%) due to the loss of water-soluble carbohydrates. The remaining proportion of dry weight losses may have been caused by the relocation of various compounds (proteins, amino acids, organic acids, nutrients, etc.) and, to a small extent, by lignification processes. It was estimated that the relocation of nitrogen compounds contributed from 6 to 9% of the total stem weight loss.

When all above-ground vegetative organs are considered, the nitrogen economy is as important as the carbon economy. If the nitrogen requirement of the grains exceeds the nitrogen uptake of the plant, then the nitrogen reserves in the vegetative parts will be used as nitrogen source. A fast depletion of these reserves may affect the photosynthetic activity of the leaves by an earlier senescence, thereby shortening the grain growth period (Sinclair & de Wit, 1975). In our experiment high grain yields were associated with nitrogen contents which were higher than in normal years. This agrees with the finding in phytotron experiments that nitrogen assimilation by the grains is favoured more by warmth than is the accumulation of carbohydrate in the grains (Spiertz, 1977). The high rate of nitrogen uptake by the grains, especially during the third week after anthesis (range 0.57-0.96 g m⁻² day⁻¹), required a high supply of organic nitrogen compounds. The reserves in the vegetative part could only satisfy about 52% of this demand; the other part (48%) came from nitrogen taken up after anthesis. Such a considerable uptake after anthesis is confirmed by Sturm et al. (1973) with high-yielding wheat crops; other authors (e.g. Austin et al., 1976; Spratt & Gasser, 1970) stated that even at anthesis the plants already contained 83% of the total nitrogen present at maturity. However, the ability of the plant to continue to take up nitrogen during the grain filling was recognized as an advantage.

Neales et al. (1963) suggested that the role of green leaves in the supply of nitrogen to the wheat grain is firstly to serve as a carbohydrate source to the roots there-

by promoting the uptake of nitrogen, and secondly as a direct nitrogen source. The first role is enhanced if the level of soil nitrogen in the root environment during grain growth is high.

The considerable uptake of nitrogen after anthesis was also reflected in the pattern of phosphorus and potassium uptake (Fig. 6). It demonstrates that healthy wheat crops under favourable growing conditions keep up their root activity for some weeks after anthesis. The continuous uptake of phosphorus during the growth period and the loss of potassium at the ripening stage confirm the results of pot-experiments with spring wheat (Slangen, 1971). Potassium is assumed to be re-located from the stem and leaves to the roots during the ripening stage. It has been stated that phosphorus is only re-distributed from the stem and not from the leaves to the grain (Slangen, 1971). However, it was concluded by Marshall & Wardlaw (1973) that the translocation of phosphorus and photosynthate are closely related in the wheat plant; the direction of movement being governed by the supply and demand for carbohydrates. In our experiment there was relocation both from the leaves as well as from the stem (including leaf sheaths); the latter was 4 to 5 times greater.

The distribution patterns of nitrogen and phosphorus are rather similar. At harvest a major part of these nutrients was stored in the grain. Additional nitrogen dressings promoted the storage in the grains, which is illustrated by the rise in nitrogen and phosphorus harvest index from 0.75 to 0.81 and from 0.91 to 0.93, respectively (Table 4). These values of the nitrogen harvest index are much higher than those quoted by Austin et al. (1976): 0.68 on average. Under Dutch growing conditions Dilz (1971) found values within the range of 0.65 to 0.75, whilst Ellen & Spiertz (1975) measured 0.78. Canvin (1976) reviewed data from literature and concluded that the nitrogen harvest index is subject to considerable variation, from 0.50 to 0.84, due to factors such as water, nitrogen and carbohydrate supply. Our finding confirms the results of Gliemeroth & Kübler (1977); they found nitrogen harvest indices of about 0.80 as a mean for three relatively dry growing seasons and of about 0.55 as a mean for unfavourable growing conditions (wet season, lodging and disease). Similar variations in nitrogen distribution were also found with spring wheat (Pearman et al., 1977). This study shows that increased nitrogen application under the prevailing growing conditions gave a higher grain yield and also a higher grain protein content. This high protein content could result from:

- the positive effect of warmth on the capability of the developing caryopsis to attract and convert nitrogen (sink strength)
- a considerable capacity for uptake and assimilation of nitrogen during the grain filling period (production source)
- a high efficiency of translocation from vegetative parts to the grains (reserve source).

The rate of these processes and of photosynthesis was promoted by additional nitrogen; so high rates of starch and protein accumulation by the grains were possible. The rise in grain yield (from 640 to 821 g m⁻²) and in protein content (from 9.98 to 13.05%) resulted in an increase of the protein yield from 63.8 to 107.1 g m⁻².

NITROGEN SUPPLY, CROP DEVELOPMENT AND GRAIN GROWTH IN WHEAT

Acknowledgments

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Differences in grain growth, crop photosynthesis and distribution of assimilates between a semi-dwarf and a standard cultivar of winter wheat

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Key words: winter wheat, semi-dwarf cultivar, nitrogen, grain yield, crop photosynthesis, carbohydrates, protein, harvest index

Summary

The crop performance of a semi-dwarf cultivar (Maris Hobbit) was compared with a standard-height cultivar (Lely), at various levels of nitrogen supply. The grain yields of Maris Hobbit were considerably higher due to a higher number of grains and a heavier grain weight. Owing to the higher grain yield and a lower stem weight, the harvest index of Maris Hobbit was higher than that of Lely: 0.47 and 0.40, respectively. The content of water-soluble carbohydrates in the stems of both cultivars appeared to be very high until 3 weeks after anthesis, despite the occurrence of low light intensities. Lely used more assimilates for structural stem material than did Maris Hobbit.

Quantity and time of nitrogen application greatly affected grain number, but affected grain weight to a lesser extent. Thus within each cultivar grain number per m² was the main determinant of grain yield. Late nitrogen dressings promoted photosynthetic production, grain weight and protein content of the grains. The low protein percentages of the grains were attributed to the low temperatures during grain-filling period. The distribution of nitrogen within the wheat plant was only slightly influenced by nitrogen dressings and cultivar differences. Nitrogen harvest index ranged from 0.74 to 0.79. Grain nitrogen was derived from the vegetative organs (63-94%) and from uptake after anthesis (6-37%). The importance of carbohydrate and nitrogen economy for grain yield are discussed.

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Introduction

Variations in grain yield between cultivars are often attributed to differences in disease resistance. However, under disease-free conditions grain yields between cultivars have also been found to vary (Spiertz, 1973). The harvest index of cereal cultivars has tended to rise progressively, with little change in biological yield (Van Dobben, 1962; Fischer, 1975; Kramer, 1978).

