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



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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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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 & Lieuw, 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 Bakhuysen, 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. Kuipers, *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): 282-296.

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): 183-197.

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 m^2 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). CO_2 -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

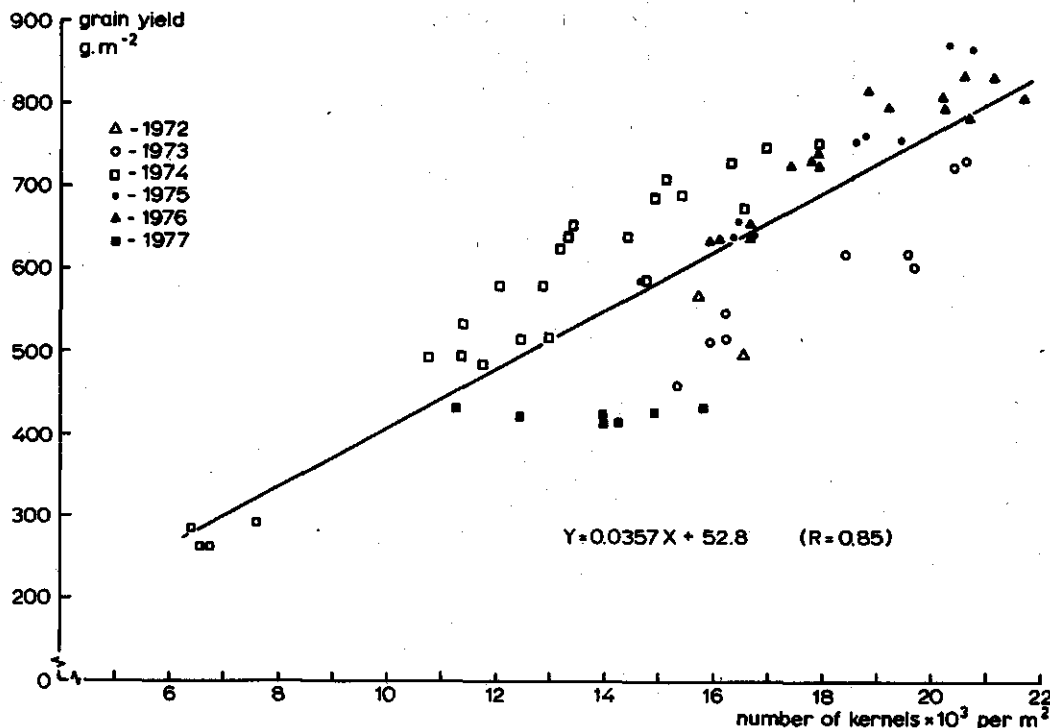


Fig. 1. Simple linear regression of grain dry matter yield (g.m^{-2}) on grain number per m^2 for six successive years with the cultivar Lely.

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 ($16 \text{ hours: } 188 \text{ W.m}^{-2}$) 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 $350 \text{ kg.ha}^{-1}.\text{d}^{-1}$ (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

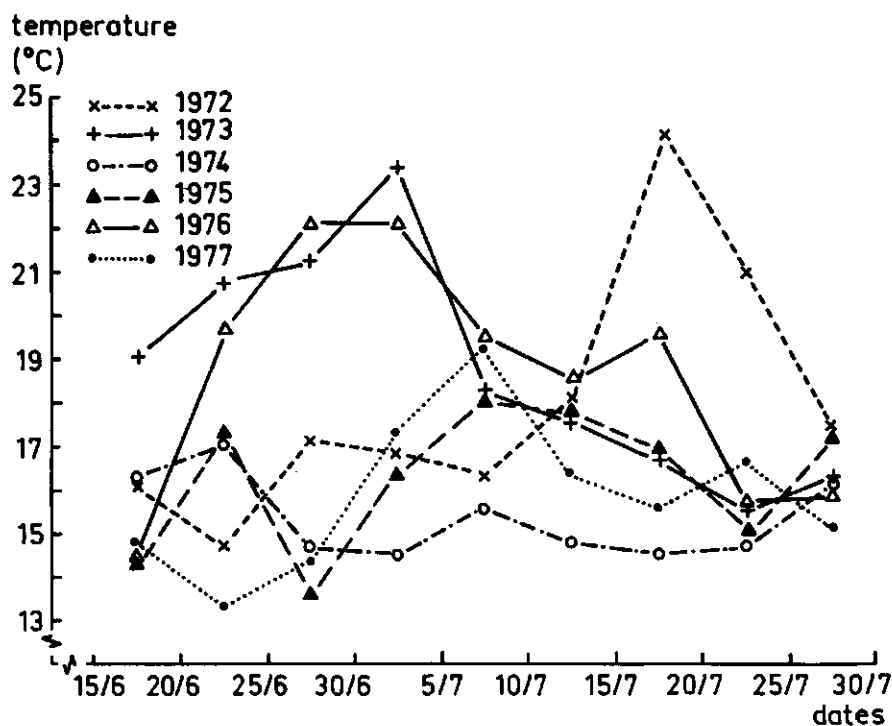


Fig. 2. Mean daily temperatures during the kernel-filling period in six successive years.