Based on theoretical considerations, Donald (1968) has outlined a wheat ideotype that should be most efficient in grain production. The main features of his ideotype are: single culm, strong stem, dwarf stature and large spike. Such a plant should be a poor competitor in a crop stand. It should also provide an improved harvest index. Austin & Jones (1976) contended that there is no single ideal model plant or ideotype for wheat. They gave a list of desirable attributes, but concluded that many of these attributes are mutually exclusive. In fact the response of the wheat plant to various growing conditions (drought, nitrogen stress, etc) is still imperfectly understood.

To study the magnitude of cultivar differences in crop response to prevailing weather conditions and to a varying nitrogen supply, observations were made on the cultivars Lely and Maris Hobbit. The former is a Dutch standard cultivar for fertile soils; which has shown a high-yielding capacity under favourable growing conditions (Spiertz & Ellen, 1978); the latter was chosen because of its attributes of superior grain set and dry matter distribution (Anonymous, 1977). Maris Hobbit is one of the semi-dwarf winter wheat cultivars that are well adapted to growing conditions in the Netherlands.

The aim of the experiment was to study cultivar differences in grain yield and grain growth pattern at various levels of nitrogen supply.

Materials and methods

The experiment was carried out in 1977 on the experimental farm of the Department of Field Crops and Grassland Husbandry, Agricultural University, Wageningen. The experiment was laid down on a fine-textured clay soil. The nitrate-nitrogen content of the top 1 m of the soil layer was found to be approximately 50 kg N per ha at the end of February 1977. The preceding crop was potatoes.

The wheat was sown on 15 October 1976 at a rate of 350 kernels per m² and a row distance of 0.25 m. The basic fertilizer dressing consisted of 500 kg N-P-K mixture (0-15-30) per ha on 15 March.

Nitrogen was applied as a split-dressing in the following treatments:

	March (F_3^*)	May (F_8 to F_9^*)	Total
N_1	50	0	50 kg N ha ⁻¹
N_2	0	50	50 kg N ha ⁻¹
N_{1+2}	50	50	100 kg N ha ⁻¹

* According to developmental stages of the Feekes scale.

Control plots without nitrogen dressing were only present with the cultivar Lely.

The fungicide applications were sequential according to the following scheme:

11 May: 4 kg Bavistin M + 5 kg sulphur per ha

6 June: 4 kg Bavistin M + 5 kg sulphur per ha

24 June: 5 kg sulphur per ha

30 June: 0.5 kg Bayleton per ha

The complete experimental field was protected against insect damage by an application of 0.5 kg Pyrimor and 0.5 kg Dimethoat per ha on 24 June and 6 July, respectively.

The experiment consisted of a split-split-plot design with cultivars and fungicide treatment in the splits. Nitrogen treatments were completely randomized and there were 6 replicates. The individual plots were 9 m long and 3 m wide. During the growing season the plots protected against diseases were sampled. The samples were taken from 2 rows of 0.50 m length. At the final harvest, 24 August, the complete plots, except for two border rows, were harvested.

The sampling procedure at the intermediate harvests and the chemical analyses were carried out as described by Spiertz & Ellen (1978).

Crop photosynthesis was measured from anthesis onwards by enclosing an area of 1 m² in a perspex chamber about 1.20 m high. CO₂ content was maintained at about 320 mg/kg during daytime; during the dark much higher values occurred. Air temperature was generally kept at 20 °C, but under high radiation conditions cooling capacity was insufficient and this resulted in the temperature rising to a maximum of 25 °C. CO₂ exchange rate was measured with an URAS infrared gas analyser by sampling ingoing and outgoing air. To prevent gas exchange at soil level the chamber was kept constantly at an overflow pressure, which varied between 0.5 and 2.0 cm H₂O. Solar radiation, air temperature and CO₂ content of air were monitored on recorders and cassette tape. These data were processed by a computer; calculations of net photosynthesis were based on at least four sampling runs.

Growing conditions

Weather

The growing season was characterized by a mild winter followed by exceptionally high temperatures during the first half of March (Fig. 1). During the tillering phase weather was unfavourable: cold, wet and overcast sky. Poor light conditions also occurred during flowering and after mid-kernel filling. High radiation and temperature occurred during the last 10 days of May and the first week of July. Much rain fell during ripening and grain harvest.

Diseases

Although yellow rust was prevalent in wheat crops in the Netherlands in the 1977 growing season, the cultivars in our experiment were only slightly infected.

Early mildew infections were controlled with fungicides. At the end of the kernel-filling period there was a late infection of brown rust (*Puccinia recondita*).

Fungicide applications caused the leaf tips of Maris Hobbitt to turn yellow.

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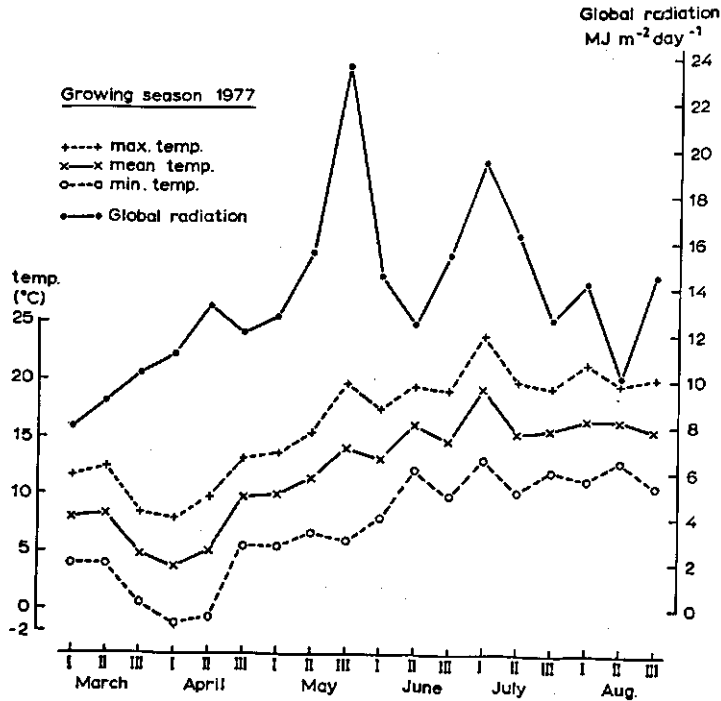


Fig. 1. Average values per decade of solar radiation and air temperature during the 1977 growing season.

Results

Grain yield and yield components

Grain yields of Maris Hobbit were considerably higher than those of Lely, although the above-ground biological yields showed hardly any difference at the highest nitrogen dressing (Table 1). Thus Maris Hobbit had a more favourable dry matter distribution than Lely as shown by the harvest index: 0.47 and 0.40, respectively. The higher grain yield of Maris Hobbit was caused by a higher grain number per ear and per m² as well as by a considerably larger grain weight. Estimates of the maximum level of grain yield are derived from the harvest of 10 August, because subsequently losses occurred due to pre-harvest sprouting. At the highest nitrogen dressing, 50 + 50 kg N ha⁻¹, Maris Hobbit and Lely yielded 813 and 635 g grain m⁻², respectively. The corresponding numbers of grains per m² were 16 400 and 14 900, whilst the grain weight ranged from 50.8 to 46.0 mg kernel⁻¹.

The cultivars responded similarly to the various nitrogen dressings. A single late nitrogen dressing of 50 kg N ha⁻¹ decreased grain number considerably more than an early dressing. This reduction was partly compensated for by an increased grain weight. A late nitrogen dressing, reduced straw yield more than grain yield, resulting in a higher harvest index. The combination of an early plus a late nitrogen gift increased grain number as well as grain weight. Thus grain yield was consider-

Table 1. Yield and yield components of the cultivars Lely and Maris Hobbit with various nitrogen treatments.

Parameter ¹	Lely		Maris Hobbit				Mean		c.v.	Fisher-test ^{2,3}			
	0	50+0	0+50	50+50	50+0	0+50	50+50	Lely		Hobbit	C	N	C×N
Grain yield a (g m ⁻²)	458	581	557	657	681	577	759	599	674	9.5	**	***	**
Grain yield b (g m ⁻²)	398	546	603	678	729	697	813	609	746	9.6	***	***	n.s.
Total dry weight b (g m ⁻²)	1018	1454	1464	1682	1620	1468	1683	1533	1590	9.4	n.s.	***	n.s.
Harvest-index b (%)	39.1	37.6	41.2	40.3	45.0	47.5	48.3	39.7	46.9	3.2	***	***	n.s.
Grain weight b (mg kernel ⁻¹)	41.7	43.1	46.2	46.0	48.9	53.5	50.8	45.1	51.1	3.5	***	***	n.s.
Grains per ear c (n)	29.1	32.3	28.1	34.8	33.6	31.0	35.5	31.7	33.4	6.9	**	***	n.s.
Number of ears d (per m ²)	361	410	425	429	438	427	462	421	442	9.2	*	n.s.	n.s.
Number of kernels e (per m ²) × 10 ³	10.5	13.2	11.9	14.9	14.7	13.2	16.4	13.4	14.8	—	—	—	—

¹ a = combine harvest at 24 August; b = intermediate harvest at 10 August; c = average of 5 sampling dates; d = average of 7 sampling dates; e = c × d.

² C = cultivar; N = nitrogen (without Lely-0).

³ n.s. = P ≥ 0.10; *0.10 > P ≥ 0.05; ** 0.05 > P ≥ 0.01; *** 0.041 > P ≥ 0.001; **** P > 0.001.

Table 2. Yield and distribution of nitrogen after anthesis in the cultivars Lely and Maris Hobbit with various nitrogen dressings

Parameter	Lely		Maris Hobbit				Mean		c.v.	Fisher-test ^{2,3}			
	0	50+0	0+50	50+50	50+0	0+50	50+50	Lely		Hobbit	C	N	C×N
% N of grain	1.46	1.42	1.72	1.73	1.31	1.52	1.52	1.62	1.44	5.9	***	***	n.s.
mg N per grain (× 10 ⁻³)	609	612	795	796	641	813	772	731	736	—	—	—	—
nitrogen yield grains (g m ⁻²)	5.8	7.8	10.4	11.7	9.3	10.6	12.4	10.0	10.7	13.1	n.s.	***	n.s.
nitrogen yield crop (g m ⁻²)	7.6	10.6	13.1	15.7	12.4	13.4	16.1	13.1	14.0	—	—	—	—
nitrogen harvestindex %	77.3	73.8	79.2	74.5	74.3	78.8	76.9	75.8	76.7	2.5	***	***	n.s.
Nitrogen loss after anthesis (g m ⁻²)	2.2	3.7	3.0	4.8	3.9	3.3	5.5	3.8	4.2	—	—	—	—
-leaves	1.3	2.2	2.4	3.8	2.1	2.8	3.1	2.8	2.7	—	—	—	—
-stem (and sheath)	0.8	1.1	1.2	1.2	1.4	1.2	1.4	1.2	1.3	—	—	—	—
-chaff	4.2	7.0	6.6	9.8	7.3	7.2	10.0	7.8	8.2	—	—	—	—
-total	73	94	63	78	87	71	82	77	80	—	—	—	—
Contribution to grain nitrogen (%)	1.6	0.4	3.9	2.9	1.1	2.9	2.3	2.4	2.1	—	—	—	—
-g m ⁻²	27	6	37	22	13	29	18	23	20	—	—	—	—
- % of grain nitrogen	—	—	—	—	—	—	—	—	—	—	—	—	—

^{2,3} See Table 1.

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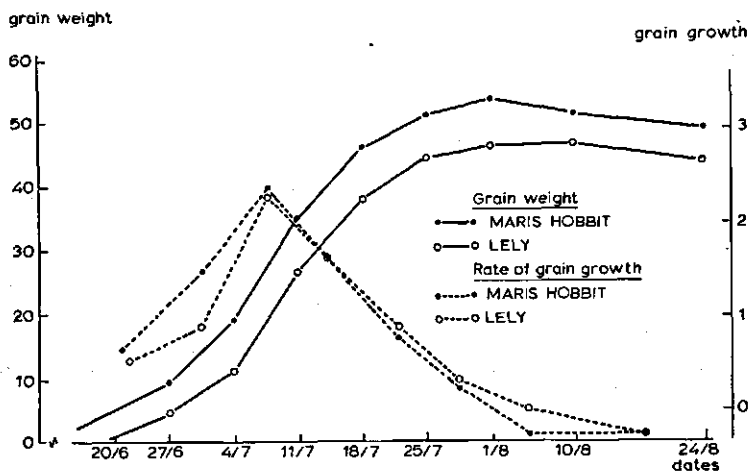


Fig. 2. Course of grain weight (10^{-3} g) and rate of grain growth (10^{-3} g day⁻¹) per kernel in the cultivars Lely and Maris Hobbit at a nitrogen dressing of $50 + 50$ N ha⁻¹.

ably increased by the additional nitrogen dressing. This marked response to nitrogen was quite unexpected in the growing season of 1977. Nitrogen mineralization during the growing season was obviously below normal.

Fungicide application increased grain yield by 420 kg ha⁻¹ in Lely, but had a slightly negative effect on the grain yield of Maris Hobbit. Harvest index and individual grain weight were not affected. These small effects of the frequent fungicide treatments show that diseases were unimportant in this experiment.