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).

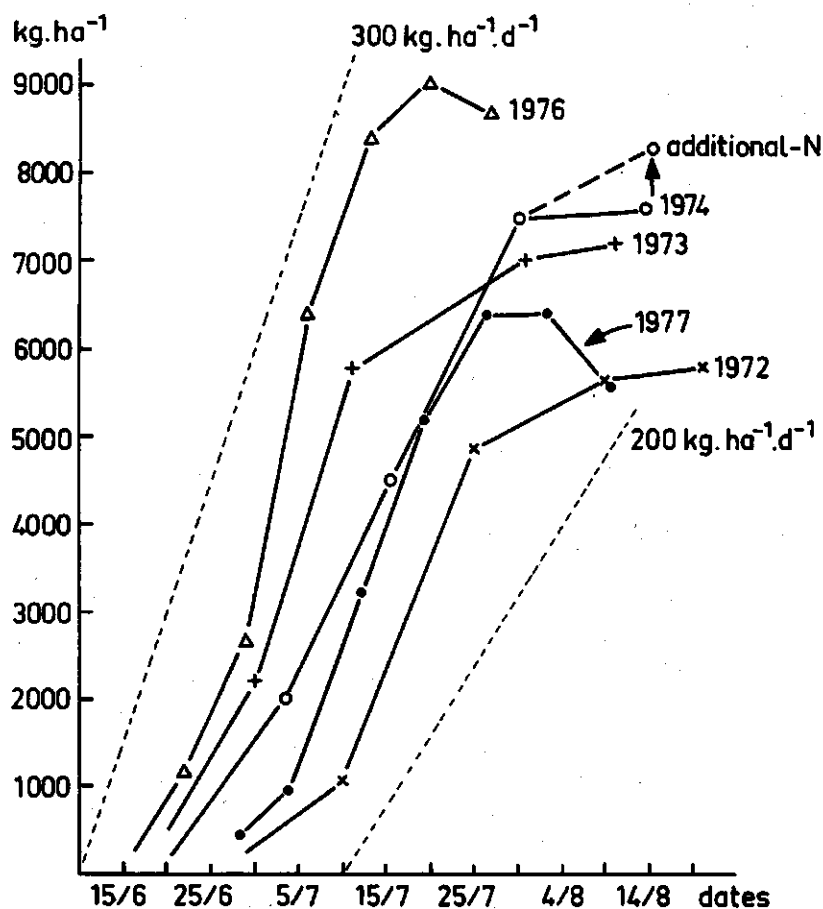


Fig. 3. Patterns and rates of grain growth for different climatic conditions in successive years with the cultivar Lely at optimal nitrogen dressings.

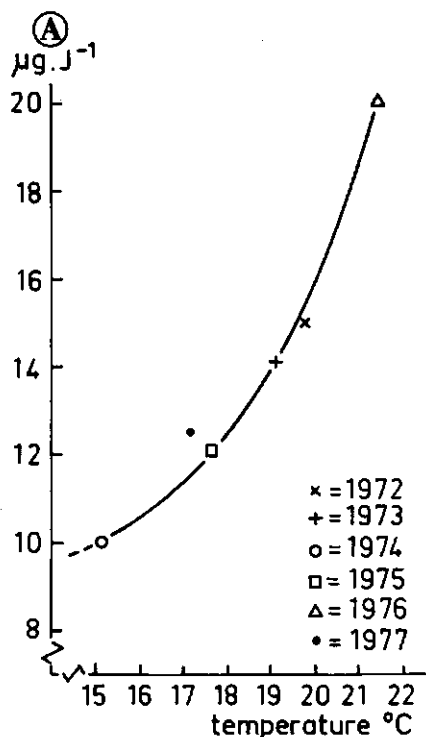


Fig. 4A. Relationship between the growth rate per unit light energy ($\mu\text{g.J}^{-1}$) and the mean daily temperature ($^{\circ}\text{C}$) during the linear phase of grain filling.