Rate and duration of grain growth

Grain growth started about four days earlier in Maris Hobbit than in Lely: 13 and 17 June, respectively. Both cultivars had a grain growth pattern characterized by a slow initial growth rate followed by a two-week period of 'linear' growth and a simultaneous decline until maximum kernel weight was reached (Fig. 2).

The lower grain weight of Lely was mainly caused by a slower rate of grain growth during the first half of the grain-filling period. Both cultivars showed the highest rate of grain growth in the period from 4 to 11 July, when a rate of about 2.25 mg day⁻¹ kernel⁻¹ was reached. From the point of maximum grain weight until final harvest on 24 August, Maris Hobbit lost 9.7% and Lely 6.4% of the grain weight. These losses must have been caused by respiration.

The effective grain-filling period lasted 42 and 48 days in Maris Hobbit and Lely, respectively. Late nitrogen dressings barely affected the duration of grain growth, but delayed a decline in the rate of grain growth after the mid-kernel filling stage. Grain growth per m² depended more on number of grains than on grain weight. The small differences in the course of grain growth per m² between an early and a late nitrogen dressing of 50 kg N ha⁻¹ were striking (Fig. 3). Mutual compensation occurred between grain number and grain weight. During the effective grain-filling period the level of nitrogen supply caused mean grain growth rates to vary from

14.7 to 18.4 g m⁻² day⁻¹ and from 17.9 to 21.0 g m⁻² day⁻¹ with Lely and Maris Hobbit, respectively. Actual growth rates during the linear phase were considerably higher: from 22.8 to 30.7 and from 28.6 to 32.1 g m⁻² day⁻¹ with Lely and Maris Hobbit, respectively. The unfertilized treatment had much lower growth rates: 11.8 and 17.1 g m⁻² day⁻¹ during the effective and linear phase of grain-filling, respectively.

Leaf area, solar radiation and crop photosynthesis

Generally, tillering and leaf growth were favoured in 1977 by a mild winter and a warm spell during the first half of March. An early nitrogen dressing increased the leaf area considerably (Fig. 4). Maximum leaf area index had already been attained at the boot stage. A late nitrogen dressing delayed the decline of the leaf area during the post-floral period. Leaf-area index and duration were slightly higher for Maris Hobbit. But average stem length was about 15 cm longer in Lely than in Maris Hobbit.

Photosynthetic production of the crop depends on the activity of the green tissues and the amount of photosynthetic active radiation. Radiation was low for a fortnight after anthesis and at the end of the grain-filling period. During the period of linear grain growth there was a spell of bright sunshine.

From anthesis onwards crop photosynthesis and dark respiration were measured weekly in the 50 and 50 + 50 kg N ha⁻¹ plots of Maris Hobbit. Due to bad weather conditions and technical restrictions, most of the measurements in the Lely plots had to be cancelled. The available data on Lely showed only minor deviations from the net photosynthesis of Maris Hobbit. This finding is confirmed by the total dry matter yields of the two cultivars.

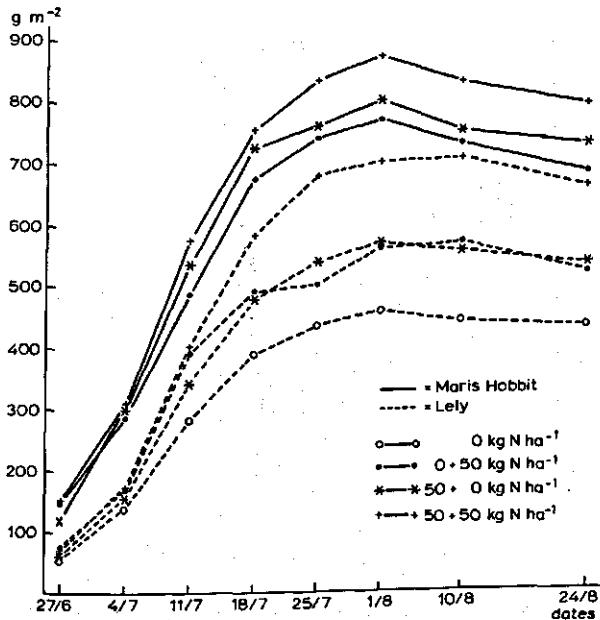


Fig. 3. Course of the grain growth calculated from grain weight, average grain number and average number of ears of the cultivars Lely and Maris Hobbit at various nitrogen dressings.

CROP PERFORMANCE OF WHEAT CULTIVARS

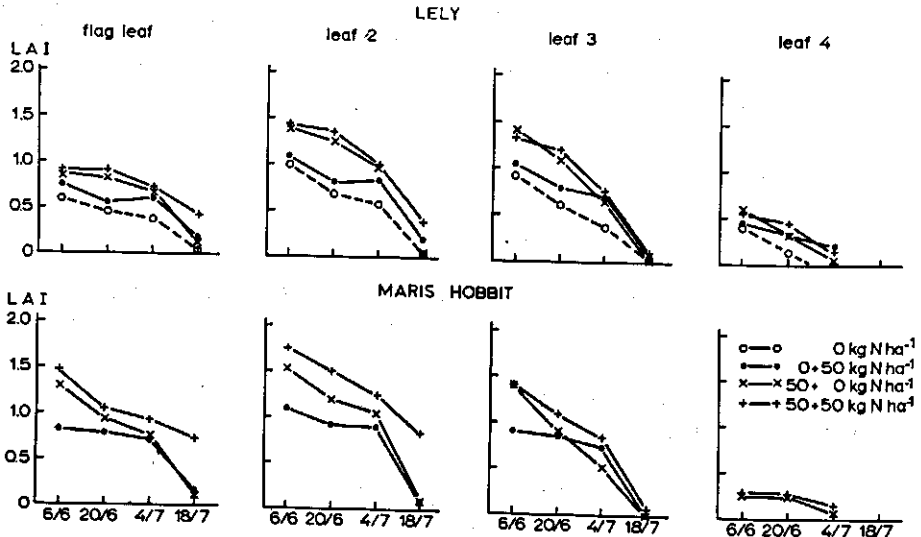


Fig. 4. Leaf area index (LAI) of the individual leaf layers of the cultivars Lely and Maris Hobbit at various nitrogen dressings.

Nitrogen had a very positive effect on crop photosynthesis. An additional 50 kg N ha⁻¹ at the booting stage slightly increased P_{max} at anthesis, but had a considerable effect on net photosynthesis from 3 weeks after anthesis onwards (Fig. 6A and B).

Estimates were derived for the daily course of net photosynthesis from the photo-

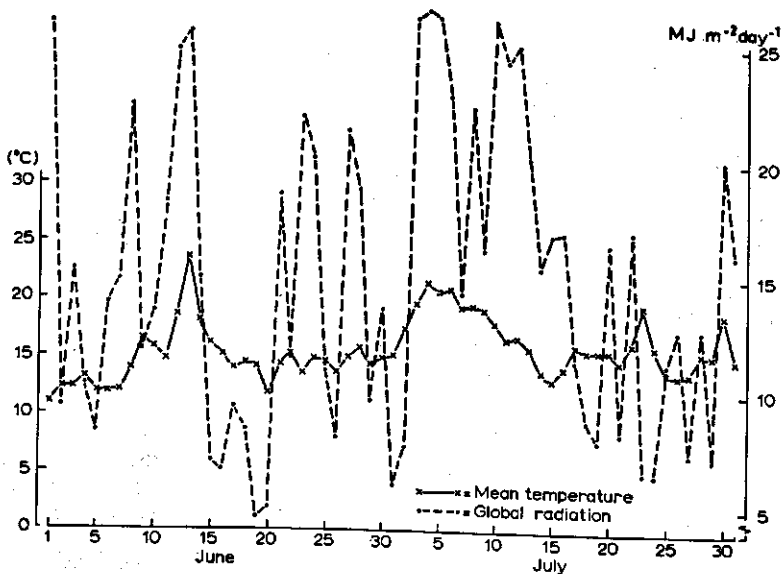


Fig. 5. Daily values of solar radiation and mean air temperature during the grain-filling period.

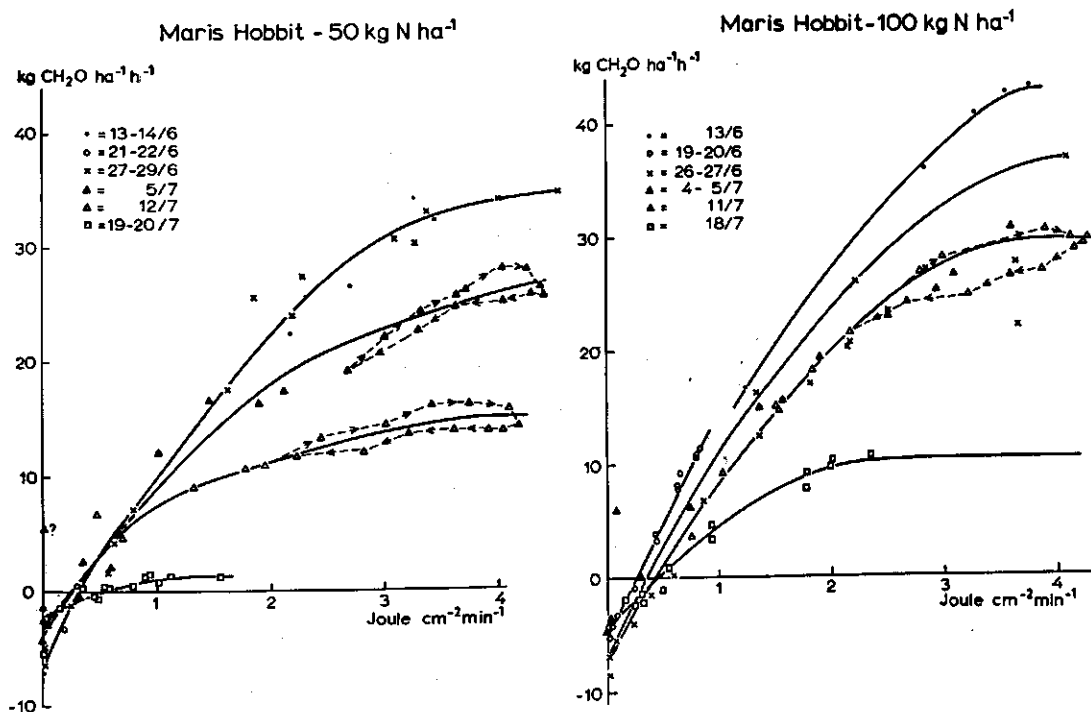


Fig. 6. Photosynthesis-light response curves for the Maris Hobbit crop. A (left): nitrogen dressing of 50 kg N ha⁻¹; B (right): nitrogen dressing of 50 + 50 N ha⁻¹.

synthesis-light curves and the diurnal course of radiation. The data presented in Fig. 7A, B and C are examples of the daily variation in the course of net photosynthesis. These data also clearly show that the magnitude of the positive effect of additional nitrogen on net photosynthesis depend on light intensity. Under low light conditions the effect of additional nitrogen seemed to be small. The net photosynthesis curves of 23 June and 12 July also show that light saturation occurred during the midday period. On 12 July the maximum photosynthetic rate had already dropped from about 42 to 30 kg CH₂O ha⁻¹ h⁻¹, whilst the light saturation period was longer than on 28 June.

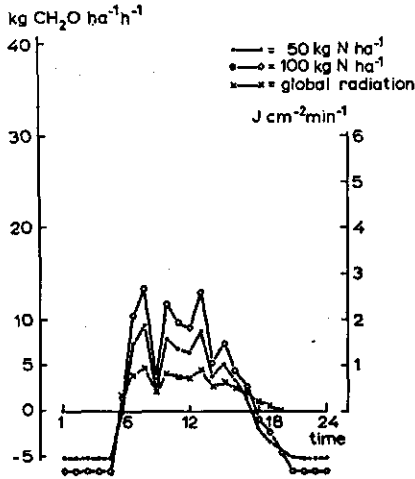
The daily amounts of net photosynthesis are the main source of assimilates for the grains. Therefore the estimates of daily net photosynthesis were compared to the growth rate of the grains (Fig. 8). It appeared that during the first weeks after anthesis there was a surplus of assimilates, whilst at the end of the kernel filling there was a deficit.