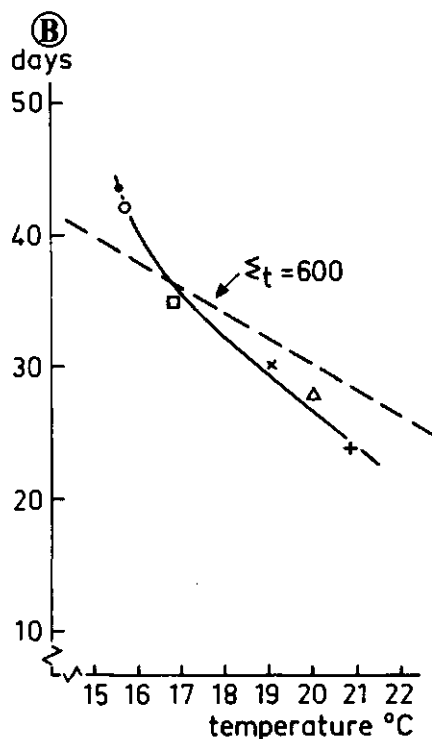


Fig. 4B. Relationship between the duration (days) from anthesis to ripeness and the mean daily temperature ($^{\circ}\text{C}$) during this period. $\Sigma t =$ sum of mean daily temperatures ($^{\circ}\text{C.d}$).

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 kg.ha $^{-1}$, which corresponded to 9.0 and 21.3% of the final grain dry matter yield with nitrogen dressings of 200 and 50 kg.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. Ruckebauer (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 kg.ha⁻¹) of the nitrogen uptake after anthesis in the less leafy crop of 1976 (Spiertz & Ellen, 1978) and about 20% (25 kg.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

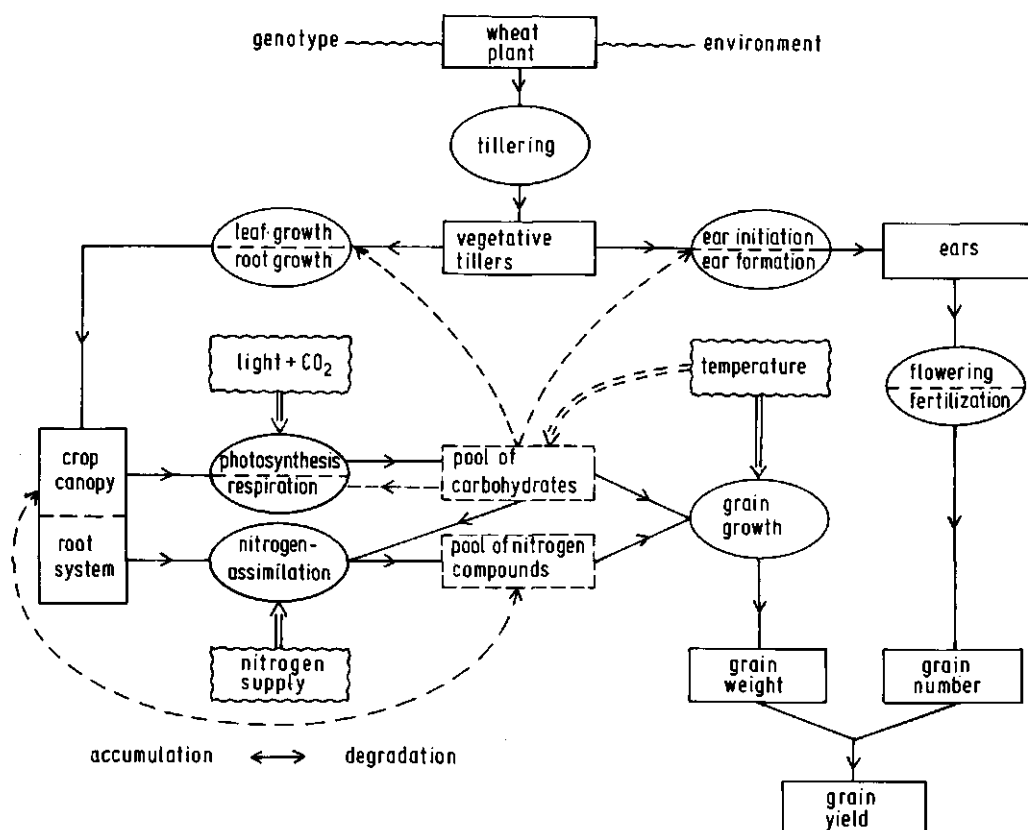


Fig. 5. Model of factors and processes related to grain growth of wheat. \square , crop components; \circ , processes; \square , environmental factors; \longrightarrow , dependence on; \Rightarrow , direct effect; \dashrightarrow , indirect effect; \longleftrightarrow , direct relation; \dashleftrightarrow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

Korrelproduktie en assimilatenhuishouding bij tarwe in relatie tot raseigenschappen, weerefactoren 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 fytootronproeven. 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 bladen 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 korrelopbrengst zijn besproken. Er wordt geconcludeerd, dat een verdere verbetering van de korrelopbrengst op een evenwichtige wijze moet worden nagestreefd, opdat de gewassen aangepast blijven aan de beperkingen van hun groeimilieu. Tevens wordt opgemerkt dat een verdere toename van de korrelopbrengst 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.