Carbohydrate reserves and distribution of dry matter

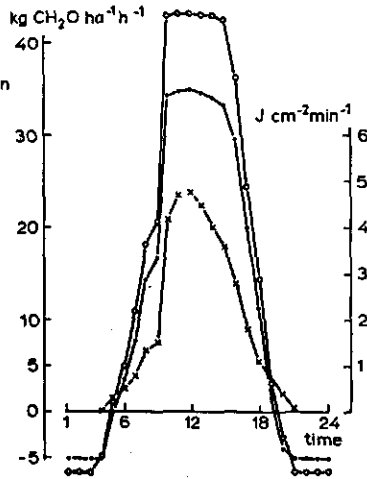
The balance of production of assimilates and utilization by the grains is reflected in the accumulation of reserves, mainly carbohydrates, in the stem. The content of carbohydrate reserves in the stem proved to be quite high, 30-40%, from ear emer-

Maris Hobbit - 1977

20 June

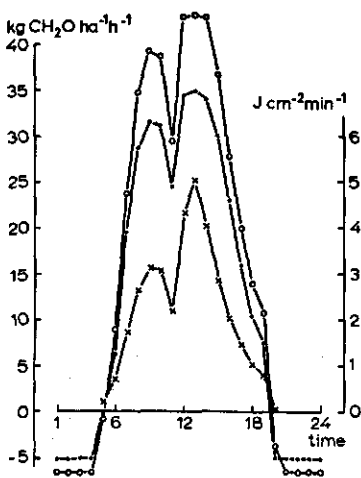


23 June

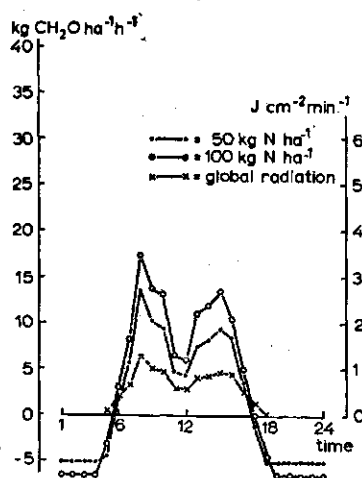


Maris Hobbit - 1977

27 June

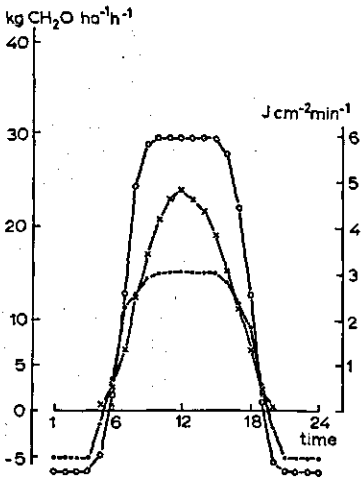


1 July



Maris Hobbit - 1977

12 July



14 July

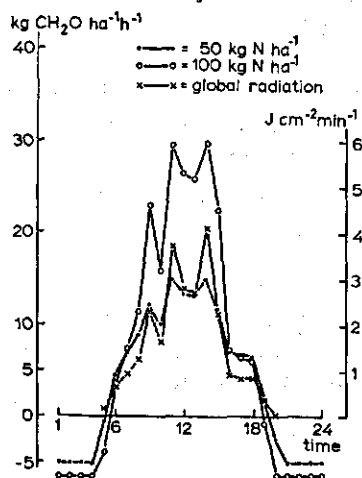


Fig. 7. Daily pattern of solar radiation and net photosynthesis at two nitrogen levels. A (top) 20 and 23 June 1977; B (middle) 27 June and 1 July 1977; C (bottom) 12 and 14 July 1977.

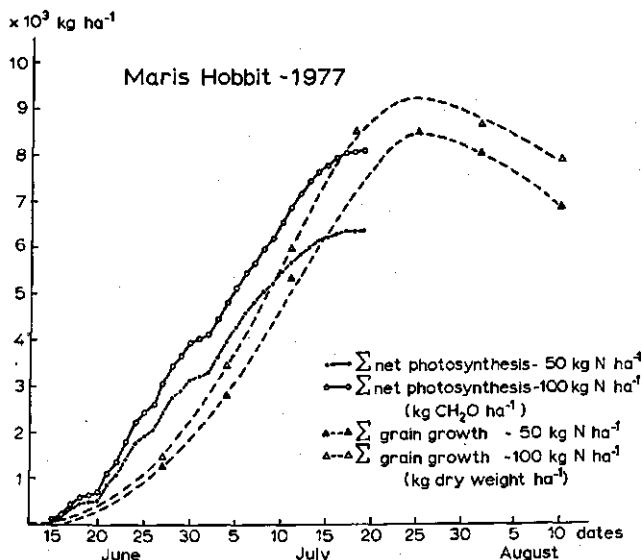


Fig. 8. Cumulative amount of net photosynthesis after anthesis and actual grain growth of the cultivar Maris Hobbit at 50 + 50 kg N ha⁻¹.

gence until 3 weeks after anthesis (Fig. 9). On average, the water-soluble carbohydrates (w.s.c.) reached a higher content in the stem of Maris Hobbit than of Lely, especially during the period of poor light conditions after anthesis. A late nitrogen dressing raised the w.s.c. content of the stem in Lely during the first weeks of grain-filling. Thus carbohydrate supply cannot have limited grain growth until 3 weeks after flowering. The sharp decline in the w.s.c. content of the stem coincides with the beginning of the linear phase of grain growth and with a drop in the photosynthetic rate of the crop.

The w.s.c. content in the top leaves varied around the 5% level, with lower values during the period of bad weather one week after anthesis, and the highest values about 3 or 4 weeks after anthesis (Fig. 9). Generally, w.s.c. contents turned out to be somewhat lower with late nitrogen applications.

Kernels and chaff were only analysed for w.s.c. at the 50 + 50 nitrogen level. The small differences between the cultivars were striking; although the grain growth of Maris Hobbit started earlier, w.s.c. contents of the grains of Lely were only higher in first 3 weeks. On average, the w.s.c. content of the grains decreased from about 45% to 7.5% during the second to fourth week of grain-filling and levelled off to about 5% during the following weeks. The w.s.c. content of the chaff decreased during the grain-filling period from about 10% to 2%.

In contrast to the small differences in w.s.c. contents between the cultivars, clear

CROP PERFORMANCE OF WHEAT CULTIVARS

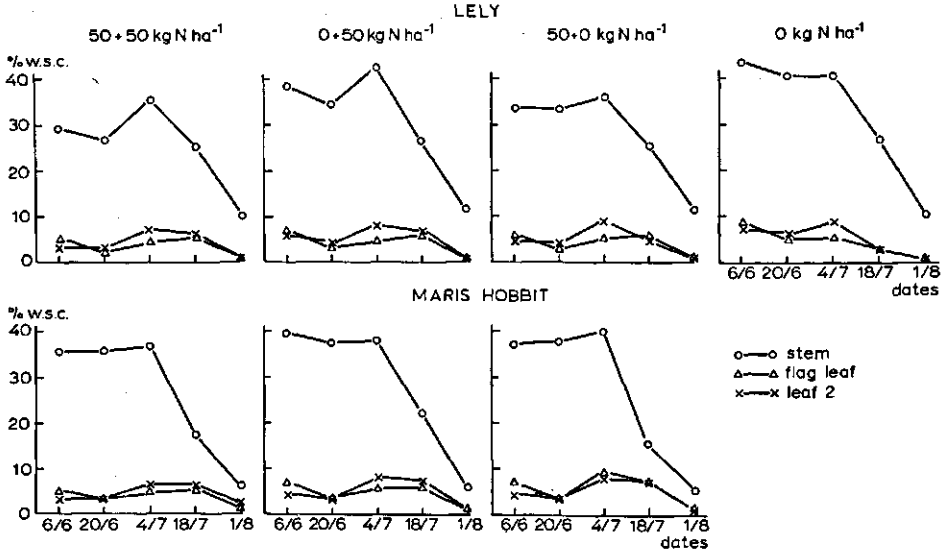


Fig. 9. Water-soluble carbohydrate content (%) in the stem of the cultivars Lely and Maris Hobbit at various nitrogen dressings.

differences in dry weight distribution existed after ear emergence. The most important contrast was the increase in stem weight in Lely, from ear emergence 4 weeks onwards, compared with a practically constant stem weight in Maris Hobbit (Fig. 10). Conversely, the ear weight of Maris Hobbit increased faster during this period than

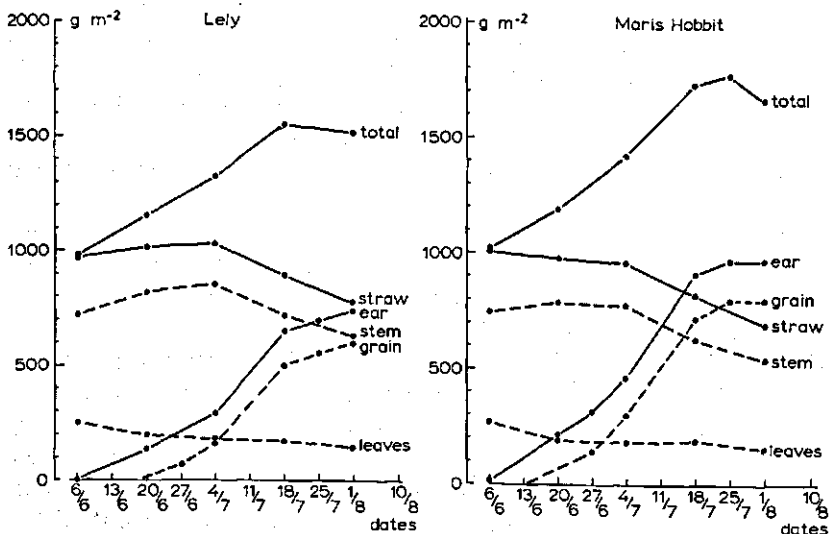


Fig. 10. Dry weight distribution after anthesis in the above-ground part of the cultivars Lely and Maris Hobbit, averaged for the nitrogen treatments.

that of Lely. This indicates competition between stem and ear growth in Lely for several weeks after emergence. However, this competition for assimilates was not reflected in the w.s.c. content.

Another consequence of the longer stem of Lely was that more assimilates were needed for the structural material of the stem. Consequently, stem weight stayed higher in Lely than in Maris Hobbit during grain growth. The dry matter weights of the leaves and the chaff were slightly higher for Maris Hobbit than for Lely (Fig. 10). It was also shown that Maris Hobbit had a higher biological yield than Lely at the end of July, but part of this difference disappeared owing to a greater loss of dry weight in grains and straw due to bad weather conditions during ripening.

Nitrogen uptake and distribution

The pattern of nitrogen uptake was characterized by

- a high nitrogen content at the first sampling date, 12 April; the amount of nitrogen in the shoots in Lely and Maris Hobbit ranged from 42 to 62 kg ha⁻¹ and from 57 to 70 kg ha⁻¹, respectively;
- a very low nitrogen uptake in the plots without N dressing during May and June; obviously, nitrogen mineralization in the soil was very low during this period;
- the nitrogen dressing at the boot stage favoured nitrogen uptake by the grains.

Compared with the dry matter yields, the nitrogen yields of the aerial parts were low; the nitrogen yield of the wheat crop in Lely and Maris Hobbit varied from 106 to 157 kg ha⁻¹ and from 124 to 161 kg ha⁻¹, respectively. The control plots of Lely yielded only 76 kg N ha⁻¹ (Table 2). Although Maris Hobbit had a slightly higher nitrogen harvest index (76.7% compared to 75.8%) nitrogen content in the grains was extremely low. The lowest value corresponded with a protein content of 7.5% and the highest with 8.8%. The nitrogen content of the grains of Lely were considerably higher: from 8.2% to 10% protein. Nevertheless these values are still below the long-term average level.

Nitrogen supply to the grains could be accounted for partly by nitrogen loss from the vegetative organs (leaves, stem, chaff) and partly by uptake after anthesis. The relative contribution by the two sources depended greatly on the timing and amount of nitrogen dressing (Table 2). On average, 80% of the nitrogen amount in the grains was contributed by the nitrogen reserves of the vegetative parts and 20% was nitrogen uptake after anthesis.

The residual amounts of nitrogen in the vegetative parts did not vary significantly; nitrogen residues in the leaves, stem and chaff ranged from 5 - 10, from 10 - 20 and from 4- 6 kg N ha⁻¹, respectively.

Discussion

Grain yield response to nitrogen was very positive in this experiment, contrary to many other field experiments in the growing season of 1977 which showed a lack of positive response at higher nitrogen levels. This lack of positive response could be due to an abnormally high level of soil nitrogen after the dry season of 1976, to the occurrence of diseases, and to low levels of solar radiation during

the tillering, flowering and ripening phases in 1977. The high nitrogen response in this experiment was the consequence of an unexpectedly poor nitrogen mineralization. This might have been caused by the irrigation of the previous potato crop, which lowered the amount of residual soil nitrogen and damaged the structure of the fine-textured heavy clay soil. On the other hand the minor influence of diseases in this field experiment also promoted crop response to nitrogen. Probably the nitrogen dressing of $50 + 50 \text{ kg N ha}^{-1}$ was nearly sufficient to allow both cultivars to achieve their full potential grain production. The low nitrogen dressings, 50 kg N ha^{-1} and the control plot without fertilization would have occasionally suffered from nitrogen stress. This enabled us to compare Lely and Maris Hobbit under conditions of sub-optimal nitrogen supply.

Grain yield differed considerably between Lely and Maris Hobbit with all nitrogen dressings. The higher grain yield of Hobbit, on average about 135 g m^{-2} , was caused by a greater number of grains per m^2 and a heavier individual grain weight. The increase in both components may have a similar cause, namely, a distribution of assimilates so that more goes to the developing ear and less to the stem. Obviously the balance between stem growth and ear growth is regulated by plant hormones. In some high-yielding cultivars it has been found that the improved ear/stem ratio is already evident by the time the first node of the stem is visible when the ear weighs less than 0.01 g (Lupton et al., 1974). Makunga et al. (1978) found that the ear of Maris Hobbit incorporated more ^{14}C supplied to the flag leaf before anthesis than other cultivars. This favoured ear formation was reflected in the dry matter distribution (Fig. 10) and also in a higher number of kernels per ear in our experiment. The upper leaves of Maris Hobbit had a larger leaf area and a greater dry weight than those of Lely. By contrast, the lower leaves of Maris Hobbit were smaller and weighed less. Differences in leaf and chaff weight were of minor importance; the lower straw yield of Maris Hobbit was mainly caused by a reduced stem weight. This pattern of dry matter distribution contributed largely to the increased harvest index of Maris Hobbit. Thorne et al. (1969) found higher harvest indices and grain yield/leaf area duration ratios for semi-dwarf compared to standard-height cultivars. The latter parameter suggests an improvement in the efficiency of photosynthesis by the crop in the use of assimilates for grain filling. Light response curves and maximum level of net photosynthesis of the $50 + 50 \text{ kg N}$ treatment resembled the data presented by de Vos (1977) for the first weeks after anthesis. Contrary to his finding, we found that nitrogen had a considerable effect on the level of maximum rate of net photosynthesis and on the decline in photosynthesis from 3 weeks after anthesis onwards. These effects of nitrogen supply on the rate of photosynthesis were mainly but not exclusively associated with differences in leaf area index. Dark respiration was also increased by additional nitrogen; this may have been mainly caused by more rapid grain growth per m^2 . De Vos (1977) also found no differences in crop photosynthesis between two winter wheat cultivars approximately 15 days after flowering.

In our experiment the number of measurements of photosynthesis and respiration in the Lely crop were too small to justify reliable conclusions to be drawn on dif-

ferences between cultivars. However, large differences in the use of photosynthetic assimilates were inferred from the growth pattern of the ear and the stem after emergence. A higher stem weight in Lely was not caused by a higher water-soluble carbohydrate content. Thus assimilates were used to a greater extent for structural stem material. Both cultivars showed very high levels of w.s.c. reserves in the stem up to 3 weeks after anthesis. The explanation for these high w.s.c. contents, up to 40% under relatively poor light conditions, might be that grain growth and respiration were more restricted by the prevailing daily temperatures (about 14 °C) than was photosynthesis.

The predominant effect of temperature on grain growth and w.s.c. content in the stem has also been established in phytotron experiments (Spiertz, 1977). In the present experiment there was no evidence of a difference between the cultivars in the utilization of the stem reserves for subsequent grain growth. This finding is confirmed by the results obtained by Rawson & Evans (1971).

Differences in the growth of the individual grains due to nitrogen treatments occurred mainly during the second half of the kernel-filling period. Obviously assimilate supply was not limiting in the early phases of grain growth. Nitrogen effects on grain weight were of minor importance for grain yield, compared with the effects on number of grains to be filled. An additional nitrogen application at the booting stage increased number of grains as well as photosynthetic production. Thus nitrogen affected sink and source capacity in a balanced way, which was reflected in the small effects on the harvest index. The small effect of nitrogen on the distribution of assimilates was also found by Makunga et al. (1978) with C¹⁴ treatments.

The higher yield potential of new cultivars is almost entirely due to an improvement in the carbohydrate economy of the plant. There have been only a small increase in capacity to take up nitrogen from the soil and to produce grain protein. Consequently, grain protein percentage has tended to fall as yielding ability has been increased (Bingham, 1976). Pushman & Bingham (1976) stated that this effect can be compensated by later nitrogen application. In our experiment this compensation was only partial.

However, there is no simple relation between yield and percentage nitrogen in the grain. In cultivars or under conditions where senescence of leaves and mobilization of nitrogen from the leaves is slow, higher grain yields may be associated with lower percentage nitrogen in the grain (e.g. 1.44% for Maris Hobbit in 1977). On the other hand, where leaf senescence is rapid, starch storage may be more adversely affected than protein storage and lower yields may be associated with higher percentage nitrogen in the grain (McNeal et al., 1972). This balance is strongly governed by temperature; high temperatures favour protein storage more than the accumulation of starch in the grain (Campbell & Read, 1968; Spiertz, 1977). Thus the low temperatures in the growing season of 1977 would have reduced protein percentage of the grain.

More than half of the grain protein may be derived from nitrogen uptake by the wheat plant after anthesis (Hucklesby et al., 1971; Spiertz & Ellen, 1978), if soil nitrogen supply and root activity are adequate. In these circumstances the nitrogen

content of the grain may remain high or even rise as grain filling proceeds (Johnson et al., 1967). In our experiment only 23% and 20% of the grain nitrogen in Lely and Maris Hobbit, respectively, was derived from uptake after anthesis. This indicates either poor root activity or depletion of soil nitrogen after anthesis. With little further uptake during grain filling, most of grain nitrogen will be derived by remobilization from leaves, stem and chaff (Austin et al., 1977). The differences in efficiency of translocation of nitrogen from the vegetative parts to the developing grains between cultivars and nitrogen treatments were very small. The overall mean for the nitrogen harvest index amounted to 76.3% within a range from 73.8 to 79.2% for all treatments (Table 2).

At high yield levels a low nitrogen content of the grains need not result from a lower grain nitrogen yield, but can be caused by enhanced starch storage per unit available nitrogen. Despite large differences between Maris Hobbit and Lely in nitrogen content of the grains (1.44 and 1.62%, respectively) nitrogen yield per grain amounted to 0.73 mg for both cultivars. Late nitrogen dressing raised the nitrogen contents of the grains considerably in both cultivars.

In a study on the importance of nitrate reductase activity for grain protein Rao et al. (1977) concluded that no single identifiable factor can be used as a physiological criterion in selecting wheat genotypes for better nitrogen utilization. Selection must consider two or more factors simultaneously, including long-term capacity for nitrogen assimilation (uptake and reduction of nitrate) and efficiency of translocation of vegetative nitrogen to the developing grains.

Considering the patterns of grain growth and yield differences we may conclude that carbohydrate supply to the grains was not yield-limiting. However, this supply corresponded to the number of grains that had to be filled. Thus grain yield depended mainly on number of grains per m². Nitrogen dressing affected grain number and photosynthetic production to the same extent. An early nitrogen dressing favoured grain number more than a late dressing; the latter increased the protein yield of the grains.

The results of this experiment confirm the great importance of ear formation for the final grain yield. It has already been shown that under various environmental conditions the formation of a larger ear with a high number of grains per ear favours a high grain yield (Ledent, 1977 Evans, 1978).

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